

Adventures of punctuated equilibria : a struggle for authority in the evolutionary sciences

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The Adventures of

Punctuated Equilibria.

A Struggle for Authority in the Evolutionary Sciences.

By

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Submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy

Deakin University, April 2001

Signed statements regarding this thesis.

This thesis is an original work by myself. In cases where reference is made to the work of others due acknowledgment is given.

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For Frances

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Abstract

The theory of ‘punctuated equilibria’ was formulated by two paleontologists, Niles Eldredge and Stephen Gould, in 1972 and has been the focus of considerable controversy within the evolutionary sciences ever since. The primary intentions of this thesis are to relate the history of punctuated equilibria and to examine how it has affected evolutionary science. Several modes of analysis have been used to illuminate the history: The sociological perspectives of Pierre Bourdieu and Bruno Latour (who see scientific debate as a ‘struggle for authority’); Rhetorical analysis of some of the key documents; Communication with practising scientists via questionnaires and correspondence; Citation Analysis. Chapter 1 gives a short summary of the history and introduces the methods and socio-philosophical perspectives used to illuminate the history. Chapters 3 and 4 examine the rhetorical process by which Eldredge and Gould constructed the ‘punctuationist revolution’. Chapters 2, 3, 5 and 6 relate the history of punctuated equilibria.

Chapter 1

Introduction.

1.1: Overview.

Evolution is one of the great stories of the modern (Western) age. It tells us of our biological origins and of our relationship to the living world. Regardless of what one may feel about the certainty of scientific knowledge it must be conceded that evolution takes its place in the tradition of origin myths along with those of other times and cultures. This thesis will provide an account and analysis of a contemporary debate about the nature of evolution (approximately 1970 to the present). Some of the people involved in this debate are well known (Stephen Jay Gould, Richard Dawkins). There are others that are not so well known but probably more influential within the field of evolutionary science[1] (John Maynard Smith) and there are others again who are probably neither famous nor particularly influential but who have interesting things to say.

Amongst these scientists there exists competition to be the pre-eminent story-teller. Each scientist believes that their story is the one that explicates evolution the best. Scientist's stories usually revolve around a core set of concepts. The focus of this thesis is the scientific argument over the veracity of one such concept – the theory of punctuated equilibria. For over 25 years now it has been the subject of substantial, and often heated, debate. Scientists, such as Alan Cheetham, Elizabeth Vrba and Steven Stanley, have taken it under their wing and used it as the basis for research programmes It has been heralded by some as the harbinger of a new evolutionary synthesis. Others such as Richard Dawkins and John Maynard Smith, have denied its significance, saying, basically, "we knew it all along, it's part of standard neo-Darwinian theory and it's not important anyway". It is well known enough among university students to have been given a nickname - "punk eek". ((Willis 1989), p.114)

Punctuated equilibria[2] was first conceived by Niles Eldredge. He presented his ideas in a 1971 article published in the journal *Evolution* (Eldredge 1971). However it is the 1972 article co-authored with Stephen Jay Gould, 'Punctuated Equilibrium: An Alternative to Phyletic Gradualism', published in the book *Models in Paleobiology*, that

[1] The phrase 'evolutionary science' is used as a group term denoting all sciences that are concerned with evolution. 'Evolutionary science' thus includes evolutionary biology, paleontology, ecology, systematics and various other sub-fields. Often the term 'evolutionary biology' is used in such a context. However I have found that such usage creates confusion – many paleontologists, for instance, do not class themselves as 'evolutionary biologists'.

[2] Note that the term 'punctuated equilibria' refers to two objects - a set of empirical statements and a set theoretical statements. The theoretical statements are designed to explain the 'facts' as described by the empirical statements and/or to extend to other areas of evolutionary explanation. A simple analogue is Newtonian gravity. There is gravity as an empirical fact (things fall to the ground), then there is a set of theoretical statements designed to explain gravity (why things fall) and/or to extend to other areas of physical explanation (why the planets go round the sun).

has become the best known is generally cited when scientists refer to punctuated equilibria in the literature.(Eldredge and Gould 1972).

At the core of punctuated equilibria is an empirical statement about the nature of data from the fossil record. This statement has two parts: first, that most species as recognised in the fossil record show little change for most of their existence (*stasis*); second that speciation is usually a geologically sudden event (*punctuation*). At this empirical level punctuated equilibria is not particularly controversial and would not be subject to challenge from outside paleontology. It is the *theory* of punctuated equilibria that has been the source of most of the controversy (the *theory* being the explanation offered for the apparent empirical facts). The authors of the theory, and others too, have used it as the basis of some rather ambitious assertions about the nature of evolution.[3]

Punctuated equilibria has been at the center of many (often controversial) challenges to neo-Darwinism. Starting with the 1972 article Eldredge and Gould have repeatedly claimed that punctuated equilibria has consequences for evolutionary biology[4] as well as for paleontology. The specifics of these claims have changed over time but the basic structure remains the same – that punctuated equilibria implies that the explanatory domain of standard neo-Darwinism, as described by the Modern Synthesis, does not encompass macroevolution[5] Many other scientists (mostly paleontologists) have joined them in challenging the validity of standard neo-Darwinism with respect to macroevolution, punctuated equilibria taking on a greater or lesser role depending on the nature of the specific assertion.[6] Other scientists, mostly evolutionary biologists, have disputed these challenges.

The first question that springs to mind here is 'Why did these scientists feel it necessary to dispute the application of neo-Darwinism to macroevolution?'. There is, of course, no simple reply to this. The answer varies from scientist to scientist and each scientist, being human, has a diverse set of motivations. However there were some principal motivations shared by almost all the scientists in question. To understand these motivations one needs to go back to the creation of the Modern Synthesis in the 1940s and 1950s – to the roots of neo-Darwinism.

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[3] Jean Gayon, in his article 'Critics and Criticisms of the Modern Synthesis' has produced a major philosophical analysis of the punctuationist position. (Gayon 1990)He observes that "its mode of argumentation may be characterized by using Lakatos' distinction between the "hard core" and the heuristic periphery of a theory …" (p.6) The hard core in this case being the statements of stasis and punctuation, which are "presented as an empirical fact" . Gayon observes that this may be combined to "*one* essential thesis: that speciation is the "fundamental event of evolution" (Gould, 1983a)". (p.7, Gayon was quoting from (Gould 1983a)) The heuristic periphery of punctuated equilibria, according to Gayon, contains "a network of explanatory suggestions and heuristic extensions woven around the central nucleus" that are "remarkable" in that they have a "plasticity nearly as great as the central claim is inalterable." (p.8) More on this later.

[4] The term 'evolutionary biology' is used to encompass all biological treatments of evolution. Paleontology is not included. As noted above the term 'evolutionary science' will be used to refer to the combination of evolutionary biology, paleontology and other scientific treatments of evolution.

[5] The word 'macroevolution' refers to evolution as measured in geological time scales (usually millions of years). Hence, strictly speaking, the data of macroevolution is situated within the field of expertise of paleontologists. The converse of macroevolution is 'microevolution', which refers to evolution as measured at human time scales (hours, days, weeks, years).

[6] The scope of these challenges to neo-Darwinism did not, as one might expect, stopped with macroevolution. The dissenters used this initial challenge as a platform for other challenges.

The Modern Synthesis, which forms the basis of neo-Darwinism, was basically the marriage of Darwin's principle of natural selection with (relatively) newly formed ideas about genetic inheritance, and the extrapolation of the combined theory to explicate all evolutionary phenomena.[7] The discipline of population genetics[8], which addresses questions of how genes behave in populations, stood at the center of this movement. Indeed population geneticists dominated evolutionary thought at the time. Contributions to the Modern Synthesis from other disciplines such as paleontology, biogeography, embryology and systematics were fundamentally statements of consistency with the population geneticists 'synthesis'. In particular, paleontologist George Simpson demonstrated that the data of the fossil record could be fully reconciled with the neo-Darwinian explication of evolution (Simpson 1944).

Population geneticists thus took a position at the top of a hierarchy of authority in the field of evolutionary science. Their core statements about the nature of genetic changes in populations became the cardinal tenets of all evolutionary science. Consider, for instance, this passage from Theodosius Dobzhansky (one of the architects of the Modern Synthesis):

> "Evolution is a change in the genetic composition of populations. The study of the mechanisms of evolution falls within the province of population genetics. Of course, changes observed in populations may be of different orders of magnitude. Experience shows, however, that there is no way toward understanding of the mechanisms of macroevolutionary changes, which require time on geological scales, other than through understanding of microevolutionary processes observable within the span of a human lifetime, often controlled by man's will, and sometimes reproducible in laboratory experiments." ((Dobzhansky 1951), p.16)

There is much to be garnered from this passage. Note first that evolution itself is actually defined as "a change in the genetic composition of populations." Evolution is not just described by population genetics (the science), evolution *is* population genetics (the phenomenon). Secondly, macroevolution, via extrapolation, is firmly under the control of population genetics. The only way to understand macroevolution is through the field

[7] There are of course other ways to understand the meaning of the term 'Modern Synthesis'. Gayon, for instance, identifies three different understandings: "a more or less extensive list of books and authors; "a "synthesis" of several (virtually all) biological sciences involved in the study of organic evolution"; "a general consensus on a *genetic theory of natural selection*". ((Gayon 1990), pp.3-4) My characterisation of the Modern Synthesis is basically the same as the third in this list although elements of the second are also present. Gayon also observes that the synthesis "was an attempt to articulate three fields of inquiry: genetics (particularly population genetics), speciation, and macroevolutionary phenomena" whilst noting that it was the genetic component that was considered more fundamental.(p.4)

[8] Population genetics is a sub-field of evolutionary biology.

observations and laboratory experiments of the population geneticists. There is not only a reduction in principle but also a reduction in practice.[9]

Examination of the functional fit between organisms and their environment has always been central to contemplations about the nature of life (its structure and its history). Population genetics during the formative years of the Modern Synthesis was no exception – the scientists' attempts to explain the existence of functional fit was central to their inquiries. It is difficult to generalise about such an enormous theme – every scientist, as one might expect, tackled the issues in a different fashion. Broadly speaking, however, the architects of the synthesis took an adaptational[10] stance. That is they believed that evolution is, by definition, the generation of functional fit and that the processes that produce adaptations are the driving force of evolution, with all other evolutionary forces having a negligible effect.

This adaptational stance is a necessary consequence of the notion that all of evolution can be accounted for by the combination of natural selection with the principles of population genetics. By definition, natural selection operating at the level of the individual produces adaptive fit over time. So, if one installs natural selection as the sole process accounting for the phenomena of evolution one must conclude that evolution is a process of adaptation to environment. This also relates to the neo-Darwinian reduction of macroevolution to microevolution in the following sense - neo-Darwinists believed that natural selection at the microevolutionary level produces adaptation at the macroevolutionary level. The belief that evolution is a process of adaptation and the belief that macroevolution can be reduced to microevolution were thus manifestations of the same perspective.

The negation of one or both of these two related maxims ((a) the installation of natural selection and thus adaptation as the sole evolutionary process; (b) the reduction in practice of macroevolution to microevolution) has been the major motivation for the dissenters from neo-Darwinism[11]. Punctuated equilibria has played a central role in the

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[9] I have introduced this distinction between a reduction in principal and a reduction in practice as it is crucial to understanding the strategy of the punctuationists. A reduction of one scientific discipline to another in principal but not in practice allows the former some measure of independence. For instance, all chemists would agree that the molecules they study are subject to the laws of quantum mechanics in principle. The laws of quantum mechanics, however, do not overly affect their practice in that they work on a level of analysis at which quantum effects are ostensibly invisible (not that this is correct for all chemistry or will always be correct). As we shall see, part of the punctuationist challenge to neo-Darwinism and the hegemony of population genetics therein has been the attempt to create a hierarchy of semi-independent levels in evolutionary science whereby the reduction in principal is preserved (and the prestige of being associated with neo-Darwinism is maintained) but the reduction in practice is broken.

[10] My dictionary of biology defines adaptation thus: "Any characteristic of living organisms which, in the environment they inhabit, improves their chances of survival and ultimately of leaving descendants, in comparison with the chances of similar organisms without the characteristic; natural selection therefore tends to establish adaptations in a population. An adaptation to a particular feature of the environment means a characteristic which is an adaptation because it reduces destruction by that particular feature." (Abercombie, Hickman et al. 1980)

[11] Note that most of these dissenters still describe themselves as neo-Darwinians, on the grounds that they continue to accept the reduction in principle of evolution to natural selection at the individual. The word 'Darwin' holds so much prestige in evolutionary science that to say that one is anti-Darwinian is to risk becoming a laughing stock. However if one defines neo-Darwinism as the version established at the Modern Synthesis then one cannot really say that the dissenters are neo-Darwinists, as it is precisely that

negation of the former maxim and a somewhat lesser but still important role in the negation of the latter maxim.[12] For paleontologists the reduction in practice of macroevolution to microevolution meant that when it came to theorising about their data they had to accede to the tenets of population genetics. Essentially they were limited to attempting to reconcile their data with the neo-Darwinian picture of evolution.

The authors of punctuated equilibria felt that this was a severely restrictive state of affairs. They yearned for disciplinary independence, to come up with theories of their own and to not have to bow to 'higher authorities'. Punctuated equilibria leant itself naturally to such a drive for independence. If evolutionary change, as detected by the paleontologist, is limited to geologically instantaneous speciation events (as is the case if one accepts the two core empirical statements of punctuated equilibria) one can argue that at the macroevolutionary level the processes described by population genetics are essentially invisible. The reduction in principle still holds - population genetic processes can still be admitted to account for the speciation events (the punctuations), and indeed for stasis- but the reduction in practice breaks down. The authors of punctuated equilibria hoped that paleontologists would thus become free to come up with their own theories and models to explain macroevolutionary phenomena.[13]

The quest for independence of theoretical practice by these scientists is one of the major themes of the history of punctuated equilibria. As will be examined in detail in later chapters the rhetorical structure of a good deal of the pro punctuated equilibria literature lends itself readily to just such an interpretation. Most of the early pro punctuated equilibria literature was couched in the language of revolution. Much of the later literature proclaims revolutionary victory. Critics have replied in kind, initially denying the need for revolution, later denying the victory of, or even the existence of, the revolution.

In a broad sociological context this aspect of the history of punctuated equilibria will be interpreted as a struggle for social capital. The struggle in this case is principally between two groups of scientists, whom I shall refer to as 'punctuationists' (mostly paleontologists) and 'syntheticists' (mostly evolutionary biologists, and particularly population geneticists). The capital is that of professional science – university positions,

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version they reject. Perhaps one could say that these dissenters are neo-Darwinians who are anti-syntheticist? For an outsider to evolutionary science the problem is more terminological than anything else.

[12] Gayon also addresses the issue of possible criticisms of the Modern Synthesis. He writes that there are "two ways of criticizing the synthetic theory as a whole. (1) To attack its most obvious central claim, that is, natural selection as the ultimate factor controlling all evolutionary processes; (2) to contest the tacit subordination between the diverse fields of research." ((Gayon 1990), pp.4-5) To an extent my (a) from the text matches his (1) and my (b) matches his (2). My negations differ from his criticisms in their more sociological perspective (his analysis is more philosophical). This difference may also be noted in our differing treatments of the concept of 'reduction'. I am more interested in how reduction affects the power structures of evolutionary science where Gayon is more interested in determining whether or not the reduction of macroevolution to microevolution meets the philosophical criteria for a reduction (the condition of connectability and the condition of derivability). (p.38)

[13] Gayon also discusses the role of punctuated equilibria in criticisms of neo-Darwinism in a similar fashion. He sees punctuated equilibria "as an attractor for a large array of critical discourse on the synthesis." (p.11) Three main categories of attraction are elucidated, the first being the decoupling of macroevolution from microevolution, which I have called the negation of the reduction in practice, which leads to "claims by paleontologists for disciplinary autonomy" (p.11). The other two categories are "an association between punctuated equilibria and radical alternatives to the synthesis" and an apparent "close connection between cladistic analysis of phylogenies and models of punctuated equilibria". (p.12)

research grants, esteem of peers, influence over the direction of research programmes, attractiveness to graduate students. My analysis of this struggle will be strongly informed by two socio-philosophers of science – Pierre Bourdieu and Bruno Latour. An explication of their ideas apart from the particulars of punctuated equilibria will thus be beneficial.[14]

1.2: The socio-philosophical perspectives of Pierre Bourdieu and Bruno Latour.

1.2.1: Pierre Bourdieu.

In the article 'The Specificity of the Scientific Field and The Social Conditions for the Progress of Reason' Bourdieu examines science in the general context of the idea of a "cultural field"[15] (Bourdieu 1975). The assumption is that within all cultural fields there is a struggle for social capital that takes the form of a competition between particular agents individual interests[16]. The agents involved in the struggle naturally employ various strategies in the pursuit of their interests and *the field itself is thus constituted by the tangled web of all these strategies*. Over time those strategies that prove to be successful will, of course, have greater influence in determining the nature of the field. Bourdieu sees the competitive struggle of science as being focussed on one specific issue – "the monopoly of *scientific authority*", where authority refers to "a particular agent's socially recognised capacity to speak and act legitimately (*i.e.* in an authorised and authoritative way) in scientific matters" (p.19) The basic question that Bourdieu attempts to answer (and that he believes an analysis in terms of a cultural field will help to answer) is 'How is it that with a "seemingly incoherent criss-crossing of individual strategies" science seems to have a 'progress of reason'?

What shall I research? What methods shall I use? Who shall I work with? Where and when shall I publish? These are the kinds of questions that scientists must answer in their careers. And every decision made by a scientist pertaining to such questions can, in respect of the struggle for authority, be read as a political one directed "towards maximisation of strictly scientific profit, *i.e.* of potential recognition by the agent's competitor-peers." Bourdieu notes that it would be a mistake to analyse a scientific struggle purely from a political perspective, quite apart from intellectual issues, but instead notes that "epistemological conflicts are always, inseparably, political conflicts" and vice versa. This is demonstrated by the assertion that those who reach the pinnacle of science in political terms must also, if they want their peers to "recognise their victory as the victory of science", convince others that their methods are the measure of legitimate scientific practice in the particular field. (pp.21-23)

[14] It should be noted that this thesis is <u>not</u> an attempt to test the sociological models of Bourdieu and Latour.

[15] Other examples of cultural fields are religion, art and politics.

[16] Note that these individual interests are not necessarily selfish self-interests. They may be underwritten by deeply held ethical or moral beliefs or beliefs in a particular philosophy or religion, for instance.

Other kinds of social capital, such as that listed above, flow from scientific authority - that is, one can convert scientific authority into other forms of social capital. Many of these other forms of social capital can of course, be reconverted into scientific authority. However it is authority that is primary, as it is the approved currency of the field. For instance, a professor at a prestigious institution has an authoritative voice by virtue of title and will also be influential in the direction of the department – who is hired or what research programmes are undertaken, for instance. In a scientific debate, however, he or she will argue that 'theory X is preferred over theory Y because of these equations and that data' not 'because I am professor Z and I have six top-flight graduate students'.

Bourdieu's crucial observation is that the struggle for scientific authority in science "owes its specificity to the fact that the producers tend to have no possible clients other than their competitors", that is the producers and the consumers of science are one and the same[17]. This is due to two factors, one of the practical nature of science and the other of the social conventions of science. On one hand "only scientists involved in [a particular] area have the means of symbolically appropriating [another scientist's] work and assessing its merits" whilst on the other hand "the scientist who appeals to authorities outside the field cannot fail to incur discredit". Within this specific struggle the critical issue is the definition of science itself, "the field of problems, methods and theories that may be regarded as scientific". In other words the struggle for authority comes down to a struggle to define legitimate practice in the field, each producer wanting their own practice to be adopted by the other producers. Agents in the struggle will, of course, attempt to impose the definition of legitimate practice that suits their own particular interests. (p.23)

Given Bourdieu's depiction of science, the structure of any particular scientific field[18] is "defined by the state of the power distribution between the protagonists in the struggle (agents or institutions), *i.e.* by the distribution of the specific capital" which is "the result of previous struggles". The form of the present struggle will then depend on the structure of the field, that is the "scientific field is always the locus of a *more or less unequal* struggle between agents unequally endowed with specific capital, hence unequally equipped to appropriate the product of scientific labour accumulated by previous generations". (pp.27-28)

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[17] It needs to be noted that the notion of consumption is being used here in a precise sense. It is of course true that non-scientific consumption of science is a very important factor in the struggle, being a major source of funding. However, as Bourdieu notes, if scientists want their work to be recognised as scientifically important it is the consumption of it by their peers and not by industry or commerce that is crucial. And internal consumption of scientific work has a different nature to external consumption. External consumers basically take scientific work and use it 'as is'. That is, they are not interested in making further scientific claims with it but rather use it to make other kinds of products. Scientists will only consume another scientists work, however, when they can use it to make further scientific claims of their own. That is, they consume the product in order to produce more products of the same kind. It is this form of consumption that Bourdieu is referring to.

[18] There are, of course, fields embedded within other fields. For instance physics is a field that is embedded in the larger field of science. The geometry of fields can get rather complicated. For instance, one could define paleontology as a field. But then parts of paleontology have an emphasis on evolution whereas other areas have on emphasis on geology. So a subset of paleontology will be embedded in the larger field of evolutionary science. Another subset will be embedded within geology. These two subsets will overlap to some extent also.

Bourdieu observes that as "accumulated scientific resources increase" there is a "correlative rise in the cost of entry". The establishment of educational conventions in schools and universities, publishing protocols, etc., causes an increase in homogeneity amongst participants. Competition in a particular field will thus be "very different in its form and intensity from the competition found in earlier states." In particular Bourdieu predicts a "decline in the likelihood of *great periodic revolutions* in favour of *countless small permanent revolutions*." (p.29)

In a well established field then, there will be a dominant group who, during the course of previous struggles (not necessarily their own struggles), have gained authority and who, by their practice, reinforce this authority by defining legitimate practice.[19] This dominant group will be "committed to *conservation strategies* aimed at ensuring the perpetuation of the established scientific order to which their interests are linked." The educational system is at the forefront of these conservation strategies, as it is "the only institution capable of securing the permanence and consecration of official science by inculcating it systematically … upon all legitimate recipients of educative action, and in particular, upon all new entrants to the actual field of production." Also within the dominant group's sphere of influence will be "the instruments of circulation, in particular the scientific journals which, by selecting their articles in terms of the dominant criteria, consecrate productions faithful to the principles of official science …". This control over the journals is a double-edged sword. On one side the literature holds out "the example of what deserves the name of science" whilst on the other dissension is suppressed by the simple action of censorship, either by "rejecting them outright", so that dissenters do not have an outlet for their produced goods, or by "simply discouraging the intention of even trying to publish them by means of the definition of the publishable which they set forward." (pp.29-30)

New entrants to the field are faced with a choice between joining the dominant group or becoming a dissenter. Regarding the former they will undertake "*succession strategies*, which are guaranteed to bring them, at the end of a political career, the profits awaiting those who realise the official ideal of scientific excellence through limited innovations within authorised limits". Regarding the latter they will undertake "*subversion strategies*, infinitely more costly and hazardous investments which will not bring them the profits accruing to the holders of the monopoly of scientific legitimacy unless they can achieve a complete redefinition of the principles legitimating domination" (p.30).[20]

Bourdieu then moves on to address the question implied by the title of the article: What social conditions need be present for there to be a situation in which "the true idea is endowed with strength because those who have a share in it have an interest in truth, instead of having, as in other games, the truth which suits their interests?" Of course

[19] W. R. Albury, who applied the ideas of Bourdieu to sociobiology, comments that elite groups in science are also able to perpetuate their dominance into the next generation of scientists by "co-opting people whom it judges to have the qualities it values most highly; and these valued qualities usually turn out to be the qualities which the elite group itself already has." ((Albury 1980), p.118)

[20] It should be noted that this characterisation of the choices facing newcomers to a field is an oversimplification. This is probably deliberate on the part of Bourdieu. The simplicity of his analysis increases the force of his argument. In an historical case study we will find elements of both strategies, in more or less quantity, in each individual scientist's strategy. One feels that the strategies may be regarded as opposite poles of attraction and that in between them there exists a complicated dynamic.

Bourdieu does not postulate some "exceptional social universe" in which agents are disinterested in their own personal interests.[21] Rather the "scientific field always includes a measure of social arbitrariness, inasmuch as it serves the interests of those who are in a position, inside or outside the field, to gather in the profits". However this does not prevent "the inherent logic of the field, and in particular, the struggle between the dominant and the new entrants, … from bringing about, under certain conditions, *a systematic diversion of ends* whereby the pursuit of private scientific interests … continuously operates to the advantage of the progress of science." (p.31-32)

In an established scientific field, (i.e. after founding revolutions) "all recourse to any weapons or powers, even purely symbolic ones, other than those which are legal tender within the field" are excluded and "it is the operation of the field itself which defines more and more completely not only the ordinary order of "normal science" but also the extra-ordinary breaks, the "orderly revolutions". This is due to the fact that as a field becomes more established "scientific resources increase, so the incorporated scientific capital needed in order to appropriate them and thereby gain access to scientific problems and tools, and thus to the scientific struggles, becomes greater and greater". Thus "scientific revolution is the business not of the poorest but of the richest (in scientific capital) among the new entrants." The conflict between succession and subversion will dissipate as the quantity of capital needed for revolution increases, the kind of capital available only to those who have come through the established, authoritatively recognised, career pathways. (pp.32-33)

The "anarchic antagonism of particular interests" transforms into a "scientific dialectic" which becomes more complete as the producer of scientific goods "likely to win recognition of their importance and of the importance of the author" (that is to be of interest to others as well as themselves) vies with competitors more or less equally "capable of applying the same means in the service of the same intentions". So, "the market in which the scientific product is put on offer increasingly becomes restricted to competitors who are increasingly well equipped to criticise it rationally and to discredit its author." In revolutions (which, as noted above, become limited to those who are rich in capital), hidden by dissensus, there will consensus on what areas are "outside the *limits* of the struggle." (p.33)

Bourdieu's basic argument is thus that the specificity of the scientific field, that the producers are also the consumers, creates the conditions for the 'progress of reason'. It is in an agent's interests to produce something that the consumers can use to produce something themselves. To achieve this the producer must obtain a certain level of technical competence (as judged by their peers). As capital accumulates this of course becomes increasingly more challenging.[22] Thus, despite the "seemingly incoherent criss-crossing of individual strategies" (p.34) science can progress[23] - there is a positive feedback loop between the producers and consumers. That is, the objective of the agents in the struggle is authority and the agents will act so as to further their own interests in

[21] Bourdieu notes that disinterestedness, as posited of scientists, is in fact "a system of specific – artistic or religious, as well as scientific –interests which implies relative indifference to the ordinary objects of interest – money, honours, etc."

[22] I would also contend that this explains the increasing specialisation of science.

[23] The use of the word 'progress' is rather problematic – it is not clear in what sense Bourdieu intends the word to be interpreted. A strict definition will not be attempted. Rather the concept of progress will be the focus of inquiry.

this respect. However because of the specific logic of the scientific field and the fact that authority in science is achieved by a combination of social power and technical competence, the longer a scientific field endures the greater will be the technical competence of its practitioners.

The question now is: In what way do Bourdieu's ideas illuminate the history of the debate over punctuated equilibria? To answer this evolutionary science must be defined as a field. Embedded within evolutionary science are various sub-fields, such as paleontology, evolutionary biology evolutionary ecology, biogeography and systematics. Each of these sub-fields can be further divided into sub-disciplines. In paleontology, for instance, there is invertebrate paleontology, vertebrate paleontology, micropaleontology and paleobotany. Population genetics is a sub-discipline of evolutionary biology. At the beginning of the debate over punctuated equilibria in the early 1970s the dominant group in the field of evolutionary science were the population geneticists. It was the principles of population genetics that defined legitimate practice in the field. The punctuationists, most of whom are paleontologists, wanted to subvert this dominance and their principal strategy involved re-defining legitimate practice, initially in their sub-field of paleontology and then extending out to all evolutionary science.

Bourdieu states that newcomers are faced with a choice between two strategies – 'succession' or 'subversion'. As noted, I believe this to be an oversimplification. Indeed, it seems that the punctuationist strategy contains elements of both subversion and succession. Basically the rejection of the reduction in practice is a subversive strategy whilst the retention of the reduction in principal is a successive strategy. The punctuationists are thus able to enjoy the best of both worlds – the prestige of the establishment, independence of practice. The strategy of the syntheticists fits easily into the 'conservation' category espoused by Bourdieu.

The debate over punctuated equilibria provides a most interesting case study for Bourdieu's crucial observation that in scientific fields the producers and consumers are one and the same. Population genetics, with the Modern Synthesis, provided a general model of evolutionary change that was adopted by all the other sub-fields. That is, population geneticists produced goods consumed by other agents in the field of evolutionary science. However the traffic was basically one way – the other sub-fields of evolutionary science, and paleontology in particular, were restricted from producing goods for population genetics. Punctuationism was an attempt to change this situation. However the punctuationists had to do more than simply produce new goods. They also had to find a market for their goods. Their strategy thus included an attempt t to define a new group of consumers[24]. This is an age-old marketing strategy – that if there is no ready market for your goods you must attempt to construct a market, to convince people that they want what you have.

In theoretical terms the Modern Synthesis, as noted above, was basically the marriage of natural selection with population genetics. Its proponents claimed that the extrapolation of this marriage could explain all evolutionary phenomena, particularly macroevolutionary phenomena. In the early 1970s the punctuationists rejected this claim and the debate over this extrapolation has continued through to the present day. This punctuationist revision of neo-Darwinism was not an attempt to totally redefine the field.

[24] Their initial target market was biologically-minded paleontologists although later they widened their aim to evolutionary scientists in general.

As noted above their strategy was to refute those aspects of neo-Darwinism that impinged on their independence and to retain the rest. The punctuationist revision of evolutionary theory can thus be seen as one of Bourdieu's 'small, permanent revolutions'.

The question at this point is: has this small revolution contributed to progress in evolutionary science? (i.e. Has there been 'progress of reason?') The punctuationist rejection of the extrapolationism of the synthesis inspired a revision of the relationship between macroevolution and microevolution. However 'progress' is not the word one would use to describe the early part of the debate (up to the mid 1980s, say). In fact, at that time it seemed as if the debate had done more damage to the field than good, with the sub-fields, after initial attempts at communication on the issue, seeming to go their separate ways. Since that time, however, there has been some measure of 'progress' on this issue, particularly in the latter half of the 1990s. I will argue that this 'progress' can be accounted for by some of the factors catalogued by Bourdieu – in particular the rise in capital of the punctuationists which brings strength to their arguments and the refinement of the arguments of both sides of the debate due to the increasing ability of their counterparts to criticise, resulting in a diversion of ends (from particular agents interests) whereby progress becomes possible.

There is a need at this point to make more specific what is meant by the word 'progress' as used in the paragraph above. As previously noted Gayon characterises the Modern Synthesis as "an attempt to articulate three fields of inquiry: genetics (particularly population genetics), speciation, and macroevolutionary phenomena." ((Gayon 1990), p.4). The punctuationists rejected this articulation. Initially, then, there was a fragmentation of evolutionary science. However in the 1990s there has been a renewed attempt to articulate these three areas. This time however, as compared to the period when the Modern Synthesis was formed, and due to a rise in status of their discipline, paleontologists have been able to address the issues from a position more or less equal to that of the population geneticists[25]. Hence it can be argued that, with a more diverse range of views being expressed and respected as more or less equally valid, there has been progress made on the subject.

This understanding of the notion of progress, that the more diverse the range of views recognised in the definition of legitimate practice in a field the more progressive it is, correlates with the philosophy of Paul Feyerabend regarding the possibility of democratic science (Feyerabend 1980). Although Feyerabend's focus was more on the need for external input (from society generally) to debates in science his idea that the greater the diversity of views expressed and accepted as legitimate in a scientific field the more democratic and perhaps progressive it is can still be applied. This is not necessarily at odds with the widely held view that the greatest breakthroughs in science are reductions. It may seem that reductions generally involve a decrease in the diversity of views expressed. However it is also possible to look at reductions as forming relationships between different views.[26]

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[25] The same could also be said of agents from other sub-fields of evolutionary science especially developmental genetics (which is basically the modern form of embryology).

[26] For instance the Modern Synthesis involved the reduction of all evolutionary phenomena to population genetics. This reduction involved an attempt at articulation of ideas from several disciplines. From the perspective of our time it may seem that some of these disciplines were basically swallowed by population genetics during the synthesis but this is not really the case. Paleontology, for example, was not a very 'scientific' discipline before the synthesis in that there was no clear distinction between amateur fossil

1.2.2: Bruno Latour.

Attention now turns to the ideas of Bruno Latour, which are strongly informed by the ideas of Bourdieu as explicated above. He assumes that science is an agonistic field, that to achieve success in this field one must accumulate allies and that one accumulates allies by convincing them to use your products. The principal text from which his ideas will been drawn is his book *Science in Action* (Latour 1987). Central to the thesis that Latour presents in this book is the notion that science is an industry whose fundamental product is the *black box*. To Latour a 'black box' is an object (either physical, like a computer, or conceptual, like a theory) which other scientists can use without needing to question its inner workings.[27] He then extends this notion to argue that the aim of science is the construction of *networks* along which these black boxes can travel. That is, a scientist's 'network' is defined as the space where their 'black boxes' can 'travel' unhindered.

In *Science in Action* Latour draws on previous work with Steve Woolgar. Their analysis of science, given in the book *Laboratory Life: The Construction of Scientific Facts*, is based on time they spent undertaking an 'anthropological' study of scientists at work in a biochemistry laboratory. The central metaphor of their analysis is that a scientific laboratory is like a factory that produces articles for science journals. They define a scale of certainty for scientific statements, ranging from type 1, the least certain, being conjectures and speculations to type 5, the most certain, being assumed 'facts' that all good scientists should know. The objective of the laboratory's articles is thus twofold - to produce new statements and to perform operations on previous statements (their own or others) that push them either up or down the scale of certainty. (Latour and Woolgar 1986)

Latour starts his analysis in *Science in Action* with the image of the two-faced god Janus. The 'double-speak' of Janus is symbolic of scientists' assymetrical appraisals of scientific statements. Latour points out that when an issue is controversial all sides of the debate justify their positions by claiming that their statements are supported by the

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collectors and professional paleontologists. Paleontology thus lacked scientific authority in comparison to other, biological, disciplines concerned with evolution. By relating the ideas of paleontology to those of population genetics Simpson (Simpson 1944) was able to give paleontological voices increased legitimacy to speak about evolutionary issues. That by the 1970s some paleontologists felt that their discipline deserved more authority than accorded to it by the Modern Synthesis is, of course, irrelevant to any judgements of the actions of Simpson forty years earlier.

[27] Latour is not the first to use idea of the 'black box' in analysing science. His definition of it is unique whilst having similarities with other uses of the terms. Kathleen Jordan and Michael Lynch give a literature review of the concept in (Jordan and Lynch 1992). They list seven different ways in which the term has been used:

1. "A set of processes, entities, or causal laws that are assumed to operate, and without the need for further inquiry
2. A reliable – even invariant – set of mechanisms that can be set to work and, for all practical purposes forgotten
3. A fixed unit containing a complex set of connections: e.g., a printed circuit board or silicon chip
4. A reified process (ritual), or standardized artifact
5. A gloss or simplification which suspends many of the features of a situation in order to focus upon others
6. An unknown basis for a palpable outcome
7. A historical amnesia about the social process of innovation." (p.105)

material world ('Nature' in Latour's terminology). Hence Nature cannot be seen to adjudicate in such controversies. Rather an issue will be settled by the scientists decisions as to whom Nature supports. This leads us to the other face of Janus – when a controversy has been settled the scientists will claim that Nature was the final arbiter. In Latour's own words there is a "clear-cut distinction between what scientists say about the cold settled part and about the warm unsettled part of the research front. As long as controversies are rife, Nature is never used as the final arbiter since no one knows what she is and says. But *once the controversy is settled*, Nature is the ultimate referee." (p.97)[28] Latour uses the term 'soft fact' to describe a statement that is in dispute and the term 'hard fact' to describe an accepted statement.

The idea of a *laboratory* is also important to Latour's analysis of science. He uses the word in a more general sense than normal, as "the place where scientists *work*." (p.64) This definition includes all places where scientists are active in their scientific pursuits. Such actions are not limited to doing research in the 'lab', but also lecturing to students, lobbying for grants, attending conferences and chatting in the tearoom. Scientists will aim to expand the influence of their laboratory – in Latour's vernacular, to create a network around it. This brings us the second definition of the term 'network' - the area of influence of a particular laboratory. (To complete a circuit of definitions we can say that the influence of a laboratory may be measured by the dissemination of the black boxes produced therein.)

The idea of the 'network' sums up Latour's perspective on science. Scientists and engineers, he states, "travel inside narrow and fragile networks… Inside these networks, they make traces of all sorts circulate better by increasing their mobility, their speed, their reliability, their ability to combine with one another. These networks are not built of homogeneous material but, on the contrary, necessitate the weaving together of a multitude of different elements which renders the question of whether they are 'scientific' or 'technical' or 'economic' or 'political' or 'managerial' meaningless. Finally, we know that the results of building, extending and keeping up these networks is to act at a distance, that is to do things in the center that sometimes make it possible to dominate spatially as well as chronologically the periphery." (p.232). This informs his attitude to studying science in the making: What do you do when you hear of some success or failure in science? In the former case look for an extension to a network. In the latter look for the restriction of a network.[29]

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[28] Latour is also not the only observer of science to conclude that the discourse of scientists regarding the validity of factual statements is asymmetric. Harry Collins, for instance, comes to the conclusion that when something is controversial in science there is disagreement as to what criteria could settle the argument, In fact decisions about which criteria are valid are a crucial part of the process of settling a controversy. However when such controversies are settled, and decisions about which criteria are valid have been made, the criteria are presented as if they were self-evident and are used to justify the verdict. See (Collins 1985).

[29] In a general sense the historical analysis of this thesis is strongly informed by Latour's attitude to studying science 'in the making'. His perspective on this can be summarised by his *seven rules of method*, which are given at intervals throughout *Science in Action*:

1. Study science "in the making" (p.13), have no preconceptions as to what constitutes knowledge and observe the creation of black boxes.
2. Do not "look for the intrinsic qualities of any given statement but … look instead for all the transformations it undergoes later in other hands." (p.59)

Of more specific relevance to my analysis of the history of punctuated equilibria is Latour's discussion of the political strategies used in scientific literature, given in the first chapter of *Science in Action*. He presents us with a basic set of rules that summarise these strategies: "weaken your enemies, paralyse those you cannot weaken …, help your allies if they are attacked, ensure safe communication with those who supply indisputable instruments …, oblige your enemies to fight one another …; if you are not sure of winning, be humble and understated. These are simple rules indeed: the rules of the oldest politics." (pp.37-8) Now, authors will not be able to turn their ideas into 'hard facts' without the help of other papers. If a paper is ignored, the work will go nowhere and the scientist will have no influence. This is the worst of all fates. For a paper to endure, for its claims to become fact, it needs a later generation of papers. A statement will be made fact or fiction by the effect of later statements.

Sometimes a dispute, a controversy, may grow around a statement or set of statements. New papers concerned with the dispute will position themselves relative to those already produced, producing alignments and oppositions accordingly. Latour identifies specific tactics used in literature during such a controversy (pp.35-58):

- *Bringing friends in*: The old 'argument from authority'. One lists respected scientists who are in favour of the ideas one is using.
- *Referring to former texts*: Includes listing allies; adding qualifying statements to a reference when those author's ideas don't quite agree with his; referring to "well-established facts so as to start his article with a black box which no one would dare to open" (p.35); referring to other articles for technical support; attacking previous claims made by other authors that contradict their own; using indirect attacks on contradictory work, i.e. using a reference to paper A so as to weaken B when B contradicts the author's claims; etc.
- *Being referred to by later texts*. When later papers assume X's work, taking it as a black box so to speak, this of course strengthens it. The more it is used like this the stronger it is.
- *Articles fortify themselves*. By guessing the objections readers may have and including ready-made answers to them, either with references to other articles or with data, presented as a graph for instance. "…any link can be

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3. "…since the settlement of a controversy is *the cause* of Nature's representation not the consequence, we *can never use the outcome – Nature – to explain how and why a controversy has been settled*." (p.99)
4. "… since the settlement of a controversy is the *cause* of Society's stability, we cannot use Society to explain how and why a controversy has been settled. We should consider *symmetrically* the efforts to enrol and control human and non-human resources." (p.144)
5. "…every time an inside/outside division is built, we should follow the two sides simultaneously …"(p.176)
6. " we will never believe that people believe in things or are irrational, we will never look for which rule of logic has been broken, we will simply consider the angle, direction, movement and *scale* of the observer's displacement." (p.213)
7. Rather than looking for special cognitive abilities in scientists, look instead for "how the observers move in space and time, how the mobility, stability and combinability of inscriptions are enhanced, how the networks are extended, how all the informations are tied together in a cascade of re-representation,…" (pp.246-7)

untied, any instrument doubted, any black box reopened, any figure dismissed, but the accumulation of allies in the authors camp is quite formidable. Dissenters are human too; there is a point where they cannot cope against such high odds."(p.49-50)

- *Positioning tactics*: Arraying the data and references in a persuasive manner. This is done by *stacking* (presenting incontrovertible statements then building new claims upon them), *framing* ("the text has to explain how and by whom it should be read.") and by *staging* ("The text builds a little story in which something incredible (the hero) becomes gradually more credible because it withstands more and more terrible trials.") (pp.52-53)

The author can present the work as following from someone else's or in contradiction to it. The reader's expectations will be altered accordingly. Accordingly the reader will be expecting either a new proposition drawn from the last one referred to or new evidence pointing to the real truth, (not like the stuff that came before). They can also qualify their own work, by saying that some things require further investigation, to insure against new and unexpected findings in the future, or they can throw caution to the wind and make a huge claim. The reader's expectations of the article will shift accordingly. Lastly, the reader cannot be allowed to come to a different conclusion to the author. Hence the text must be laid out so that "…there is only *one way* to go." "No matter where the reader is in the text, he or she is confronted with instruments harder to dispute, arrays of stacked black boxes." If the author is completely successful in this enterprise the " text is said to be **logical**." "This is where **style** starts to count; a good scientific writer may succeed in being 'more logical' than a bad one." A reader still dissenting will be confronted with "facts so old and unanimously accepted that in order to go on doubting he or she will be *left alone*." (pp.57-58)

The tactics listed above will illuminate my analysis of the rhetorical structure of the key articles in the debate over punctuated equilibria. Latour also lists four *translations* used to gain the interest of others. (pp.108-121) These translations are also particularly illuminating in view of the struggle for social capital, in that they help one to identify specific strategies used by scientists:

1. *I want what you want*: Tailor your work so that it is aimed at the goals of others. "The first and easiest way to find people who will immediately believe the statement, invest in the project, or buy the prototype, is to tailor the object in such a way that it caters for these people's **explicit interests**." (p.108) The disadvantage of this strategy is that you may be made marginal, others may take the kudos for your work and/or you may lose control over the direction of the research.
2. *I want it, why don't you*: Better if people can be convinced to follow us instead. Problem is they probably won't want to, especially if they are already powerful and we aren't. This strategy rarely works.
3. *If you make a short detour …*: Convince others that your route is a shortcut to the final result. A community of interest may be built up, but may dissipate just as quickly if the detour starts to appear unpromising. Problem is if the main route does

not appear blocked you will not convince anyone to change course, and once a return is made to the main road, your partners may take credit for having found the way through.

4. *Reshuffling interests and goals*: The third strategy has obvious defects. We may not want the interested parties to know how long the detour is, we may want to convince them that our route is better even if theirs doesn't appear blocked, we want to appear as the driving force. There are tactics that can be used to achieve these goals: Help people to reinterpret their goals - convince them that your solution will help them achieve their goals; Invent new goals, convince people that it should be theirs, then show them your solution - sales and marketing people do this all the time; "The ability to invent new goals is *limited* by the existence of already defined groups. It would be much better to *define* new groups that could then be *endowed* with new goals, goals which could, in turn, be reached only by helping the contenders to build their facts." (p.115); If an enrolled group, even a newly invented one, can see a gap between their goals and the current direction, they may become disenchanted - hence it may become necessary to make a detour hard to see, make them think they're travelling in a straight line.

It is, perhaps easy to see how these 'translations' illuminate the history of the debate over punctuated equilibria. Eldredge and Gould, from the start of their campaign, were involved in an attempt to define a new group in evolutionary science – the biologically informed, theoretically minded, macroevolutionary focussed paleontologist. They attempted to construct new goals for these paleontologists, goals that were loftier than those of their predecessors. Their strategy was identical to Latour's fourth translation, 'Reshuffling interests and goals' – 'invent new goals, convince people that it should be theirs, then show them your solution'.

1.3: Rhetoric.

Analysis of the use of rhetoric in the debate over punctuated equilibria is a major focus of this thesis. In particular chapters 3 and 4 present rhetorical deconstructions of the key punctuated equilibria articles written by Eldredge and Gould whilst the same treatment is given to several articles critical of punctuated equilibria in chapter 5. There are two principal motivations for these deconstructions: First, to illuminate the history by precisely identifying the range of strategies employed by Eldredge and Gould in their 'punctuationist' struggle and, in the case of the critics, identifying the counter-strategies; Second, to study the structure of scientific communication and criticism in a general sense.

The deconstruction of Eldredge and Gould's rhetoric relates intimately and uniquely to my analysis of the history of punctuated equilibria. The language used by Eldredge and Gould in these key articles, and the structure of their arguments generally, set the tone for much of the later debate. Punctuated equilibria was (and still is) presented as a revolutionary idea. Epistemologically there was no necessity for this. With a different presentation punctuated equilibria could have been added to the Modern Synthesis and barely a ripple produced. For Eldredge and Gould, however, this was not

satisfactory. They did not like the political structure of the field of evolutionary science and set out to change it. Their revolutionary presentation of punctuated equilibria was entirely intentional. The rhetorical structure of the literature of the critics of punctuated equilibria also intimately relates to analysis of the history of the debate, as it provides, at least in part, an explanation for the course of the debate - the position they took shaped the nature of the struggle. By analogy, if we look at the struggle as a war, then these chapters may be seen as analyses of some of the key battles.

The second motivation for the rhetorical deconstructions is to study the structure of scientific communication and in particular the way that scientists criticise in a general sense. Many of the assertions made about the nature of scientific communication are intended to have universal applicability. And, of course, this aspect of the study still relates to the history of the debate over punctuated equilibria. The way that the scientists involved attempted to communicate and criticise each others ideas is integral to the nature of the struggle. I have introduced some new terms into the analyses – *debasement* and *reconstruction* – in order to precisely describe the form of scientific criticism in the punctuated equilibria debate. These terms are intended to have applicability across the field of science. It will be argued that scientific criticism invariably takes the form of debasement or reconstruction or a combination of both.

Discourse analysis, of course, is not new to studies of science. In 1978, for instance, Joseph Gusfield used the methods of literary criticism to analyse a scientific paper. (Gusfield 1978) He observed that in a scientific paper the writer hopes to "persuade the audience that the results of the research are *not* literature, are *not* a product of the style of presentation. The style of non-style is itself the style of science." The language used is thus a "significant part of the scientists' display of the external world." (18) Like any good story, the opening sections of a scientific paper set up "a tension that the paper will proceed to resolve." However the scientist does not want to be seen as influencing the resolution. Rather he or she wants to be trusted as an observer. This result is achieved through "an emphasis on the externality of the source of action and through the passive character of the agent." For example, a scientist will write 'it was decided to use method X …' not 'I decided to use method X' or 'The data indicate Y …' not 'We concluded that the data inferred Y …'. The use of this type of language places the action in an external reality. The author gains credit for being a reliable medium through which this reality is related to the readers. (pp.17-20)

Gusfield notes that in the attempt to achieve this 'reliable medium' status authors attempt to rid their language of any emotion or feeling, presenting the work in a clinical form. This, they hope, will persuade the reader that he or she is an objective observer. After presenting the 'facts' (in the form of data, etc.) the author tells the readers how to interpret them. Once again though, the passive voice is taken to give the impression that it is the data leading to the conclusion and not the author. The fact that the author is acting as a spokesperson for the data is hidden.

The notion that science has a particular rhetoric does not necessarily demean its sagacity. Gusfield does not believe that this form of analysis of science is inconsistent with it being a "truth-begetting instrument." It does point, however, to the existence of "multiple realities" that can be "constructed". Hence it is inconsistent with a view of science as "positive knowledge." This sort of analysis will help us to "recognise the

context of unexamined assumptions and accepted concepts" in scientific works, and hence makes a contribution to the social analysis of science. (pp.31-32)

In 1983 Karin Knorr-Cetina and Michael Mulkay identified four themes linking the diverse approaches to sociology of science, the third of which was linguistic analysis ((Knorr-Cetina and Mulkay 1983), p.2).[30] By 'linguistic analysis' they meant the study of scientific communication. The idea is that the transmission of scientific ideas cannot be dissociated from the language used. Interaction becomes the focus for study. Some of these approaches are: Literary 'inscription', as by Latour and Woolgar in (Latour and Woolgar 1986); Expanding analysis to include all scientific discourse, like talks, informal conversation, strategies of persuasion, etc.; Focusing on scientists discourse as an object of study rather than relying on their accounts as reliable indicators. The approach taken in this thesis is most similar to the latter.

The general approach taken to rhetorical deconstruction in this thesis is most strongly informed by the book *Understanding Scientific Prose*. (Selzer 1993) This book presents thirteen deconstructions of the rhetoric of the famous paper 'The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme' (Gould and Lewontin 1979) written by Gould and Richard Lewontin and a concluding reply by Gould himself. The authors in *Understanding Scientific Prose* use a variety of approaches to identify the strategies employed by Gould and Lewontin, or, in other words, to attempt to work out how Gould and Lewontin attempt to 'construct' scientific knowledge. Most particularly informative to this thesis are the articles by Dorothy Winsor ('Constructing Scientific Knowledge in Gould and Lewontin's "The Spandrels of San Marco".', pp.127-143), Gay Gragson and Jack Selzer ('The Reader in the Text of "The Spandrels of San Marco".', pp.180-202), and Greg Myers ('Making Enemies: How Gould and Lewontin Criticize.', pp.256-275).

Winsor endeavours to apply ideas from Latour and Woolgar (1986) and Latour (1987). Using the five statement types of Latour and Woolgar[31] she analyses the way that Gould and Lewontin used the wording of their article to make some statements less certain (particularly those attributed to the 'adaptationist programme' that they attack) and others more certain (she observes that during the article Gould and Lewontin's own claims moved from type 3 to type 4). Winsor also observes the use of the tactic that Latour labels 'stacking' (see above). During their article Gould and Lewontin moved from discussion of shells, to shell patterns to assertions about adaptation. As will be discussed in the relevant chapters Eldredge and Gould also use 'stacking' tactics in their punctuated equilibria articles.

Gragson and Selzer compare the rhetoric of an article by the evolutionary geneticist John Maynard Smith with the 'Spandrels' article by Gould and Lewontin (these

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[30] The full list is: "a concern to include the technical content of science within the scope f sociological analysis"; the choice of internal or external methodology; linguistic analysis; the "rejection of traditional distinctions between the social and the scientific". ((Knorr-Cetina and Mulkay 1983), pp.1-2)

[31] Specifically these statement types may be interpreted in the following fashion:

1 Speculation
2 'In our opinion' or 'We believe' – qualified facts, or facts not considered proved 'It is not yet clear how X is Y, but it appears that thus is so'
3 'Z demonstrated X is Y' or 'X has been shown to be Y' modalised statements
4 'X is Y'
5 No statement necessary at all. So accepted as to not need any explanation.

two articles were published in the same volume of *Proceedings of the Royal Society*). They focus their analysis on the manner in which the authors construct an image of 'the reader' in their texts. This 'reader' is a fictional character that Selzer and Gragson use to deconstruct the rhetoric of the articles. That is, Maynard Smith, Gould and Lewontin assume that those reading their articles will have certain attributes, and they also foist certain attributes upon their readers by way of suggestion. Thus one way to examine the relationship between the author/s of a text and the intended readers is to determine what the authors ideal reader would be like.

Selzer and Gragson note that in both Maynard Smith's article and that of Gould and Lewontin the reader is assumed to be literate in the language of evolutionary science and to be part of that "community of shared beliefs" about evolution. However after that initial assumption the two articles diverged rapidly. Maynard Smith employs standard scientific language (impersonal, objective, authoritative) whilst Gould and Lewontin use emotive language and appealed to a wider range of the reader's experience than the purely scientific.

According to Gragson and Selzer, Maynard Smith places the reader as a conventional scientist (one who is "objective, fair-minded, sober, reasonable") but who is also "subordinate" to the author (who assumes a position of authority). The standard register of scientific literature, the passive voice[32], is predominant, making Maynard Smith seem impersonal and objective to the reader. He then "projects those same qualities onto his fictional reader by serving up an occasional 'we' or 'our' or 'us' without clear antecedents." He uses emphatic, declarative sentences which, "combined with confident diction such as 'it seems certain" and "it is hard to see", create an authoritative voice that by implication dominates the reader in the text and admits a polite margin of doubt that only those who wish to seem ignorant can actually question and even his use of the personal 'I' is decisive and commanding. All in all Maynard Smith's use of language establishes "him as masterfully in control of the situation. … readers are guided into becoming patient and passive, if attentive and entertained, bystanders. These fictional readers may be mainstream professional biologists, but they are put into a quiescent role by Maynard Smith's performance. Though they are in fact faced with an argument, not a presentation of facts, they are directed to take notes on information presented by an authority rather than invited to take issue with an argument." (pp.185-192)

Scientists are also Gould and Lewontin's target audience. Apart from being published in the *Proceedings of the Royal Society*, their article has the standard format of the scientific article (like an abstract, identification of the authors with their credentials, etc.) After this, however, the article makes a strong contrast with Maynard Smith's – it is no ordinary scientific article. The active voice ('we', 'us', 'our') is predominant and the authors appeal to human authorities (such as philosophers) and material evidence (such as their metaphor of the 'spandrel') that are not of science. They appeal to "the reader's cosmopolitan self. It is as if the reader is being consciously recast into the broadly urbane reader implied in *Smithsonian* or *Natural History*." Gould and Lewontin construct "their readers in another image: not objective but interested; not impersonal but flesh and blood;

[32] For example: 'it is hard to say'; 'the second prediction was'; 'this prediction has been well supported by observation'; In Maynard Smith's text there are "sayings without sayers, …, predictions without predictors, observations without observers'. He even refers to his own work in the third person. (p.187)

not reserved but involved; not dispassionate observers of reality but enthusiastic partisans; not blinded by narrow specialization but enlightened by broad experience." (pp.192-193)

So, in contrast to Maynard Smith who takes a position of authority over the reader Gould and Lewontin attempt to identify with the reader, setting up an 'us v. them' scenario where the 'we' are broad-minded intellectuals and the 'them' are 'narrow minded specialists'. (pp.195-197) A dichotomy is constructed, one in which the reader seems to have little choice as to which side to take. This rhetorical tactic is frequently used by Gould – indeed it is also used in Eldredge and Gould's key punctuated equilibria texts.

Myers introduces his analysis by observing that Gould and Lewontin employ an unusual overall strategy in 'Spandrels', in that rather than identifying themselves with the consensus view they set themselves in opposition to it. That is, they set themselves outside the mainstream research community then ask their readers to join them. As Myers remarks, this "is a high-risk strategy. But when successful … the gamble has a high payoff; the new center of a field forms around the position that was previously defined as outside it." (p.258) Myers then moves on to look at Gould and Lewontin's use of language in respect of this 'gamble'.

Myers distinguishes four different utilisations of the word 'we' that might be used in Gould and Lewontin's text (recalling that Gould and Lewontin's article was written in the active voice). These four 'we's are:

1. Gould and Lewontin themselves.
2. All pluralists (who, by implication, agree with Gould and Lewontin).
3. The whole community of evolutionary scientists.
4. Intelligent and reasonable readers.

Gould and Lewontin's aim is to move readers from the third 'we' to the second. There are many tactical manoeuvres that might help to achieve this goal. For instance one can blur the antecedents, so that, for instance the second we and the fourth we are indistinguishable.[33] Myers also analyses Gould and Lewontin's use of emotive adverbs and adverbials, and the way they construct an us v. them scenario where the them are a group that readers would not want to be associated with (Gragson and Selzer make a similar point – see above). The rhetorical analysis of this thesis will also include a dissection of the use of the word 'we' (although this time, of course, the texts of Eldredge and Gould are examined, not Gould and Lewontin). This type of analysis is most informative in that it reveals an important component of the structure of Eldredge and Gould's strategy – their attempt to define a new group of evolutionary scientists. Eldredge and Gould's use of adverbs and adverbials in their texts is also very important in their attempt to inspire their readers to reject the status quo of evolutionary science and accept punctuated equilibria.

The reason for the presentation of detail re the three articles from *Understanding Scientific Prose* is that Gould and Lewontin's article was mainly Gould's handiwork (p.320), and the rhetorical style of 'Spandrels' is similar to that of Eldredge and Gould's

[33] Myers observes that Gould and Lewontin, in their article, deliberately avoid using the second 'we'. Rather they leave the position open, avoiding the use of hard lines that the reader might object to.

punctuated equilibria articles. Hence the analytical techniques described in turn by Winsor, Gragson and Selzer, and Myers can readily be turned to analysis of Eldredge and Gould's texts – the approach taken to rhetorical analysis in this thesis will take elements from all three of these articles. Added to these techniques is a method of analysing scientific criticism titled *D & R* (short for debasement and reconstruction). *Debasement* and *reconstruction* are names for rhetorical tactics used in scientific controversy, he combination of which produces a formidable critical strategy. My postulate is that all scientific criticism takes either one of these two forms or both combined.

Commonly the word 'debase' means to profane, adulterate, cheapen, befoul. In the context of this thesis, however, it has a very specific definition although elements of the common definition are present in the background. To *debase* is to *invalidate the basis of another scientist's statement/s*. Invariably debasement involves a challenge to the validity of the practice of another scientist. It thus relates to the attempt to set criteria, to impose the definition of valid scientific practice. There are two forms, relating respectively to the material and the theoretical nature of science. In terms of the material world a dissenter can challenge the integrity of the data used to support a particular statement or set of statements by contending that it wasn't collected in a valid fashion. In respect of theoretical practice a dissenter can challenge the validity of the theoretical assumptions underlying a statement or set of statements. Of course no hard line can be drawn between material and theoretical debasements – most debasements will have elements of both. Indeed a typical example of a debasement is for a scientist to say that the data produced by a particular experiment is no good because the theory underlying the experiment was either erroneous or was incorrectly applied.

Reconstruction refers to the procedure by which scientists use the work of others to support their own interests. Invariably this involves *removing an object or objects* (either data or statement/s) *from their original context and reformulating them so that they uphold their own statements*.[34] A scientist engaging in reconstruction is thus performing a translation of interests – moving an object from one place, transforming it then re-presenting it in such a way that it furthers his or her own interests. Once again there are two forms or reconstruction relating respectively to the material and the theoretical. In terms of the material world a scientist can claim that another scientist's data uphold their own statements. Regarding theory a scientists can take another scientist's theoretical construct and use it to support their own assertions. Once again no hard line can be drawn between the theoretical and the material. A typical example is for a scientist to take another scientists data, including the assumptions that underwrite the collection of the data, and use it to support their own theoretical statements. Reconstruction is also, of course, often used as a prelude to debasement – a scientist will reinterpret another's statements in such a way that they can then debase said statement.

Without reflection one might not anticipate that these two tactics could be combined. Indeed the combination seems tantamount to self-contradiction. One might as well say 'Your data are no good and it supports my theory anyway' or 'Your theory is no good and it supports my ideas anyway.' However, as will be shown in Chapters 3, 4 and

[34] Note that reconstruction does not necessarily involve criticism. One can reconstruct the data of one's apparent supporters also. For instance a scientist might say 'I like what Dr. X produced in this experiment, and if we look at the data this way we can see that it supports my conjecture Y.' Debasement however, is by it's nature always critical. One does not want to remove the basis of one's supporters statements.

5 when scientists criticise one another their arguments are often comparable to such statements. They will, for instance, debase another scientists data on the basis that their practice was deficient in some way, then show how that very same data can be reinterpreted to support their own ideas.

R&D is, of course, a political strategy. Debasement is a form of criticism that is based on the setting of criteria, imposing the definition of science. Hence it is the principal rhetorical tactic used in the conflict of interests as described by Bourdieu: "what is at stake [in science] is the power to impose the definition of science … best suited to [one's own] specific interests …" ((Bourdieu 1975), p.23) Another way to define debasement, then, is 'an attempt to erode the authority of another.' Harry Collins also comes to the same conclusion, although from a different angle. He observes that the opinion of a scientist or scientists as to whether an experiment was properly executed is coincident with whether it produced the right results (what he calls the 'experimenter's regress'). A controversy can thus only be settled when a set of criteria are imposed. Debasement is thus the most important tactic in a scientific controversy (see (Collins 1985)).

The idea that reconstruction is an important rhetorical tactic in scientific literature has its most apparent precursor in the analysis of Latour. It relates to the idea of 'Positioning Tactics' as explicated above. Scientists will attempt to build an arrangement of data and references, both their own and others, that makes their new claims as persuasive as possible. Latour also points to another aspect of reconstruction, that scientists attempt to construct their 'black boxes' in such a way that they avoid being subject to such treatment. Scientists don't want their products to be dissembled, they want them to be used as they intended them to be. They want them to be mobile and combinable with other products but also stable – this is the essence of Latour's idea of a 'network'. ((Latour 1987), p.223)

1.4 : Jean Gayon's analysis of punctuated equilibria.

As noted above, Jean Gayon performs an analysis of the rhetorical structure of the (generalised) punctuationist argument in his article 'Critics and Criticisms of the Modern Synthesis.' ((Gayon 1990)) He uses Lakatos' idea that research programmes possess a 'hard core', being a set of statements that are non-malleable, and a 'heuristic periphery', a tangle of flexible webs woven around the hard core. Gayon argues that the hard core of punctuated equilibria is the two coupled theses of stasis and punctuation, which may be combined in the statement that speciation is the fundamental evolutionary event. He observes that these central claims have the non-malleable characteristic of a 'hard core; in that they are presented as "empirical fact". From this hard core "punctuated equilibria expands into a number of heuristic proposals, notable for their "plasticity", such as "discussions of species selection or species drift, … various paleobiological programs …[and] the debates on developmental constraints". Gayon concludes that punctuationism, in the periphery, is quite distinct from the specifics of the theory of punctuated equilibria (being the two central claims). The "rhetorical transition" from core to periphery punctuationism "becomes a deliberate reconstruction of the epistemology … and metaphysics … of evolution." (pp.7-9)

Examination of the metaphysics of punctuationism helps to place the current debate in an historical context. Gayon identifies two metaphysical themes that relate to the idea of evolutionary hierarchy. The first is the question of whether "absolutely simple things exist" (as in fundamental particles, for instance). According to this view nature is an aggregate of such simple things. The alternative is that there are no absolutely simple things and that everything is made of parts which are themselves made of parts, etc, etc. According to this view the structure of nature is ultimately to be found in its organisation and not in its parts. One would say then that the reductionism of the Modern Synthesis belongs to the former view and punctuationism to the latter. The debate over these two world-views is centuries old, hence one could say that the modern debate is a continuation of a venerable tradition. (p.34) The second theme that Gayon identifies is "transcendence": "In this [metaphysical] sense, hierarchical is defined as any reality the principle of which is sacred". That is each level in the hierarchy is an independent order of reality, incommensurable with other levels (the word sacred implies that each level must be undisturbed by the others).

There is a third metaphysical theme that also relates to punctuated equilibria – the problem of discontinuity and progress. Basically one can argue that if history is discontinuous then progress is not inevitable. The history of science is a good example of this problem. After Thomas Kuhn published *The Structure of Scientific Revolutions* (Kuhn 1962), proposing that the history of science was marked by large discontinuities, the question arose amongst many historians and philosophers of science as to how this corresponded with the widespread notion that science was marked by gradual progressive understanding of the universe. It was proposed that historical discontinuity is not compatible with such progress and that if progress is to be preserved then one has to explain it in some fashion other than one of gradual increase. The debate over this question was and is strongly informed by Marxism.

One of the authors of punctuated equilibria, Stephen Gould, who acknowledges a strong Marxist influence, has consistently made similar assertions about the nature of history. However in this case he is referring to the history of life rather than human history. His claim has the following structure – if most evolutionary change occurs at geologically instantaneous points in time (that is, if evolution is punctuated) then such change is ostensibly random with respect to long term trends and that evolution thus cannot be viewed as a progressive process (i.e. with increasing complexity, for instance, as has often been assumed). (see, for instance, (Gould 1997b)) The debate over punctuated equilibria thus has a place in a general metaphysical discussion about the nature of history – the rivalry between the linked notions of gradualism and progress one hand and discontinuity and randomness on the other.

Gayon also provides a philosophical dissection of the syntheticists' reduction of macroevolution to microevolution and notes that the syntheticists do not seem to believe in a strict reduction. Rather they use the word 'extrapolation', which he contends is a compromise between their belief that macroevolution is reducible to microevolution and their inability to extend microevolutionary calculations into macroevolutionary time. Gayon thus determines that there is no complete reduction and hence that "there is an obvious autonomy of paleontological theories." Using the two philosophical conditions

for a reduction[35] as criteria he concludes that derivability is not satisfied. This philosophical treatment correlates nicely with the treatment of reduction given in this thesis - connectability equates with reduction in principle and derivability with reduction in practice. Gayon's judgement that derivability is not satisfied is thus a philosophical justification for the punctuationist rejection of the reduction in practice. However it should be noted that for Gayon reduction is all or nothing, where the punctuationists retain the reduction in principle. (pp.37-38)

1.5: A note on the nature of communication.

Humans are not entirely instinctual creatures. We have the capacity to understand things intellectually as well as instinctively. This is important, as often people will say things that we don't agree with or don't understand or both. Using our intellect, however, it is possible for us to make sense of what the other person is saying. Even though we do not have enough shared experiences with them to immediately know what they mean, we can imagine what causes them to make such statements and thus come to some understanding. That is, we assimilate the experience of the other by listening to what they say and making a real conscious effort to understand their point of view. Their experience becomes, at least partly, ours also. We come to understand the interpretive structure of their mind and by the same process they may come to understand ours. This is called *communication.*

In general if there is a conflict of opinion between two people it is not because one of them is right and one is wrong. Instances in which it is possible to say categorically that there is a right and a wrong side are either trivial ("that's a tree" "no it's not") or are based on moral judgements ("murder is bad"[36]). In general each person's perspective has a sound basis in their own experience. Given this the question arises as to how conflicts of opinion can be resolved? The answer is the process of *communication*. If one does not agree with another on some point, then the path to resolution involves a bipartisan attempt to understand the perspective of the other, to let their experience become ours and vice versa. If there is a real, conscious attempt to address the issues on their terms, and vice versa, conflicts invariably dissipate. There may still be differences of opinion, but there will also be respect for the position of the other. *Common ground* will be established - that is, there will be agreement as to what the issues actually are. And, even more importantly, a *common language* will develop - understanding the perspective of the other allows us to speak to them in terms that will not be misconstrued. There will be understanding where there was incomprehension, discussion rather than argument and respect instead of disdain. The protagonists will have *empathy* for each other's position. .[37]

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[35] These conditions are: "the concepts of the reduced theory must be defined in terms of the reducing theory (the condition of connectability)"; "one must be able to deduce the laws of the reduced theory from the laws of the reducing theory (the condition of derivability)."

[36] Even this 'evident' statement is not so clear cut – consider the grey area between murder and war.

[37] *Empathy* should not be conflated here with *sympathy*. There are very important distinctions between the two concepts. For instance in his book *People Skills* (Bolton 1986) Robert Bolton, a communication skills

In the sense of the above discussion, the dialogue between scientists is no different to that between other humans, whether that dialogue be oral or written. Most new science is marked by at least some disagreement between the scientists involved. The way that such disagreements are handled by the people involved affects the resolution of the issues (or, indeed, whether any resolution occurs at all). The history of the debate over punctuated equilibria and associated ideas about macroevolution is no exception to this. Both sides of the debate have expressed interest in communicating with the other and the methods they have used to attempt such communication has had a strong affect on how the issues have been resolved.

In the simplest terms the history of the debate over punctuated equilibria can be read as one between evolutionary biologists (particularly population geneticists) and paleontologists. These two scientific disciplines are naturally concerned about evolutionary issues and when it comes to macroevolution their concerns overlap. Evolutionary biologists like to feel that the phenomena they study can be extrapolated in some way such that their analyses are relevant to the history of evolution and not just the ecology of the present, and paleontologists like to feel that they do more than name species from the fossil record - that they, too, can make assertions about the nature of evolution, particularly over large spans of time. The problem has been that historically these two disciplines simply haven't talked to each other at all. Most of the scientists in question are academics at universities, and in those universities paleontology and evolutionary biology are separated by the structure of the departments – evolutionary biology is usually part of the biology department and paleontology is usually in with the geology department. Quite often that means that evolutionary biologists and paleontologists are in different buildings. Literally, the scientists from the two disciplines don't talk – they do not, as a matter of course, see each other in the hallways or coffee lounges, there is no routine sharing of ideas.

The problem is that when it comes to punctuated equilibria and associated macroevolutionary issues the concerns of the two disciplines overlap to a large degree. However discussions of such issues by either side have generally been marked by a disregard for the concerns of the scientists from the opposing camp. In general, even when they are purporting to answer the assertions of the other discipline, no real attempt is made to find a common ground upon which to base the discussion.. Few attempts have been made at a cross-disciplinary analysis of macroevolutionary issues. In fact there is not even agreement on what the issues are (no *common ground* has been established) and there has been no attempt to establish a terminology that is agreeable to the concerns of both sides (there is no *common language*). Of course, it is natural for any scientist to use the methods and language of their own discipline in an analysis of a particular theory, idea or phenomena. Such is the nature of contemporary expertise. Scientists generally do not feel qualified to make comments about scientific work from other disciplines, and they tend to object when others do so. However it is not impossible for the two

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consultant, sees empathy as being a "feeling with" another person whereas sympathy is a "feeling for" another person. Sympathy, in this sense, is "often condescending" ("Oh you poor thing") (p.271). Empathy, however, being merely identification with the other person, is more likely to "foster constructive changes in others" (p.272). Bolton, in fact sees empathy as being one of the three essential elements of effective communication. (The other two are genuineness and nonpossessive love)

disciplines at the forefront of the punctuated equilibria debate to combine their expertise. This is shown by the rare but important studies that have actually done just that, such as the (ongoing) collaborative investigation into fossil and extinct bryozoans by Alan Cheetham and Jeremy Jackson (see Section 6.1.4).

In the early 1980s a prognosis for the relationship between evolutionary biologists and paleontologists would have been more positive than one made in the late 1980s. Despite the fact that there was some heated debates occurring at the time there was evidence of concerted attempts from both disciplines to find a common ground on which to discuss macroevolutionary issues. In 1980, for instance, a conference was held in Chicago in to discuss macroevolution that included scientists from both disciplines. Notable evolutionary biologists like John Maynard Smith and G. Ledyard Stebbins wrote articles that welcomed the input of paleontologists to evolutionary theory ((Maynard Smith 1984), (Stebbins 1982)). There was hope of a new synthesis in the study of evolution, one that would include the concerns of modern paleontologists. Gould wrote several articles between 1979 and 1983 that attempted to discuss issues of common concern and/or announced that the structure of evolutionary biology had changed because of the contributions of paleontologists (see, for instance, (Gould 1979a), (Gould 1980c), (Gould 1980b), (Gould 1982a), (Gould 1982b)). By the late 1980s, however, it became evident that the attempt at forming regular channels of communication between the two disciplines had failed. (The reasons for this are discussed in Chapter 5.) Any hope of a new synthesis vanished.

1.6: Other Historical Accounts of Punctuated Equilibria.

As far as I am aware, this thesis is the only book length account of the history of punctuated equilibria. There are, however, many shorter historical accounts, almost all of which have been composed by protagonists in the debate. In fact the history of evolutionary science and the relationship between paleontology and evolutionary biology has been one of the major points of contention within the debate.[38] The reason that history has been such a crucial aspect of the debate is that the punctuationists have from the start claimed that the history of evolutionary science was marked by an undue emphasis on gradualism and that this was caused by an over-reliance on natural selection as the sole creator of evolutionary patterns. This epistemological history, they charged, was reflected in the social history, in which pre punctuated equilibria paleontology had not been a respected discipline within evolutionary science. The punctuated revolution, according to the punctuationists, had remedied the situation by challenging the omnipotence of natural selection and asserting the independence of paleontology. The syntheticists, in turn, denied the punctuationist history. They asserted their own version in which varying rates of evolution had always been a part of evolutionary science and paleontology. They did, in general, concede that before the 1970s paleontology was in the doldrums but denied that this was related to an over-emphasis on gradual evolution. Thus many of the historical accounts of punctuated equilibria, having been produced by actors

[38] Indeed this thesis could well have a subtitle ‘The Use of Historical Constructions in Scientific Debate.’

in the drama and indeed being crucial parts of the drama, will be discussed in the following chapters and at this point a brief summary of them will suffice.

One of the most consistent commentators on punctuated equilibria has been the philosopher Michael Ruse. He does not, however, attempt to adopt the usual 'objective' stance of a philosopher. Rather he professes to be an 'ultra-Darwinist', someone who believes in the power of natural selection to explain all of evolution (and more besides). He has thus been a protagonist in, rather than an observer of, the debate over punctuated equilibria. Ruse has published three major studies of evolutionary science.

Darwinism Defended: A Guide to the Evolution Controversies (Ruse 1982), is a comprehensive summary of the state of neo-Darwinism as of the early 1980s. Ruse's 'ultra-Darwinian' perspective is most clearly displayed in a chapter titled "Neo-Darwinism: The Total Picture" in which he sets out his judgment of the current state of evolutionary theory. He characterised the neo-Darwinian as one who accepts that population genetics has total authority over evolutionary explanations: "neo-Darwinians recognize that throughout the world there is a strong tendency towards overpopulation and that this sets up conflicting selective pressures. Hence neo-Darwinians feel justified in turning to the theory that combines selection with modern principles of heredity: population genetics.". According to Ruse population genetics provides the "focus" for all the other disciplines concerned with evolution (paleontology, biogeography, embryology, systematics), which are "brought beneath the umbrella". (p.115-151)

Ruse devoted a 20-page chapter to punctuated equilibria - 'The Challenge from Paleontology' (pp.207-226). Not surprisingly he gave a rather negative appraisal. His major bone of contention with the punctuationists was on the topic of adaptation. The punctuationists, he wrote, "seriously underestimate the overwhelming evidence that we have for ubiquitous or near-ubiquitous adaptation in the organic world" (he cited two notable evolutionary biologists in support of this position – Maynard Smith and A. J. Cain). He then concluded that "the deemphasis of adaptation that occurs in the writings of the punctuated equilibria theorists seems untenable."

The Darwinian Paradigm: Essays on Its History, Philosophy and Religious Implications (Ruse 1989), is basically a sequel to *Darwinism Defended*, with further investigations of the same themes. Once again a whole chapter was devoted to punctuated equilibria - 'Is the Theory of Punctuated Equilibria a New Paradigm, p.118-145. Ruse began with a brief account of the history of punctuated equilibria which he saw as having gone through three distinct phases. The first phase, which occurred directly after Gould and Eldredge's 1972 paper, was a "fairly straightforward extension of orthodox Darwinism." The second phase, which began in the late 1970s and continued up to the early 1980s, was more radical, with an assault on the hegemony of natural selection and adaptation. The third phase retreated from this extremism but was by no means a total surrender. "Now", he wrote, "we are presented with a *hierarchical* view of the evolutionary process." This hierarchical view, according to Ruse, includes a de-emphasis of the importance of adaptation and a re-emphasis of the importance of species as evolutionary units rather than classes.

Mystery of Mysteries: Is Evolution a Social Construction? (Ruse 1999), is Ruse's contribution to the debate over the 'Social Construction of Scientific Knowledge'. He uses the history of evolution as a case study in which to illustrate his philosophical

position. Ruse examined the ideas of Stephen Gould in an eighteen page chapter – 'Speaking Out for Paleontology' (pp.135-152). Strictly speaking, Ruse was not addressing the punctuationist research programme as such. However he strongly identified Gould with that programme and demonstrated considerable antipathy to both. He concluded that Gould's ideas, punctuated equilibria included, are more often a product of external, social forces rather than internal, scientific ones.

Over the years both Eldredge and Gould have produced historical accounts of punctuated equilibria. Eldredge's *Time Frames: The Rethinking of Darwinian evolution and the Theory of Punctuated equilibria*, for instance, contains Eldredge's personal perspective on the trajectory of punctuated equilibria. (Eldredge 1986) Eldredge and Gould's joint article 'Punctuated Equilibrium Comes of Age', written to mark 21 years since the theory's inception, contains a comprehensive account of their version of history and the significance of punctuated equilibria. Gould himself, it must be remembered, is almost as much an historian as a scientist and the tally of his historical publications runs into the hundreds. Many of these contain sections concerning the history of punctuated equilibria – too many in fact to list here. Suffice to say that many of these historical accounts are the focus of discussion throughout this thesis as they have been a crucial part of their overall punctuationist campaign.

Eldredge and Gould have not been the only punctuationists to write historical accounts of punctuated equilibria. 'Punctuated Equilibrium at Twenty: A Paleontological Perspective' by paleontologist Donald Prothero, for example, is almost the archetype of the punctuationist historical perspective (Prothero 1992). In the article he:

- Discussed the years before punctuated equilibria, when "paleontology had the well-deserved reputation of being a stagnant backwater among the sciences".
- Recorded the birth of 'paleobiology' in the 1970s.
- Moved through the debate of the 1970s and 1980s, during which many paleontologists "denied its importance" and "trotted out their favourite example of gradual evolution" many of which "turned out to be ambiguous, or actually demonstrated punctuated equilibria better than gradualism".
- Summarised studies from the 1980s and early 1990s that confirmed stasis (including his own).
- Documented the decoupling of macroevolution and microevolution, the associated paleontological independence movement and the consequences for evolutionary biology. (It must be said that Prothero gave a rather balanced account of this topic. Rather than presenting a partisan view he merely pointed out that most neo-Darwinists "come from a reductionist viewpoint", that the "opposing camp sees the world as hierarchically ordered" and that this "fundamental difference in worldview" has meant that "debaters [have been] talking past each other".)

There are very few non-partisan histories of punctuated equilibria. One such account was given by the historian Brian Leith in 1982. He devoted one chapter of his book *The Descent of Darwin* to a discussion of punctuated equilibria and associated challenges to synthetic theory ('Why Don't We See Gradual Transitions in the Fossils?', (Leith 1982), pp.79-95). After discussing the historical origins of the debate (ie Darwin's penchant for gradualism and his assertion that breaks in fossil sequences were

imperfections in the record) Leith summarised the discussions that had taken place up to then. He concluded that "whilst the theory of natural selection is not actually contradicted by the researches of the macroevolutionists [punctuationists], it may simply prove inadequate in explaining the large-scale events … it was designed to explain", predicted that the issue "may prove to be a bitter battleground" and advised that "population geneticists should not guard so jealously *all* aspects of evolution."

Journalist Andrew Brown's *The Darwin Wars* is a large-scale publication that deals with disputes over natural selection and adaptation in a largely unbiased fashion. (Brown 1999). Brown's book provides a popular account of the division in evolutionary science between the sociobiologists and their opponents, whom he labels, respectively, 'Dawkinsians' and 'Gouldians'. He summarises their differing world-views thus: "Dawkinsians will stress the power and reliability of natural selection, and its ability to produce adaptations to almost anything; Gouldians reply that there are large numbers of starting points eliminated by chance or mass extinction, and that in consequence there is much that natural selection will never be able to accomplish."

Some major parallels between Brown's book and this thesis are thus apparent. His 'Gouldians' and Dawkinsians' loosely correspond with the groups that I have called 'punctuationists' and 'syntheticists'. Both he and I identify the centrality of natural selection to evolutionary explanation to be the focus of debate between these two groups. However Brown focusses almost exclusively on debates about sociobiology and genetic selection (punctuated equilibria is mentioned only very briefly at two separate points in the book) whereas I focus on debates about punctuated equilibria and related ideas. By way of analogy, Brown and I have described the same building, but from different sides.

Chapter 2

Materials, prehistory and the 1970s.

(An overview of material aspects of the debate, a summary of relevant events leading up to the formation of the theory and an account of the trajectory of the theory in the 1970s.)

2.1: Material aspects of the debate (fossils and flies).

2.1.1: Paleontology.

Brian Leith, in his book *The Descent of Darwin* (Leith 1982), gives a good account of the nature of the fossil record, and how it is possible for scientists to hold such diametrically opposing positions regarding its nature. It appears that data collected from the fossil record is equally as esoteric and cryptic as data from any other scientific field. Fossil data must be ordered by the perspective of a world-view or it just won't be anything more than a collection of pictorial reliefs on rocks. Leith points out that there have been two long-standing, opposing, traditions for interpretation of fossils, dating from well before Darwin – uniformitarianism and catastrophism - and that the current dispute over punctuated equilibria can be seen "as a direct descendant" of the conflict between these traditions.[39] (p.80)

Leith notes that if collecting data from the fossil record were simply a case of digging vertically "into the earth's surface" and thus retracing "the history of an area chronologically with increasing depth" then there would be no room for dispute. (p.82) However this is not the case. Rather the "fossil record is patchy and discontinuous" like "a ruler that has been chopped into thousands of short sections then scattered around randomly." There are also several other factors that mean the jigsaw is not only scattered but also incomplete: In a particular deposit there will be times when erosive rather than sedimentary forces have acted and no fossils will be left; Mostly only "hard bony or woody tissue" will be fossilised – soft body fossils are extremely rare, so "only a fraction of all living creatures in any one place or time" will generally leave an impression; both the earth's surface (via plate tectonics) and most living things themselves are mobile, so it can't be assumed that a fossil from a particular place necessarily lived in that place. (pp.83-84)

Despite the obvious imperfections of the fossil record, there is unanimity amongst evolutionary scientists on one point - it is full of breaks. That is, frequently species disappear suddenly and are replaced by their descendants. The moot point regarding these breaks is whether they represent actual biological phenomena or are artefacts of the fossilisation process. Darwin, for instance, generally espoused gradual evolution and thus held the latter view. From the perspective of his worldview the breaks were imperfections

[39] I would agree with Leith that metaphysically this is true. However there is no direct line of descent re research programmes.

in the record. The punctuationists by contrast see the breaks as the result of actual events (the 'punctuations' of punctuated equilibria).

The crux of the difference between these two world-views is not the breaks themselves which, being constituted by a lack of data, give no information but the parts in between. If species gradually evolve over time, as Darwin advocated, then any breaks in the record (due to lack of deposition or erosive forces) will necessarily show a jump in evolution from one species to something substantially different. During the time when no fossils were recorded the species just kept on evolving. However if species are predominantly unchanging stable entities, as the punctuationists advocate, then a gap in the geological strata due to non-deposition or erosion will not necessarily show change and the jumps in the fossil record document real biological events – speciation events. ((Leith 1982), p.85)

There are three principal divisions of fossil types, each with its own paleontological discipline – plants (paleobotany), invertebrates (invertebrate paleontology) and vertebrates (vertebrate paleontology). Paleobotany has connections with systematic botany and floristics and has not been a major contributor to ideas about evolution. (Hence it has no great relevance to the debate over punctuated equilibria.) Vertebrate paleontology has limited relevance to the debate over punctuated equilibria. There are a few vertebrate paleontologists who have been significant actors in the debate but most of the prominent paleontological protagonists are invertebrate paleontologists.[40] The material reason for this is that vertebrate fossils simply do not occur with anywhere near the same frequency as invertebrate fossils. In general, making macroevolutionary claims using data from vertebrate paleontology is like trying to generalise about a social trend from a survey of ten people.[41] Also, the organisms that vertebrate paleontologists study are relatively complicated. Hence they are generally concerned with the reconstruction of extinct animals (a practice closely allied with comparative anatomy) and, increasingly, how they may have behaved and interacted with their environment. Invertebrate paleontologists, by contrast, generally deal with simple animals (whose morphology is thus relatively easy to reconstruct) abundantly represented in the fossil record. They thus have large samples to catalogue, draw graphs with, make statistical analyses of and to make assertions about macroevolutionary trends with.

One of the main activities of paleontologists is the construction of phylogenetic tress. (Which species are whose ancestors? who evolved from who? etc.) In recent times there have been two opposing traditions in this form of analysis, the cladistic approach and the phenetic approach. The cladistic approach was formulated by the systematist William Hennig in the 1960s and is based on the principal of parsimony. In a zoological cladistic analysis one restricts examination of the relationship of different species solely to the presence or absence of shared characteristics, makes no assumptions

[40] The vertebrate paleontologists involved in the debate may be few in number but they have been important. In particular Phillip Gingerich, who was the most prominent paleontological critic of punctuated equilibria in the 1970s, used mammalian fossil data in his attempt to refute the punctuationists' claims. And Elizabeth Vrba who has been a strong ally of Gould, Eldredge and Steven Stanley is a vertebrate paleontologist. She mainly uses fossils of antelope species from Southern Africa. In both cases the species concerned are exceptionally well represented in the fossil record compared to most vertebrates.

[41] Before the Modern Synthesis vertebrate paleontologists were in fact the main source of assertions about macroevolutionary trends. However invertebrate paleontology has, since the Modern Synthesis, increasingly usurped this role. The reasons for this are discussed in Section 2.2.2.

about who may be ancestral to whom and ignores the rest of the organisms morphology. Cladists transfer these principals into their phylogenetic reconstructions by maintaining the principal of parsimony – that is, they choose the arrangement that minimises the total number of changes from taxon to taxon, with each morphological trait considered separately. The more traditional phenetic approach is based on simultaneous consideration of all traits.

Cladism has been a controversial movement in evolutionary science (see (Leith 1982), pp.96-109 for an extended account) however it has not had a large influence on the direction of the punctuated equilibria debate. Each of the opposing camps from the debate contain scientists both for and against cladism. Indeed even the authors of punctuated equilibria are divided on this issue, Eldredge being a cladist and Gould being a pheneticist. However there have been a few important instances where the debate over cladism has intersected the punctuated equilibria debate.

In the late 1970s and early 1980s the taxonomist Beverley Halstead wrote a series of letters to the journal *Nature* objecting to the 'Origin of Man' exhibit at London's Natural History Museum, which was based on the cladistic approach. In his letters Halstead linked cladism, punctuated equilibria and Marxism. Halstead was at least partially correct in linking punctuated equilibria with Marxism as in some ways the punctuated perspective of natural history has a lot in common with Marxist reconstructions of human history. Indeed some of the punctuationists (Gould in particular) have professed to be influenced by Marxism. However he was mistaken in linking the cladism of the museum exhibit with punctuated equilibria. Nonetheless, his letters sparked a prolonged controversy in the pages on *Nature*. (again see (Leith 1982), pp.105-107 for an account of the museum/*Nature* controversy.)

This conflation of cladism with punctuated equilibria is at the root of all intersections between the two controversies. Many critics have assumed that cladism and punctuationism are the same thing. This is perhaps due to the fact that when cladism is applied to phylogenetic trees it has the effect that new species cannot be named until there is a speciation event. Thus it seems that phylogenetic analyses based on cladistic analysis are punctuated by convention – a species keeps the same name no matter how much change takes place until the paleontologists decide that a speciation event has occurred. However this is a rather shallow view of the cladistic approach. Just because the cladists do not change the name of a species over time does not mean that they ignore the morphological variation of that species over time. Cladists are just as likely to find against stasis as for it in a particular lineage despite the fact that they keep the name constant.

Richard Dawkins, for instance, made just such a mistake when he criticised punctuated equilibria in his book *Climbing Mount Improbable*: "If a specimen is intermediate in actual form (as many are) zoologists' legalistic conventions still force them to jump one way or the other when naming it. …that there are no intermediates has to be true *by definition* at the species level, but it has no implications about the real world". Dawkins assumed that once a paleontologist names a species in the fossil record their analysis of that species ends, commenting that the "proper way to look for intermediates is to forget the naming of fossils and look, instead, at their actual shape and size." ((Dawkins 1996), p.96) In practice the identification and naming of a species is usually just the beginning of a paleontologist's analysis. Attention is then turned to

examination of changes in the morphological variation of that species over time. They may find stasis (which doesn't necessarily mean no change but rather no net change over time) or they may find gradual change or a mixture of the two.

2.1.2: Population Genetics.

Since the Modern Synthesis population genetics has been the first-port-of-call for evolutionary explanation. That is, interpretations of evolutionary data from any sub-field of evolutionary science have had to be rendered consistent with the tenets of the population genetics or be subjected to ridicule and disdain. Witness the derision administered to the 'hopeful monsters' of Richard Goldschmidt. In essence Goldschmidt proposed that at times evolutionary change can occur in one generation via large mutations - the very antithesis of the principles of the population genetics. In evolutionary science the name 'Goldschmidt' has become a euphemism for absurd and foolish.[42]

The dominance of population geneticists in the Modern Synthesis stemmed from their ability in the preceding decades to establish the data of their field and their interpretations of that data as the most important area of inquiry for evolutionary science. In particular they secured authority over the mechanisms of heredity, which had been the biggest problem for Darwinian evolutionary theory (see (Sapp 1983) for a full account of this period). The origin of new species had also been a major difficulty for Darwinism until the biologist Ernst Mayr managed to provide an explanation for the phenomenon. His notion of allopatric speciation[43] was a crucial part of the Modern Synthesis as it

[42] Gould has been the only prominent evolutionary scientist to defend the ideas of Goldschmidt in the last thirty years. (In a general rather then a specific sense. See (Gould 1977c), and the introduction to (Goldschmidt 1982(1940))). He documented the ridicule afforded to Goldschmidt then charged that such treatment is unwarranted. Gould did not advocate 'hopeful monsters' as such, but rather promoted the idea that there are lessons to be learned from Goldschmidt's ideas. The first of these was that small genetic changes can have cascading affects on the development of organisms resulting in large final differences in the adult. Goldschmidt's experiments, according to Gould, "demonstrated that large final differences reflected the action of one or a few "rate genes" acting early in growth." Hence, said Gould, "if we do not invoke discontinuous change by small alterations in rates of development, I do not see how most evolutionary transitions can be accomplished at all." ((Gould 1977c), p.30) The second lesson was that evolution should be studied at a hierarchy of levels - "The systematic mutation, the saltatory origin of nearly all new species, may be rejected, but Goldschmidt's vision was sound and it supplied (or rather resupplied) an essential ingredient that strict Darwinism had expunged from evolutionary theory: the idea that evolution works through a hierarchy of distinct levels with important independent properties (however strong the ties of feedback that Goldschmidt denied)." ((Goldschmidt 1982(1940)). p.xi) Gould thus used Goldschmidt as an ally to challenge the primacy of natural selection in evolutionary science.

[43] The basic idea of allopatric speciation is that speciation will usually only occur when populations are separated by some physical barrier. If two populations of the same species are regularly in contact with one another speciation is unlikely because there will be constant gene flow. However if a physical barrier of some sort (ie a new river, mountain chain, etc.) separates the populations there will of course be no gene flow. The isolated groups will face different selection pressures (or genetic drift) and, if they stay isolated for long enough they will become so different that when and if they do eventually meet again they will no longer be able to interbreed – that is they will become separate species. Important to Mayr's theory was the idea of 'peripheral isolates' and the concomitant 'founder effects'. Speciation, said Mayr, was most likely when a small population on the periphery of the range of a species became isolated. In this small population only a percentage of the total gene pool of the population would be represented. Certain genes would thus

provided a solution for one of the major evolutionary puzzles that was consistent with both Darwinism and the tenets of population genetics.

Population geneticists obtain their data from one of two sources: controlled populations in laboratories (the fly species *Drosophilia* is the most common species used in such environments) and studies of species in the wild. They therefore have an almost unlimited pool of possible data that could be collected. However in terms of vindicating and explicating the application of population genetics to evolution they have some major difficulties. Firstly it has been well demonstrated time and again that selection pressures applied to populations in the laboratory can produce remarkable 'evolutionary' changes over short periods of time. Hence it can be inferred that under suitable conditions in the wild natural selection will produce evolutionary change. However, as is perhaps obvious, these studies have limited applicability to wild populations, where selection pressures will not be as constant. It is also very difficult to isolate selection pressures in the wild This leads to the second major problem in applying population research to evolution. It is difficult for scientists to know precisely what selection pressures are being applied to any particular population. Also wild populations are rarely isolated enough for biologists to be sure that gene flow from other nearby populations are not affecting their data.

The focus of this thesis is the disputed territory of macroevolution. When it comes to macroevolution population geneticists have a major problem with the difference between the periods of time that their studies are able to encompass and the time-scale of evolution. It is very difficult for them to actually observe any major evolutionary change in the time they have available, and therefore it is perhaps not surprising that the number of empirical studies purporting to illustrate how population genetics can be extrapolated to macroevolution is small. Indeed it seems that, empirically, the case for population genetics is based on a handful of examples that are repeated *ad nauseam* by the textbooks of evolutionary biology.

The most famous illustration of 'evolution at work' concerns the moth species *Biston betularia*. In parts of England over the course of the last hundred years or so this species changed color, apparently because of industrial pollution. It then changed back again when the pollution stopped. Initially the moths were mostly of a light-coloured form. They became mostly dark in colour during the polluted period. When the pollution stopped they changed back to being light in colour. The explanation offered for this phenomenon proceeds thus: The habitat of the moths is the trunks of a certain kind of tree. This tree has light-colored bark and the moths, being predominantly light-coloured had some measure of camouflage to protect them from being eaten by birds. However the pollution (caused by the burning of coal) darkened the bark of the trees. The light coloured moths thus became easy pickings for birds. However within the spectrum of morphological variation for the species there is a dark coloured type. Individuals of this type were thus advantaged by their new found camouflage and quickly became the predominant type. That is, the dark-coloured individuals became more likely to survive and leave offspring than light-coloured ones, and the colour of the offspring is more than likely to be the same as that of the parent, hence during the polluted period the dark-

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have a pre-emptive chance of becoming established in the new species – this is the founder effect. Also in a small population the effects of natural selection and genetic drift are magnified and mutations are able to become fixed in the roup more rapidly. Speciation in the 'peripheral isolate' can thus occur in a relatively short period of time.

coloured variety became the most common form. After the pollution stopped and the trees went back to their normal colour and the selection process reversed and soon the light coloured form dominated again. (See (Bishop and Cook 1975) for a full scientific account of this phenomenon.)

This story is supposed to illustrate how natural selection can cause evolutionary change via a process of adaptation. The species as a whole changed form over time as it adapted to the new environment. However the cause of the change is not to be found at the species level. Rather it was caused by differences in the probability of survival, and therefore probability of breeding, of individual moths - that is, by *natural selection* of the moths. However in terms of justifying the extrapolation of population genetics to larger scale evolutionary phenomena this story has a major weakness - the change recorded was minor relative to the kinds of evolutionary change that can be seen in the fossil record. The color variations were already in existence and the differing environments simply caused changes in the relative frequency of these variations - no new species was formed. A process of adaptation is illustrated and the application of population genetics to microevolution is corroborated but it provides no support for extrapolation to macroevolution.

The previous story is not exclusively a population genetics one, in that the genes that code for the moth's colour have not been identified. Indeed Darwin could quite easily have come up with the same story. It is assumed that there is a simple gene complex coding for color that natural selection can work on (this is a common assumption made in evolutionary biology). The archetypal population genetic story, in which the genes involved have been precisely identified, is that of sickle cell anaemia. The essence of the account is this. There is a gene (call it 'S' with other, 'normal' genes being called 'A') that causes a number of debilitating, and eventually lethal, effects when one is homozygous for it.[44] In most parts of the world gene S is extremely rare. However it is recessive[45] with respect to its debilitating effects and when one is heterozygous[46] some measure of resistance to malaria is offered. It so happens that in some parts of Africa, where malaria is rife, gene S is actually very common, with up to 90% of the adult population being heterozygous. (The account given here is based on information from (Anonymous 1995))

A population genetic calculation of the 'fitnesses' of the different alleles (gene combinations) is thus possible. The details of such a calculation are not important here, but one can imagine the form it would take. A certain proportion of the adult population will be homozygous for A, the rest being heterozygous (individuals homozygous for S die as children). Knowing the frequencies of the genes and assuming that breeding between adults is random with respect to these genes it is possible to calculate the frequencies these genes will have in the next generation. In the new generation individuals bon homozygous for S will not survive to breed, but heterozygous individuals will be more likely to survive and breed than those homozygous for A. By comparing the frequencies of the genes between generations one can thus give 'fitness' values to the different genes. In simple terms, the worse the malaria in a particular area the 'fitter' the S gene will be and the greater its representation.

[44] That is, when one has two copies of it - one from each parent.
[45] That is, when one gets S from one parent and A from another the effects of S are not expressed.
[46] That is, having one S and one A.

The sickle-cell story is thus an example of how the principal of natural selection in combination with the ideas of population genetics can explain the changing distribution of genes in a population over time. And, as was seen in the quote from Theodosius Dobzhansky (see Section 1.1), population geneticists defined evolution as a change in the genetic composition of populations. The sickle-cell anaemia story is held up as an example of evolution in action. However with respect to macroevolution it suffers from the same problem as the moths-that-changed-colour story. It offers no support for the notion that population genetics can explain the patterns of macroevolution.

Another common story that purports to illustrate the validity of the population genetic view of evolution is that of the Herring Gull and the Lesser Black-Backed gull. These birds constitute distinct species in Scandinavia and Britain yet they are linked by groups of interbreeding populations that circle the Northern Hemisphere. This is thus supposed to illustrate the way that speciation occurs. Species change gradually over time via natural selection and, perhaps, genetic drift. At their peripheries they can become so different to the rest of the population that they are no longer capable of interbreeding. This story lays a much stronger claim for an extrapolation to macroevolution than the previous two, the evolution of these birds taking place over a much longer time period (as compared to other phenomena that population geneticists study) and over a large geographical area.

Indeed John Maynard Smith uses this example to place doubt on the punctuationist explanations for the phenomenon of stasis in the fossil record. After recounting the gull story he comments: “Stasis in time is, therefore, a puzzle since it seems not to occur in space.” ((Maynard Smith 1993)[47], p.152) One imagines that the punctuationists would counter this story by saying either that the gulls are not sufficiently differentiated to count as good paleontological morphospecies[48] or that their speciation is an example of a macroevolutionary punctuation. That is they would say either that the evolutionary change accrued by the birds is negligible with respect to macroevolution or that in macroevolutionary time-scales it would be seen as an instantaneous event.

The most famous evolutionary story is that of the Galapagos finches.[49] The Galapagos islands are very isolated and their colonisation by only a single finch species is well documented. From that single species over a dozen new species have evolved, each using different environmental niches to survive and each having a morphology to suit their particular lifestyle. These finches offer population biologists excellent material for study. Their isolation ensures that migration and gene flow from adjacent populations does not affect them. The populations are relatively small (usually a thousand or less) so it is possible to follow the genealogies quite precisely. The finches of the Galapogas are thus a small natural experiment in evolutionary change.

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[47] This book is a collection of Maynard Smith’s essays. The article from which the quote was lifted was first published in 1981 and is a defence of population genetics right to explain all of evolution.

[48] A morphospecies is one that is distinguishable by its morphology alone. Usually there is coincidence between morphospecies and species in general but there are some species (mostly arthropods) that are indistinct apart from their breeding habits. This represents a problem for paleontologists, as they have no possibility of observing colour and little of observing soft-bodied features, let alone breeding behaviour and their special classifications can thus be criticised for a lack of sufficient discrimination.

[49] Most of the information offered here is from (Weiner 1995).

The first thorough study of the finches informed by the Modern Synthesis was performed by David Lack.[50] His 1947 monograph *Darwin's Finches* is considered a classic in the field and is still widely cited. He was the first biologist to observe the finches in the wild over a long period of time and to record their behaviour (particularly their feeding behavior). Each finch species has a distinctive beak and the differing beak-shapes are the result, according to the story, of adaptation to different feeding habits. That is, each species took advantage of different environmental opportunities, some feeding on cacti, others on small seeds, some on big seeds, some on insects, etc. What Lack noticed was that on each island no two species had similar shaped beaks although across the archipelago there were species that have similar beaks. Lack saw this is an example of Darwinian competitive struggle, that if two species lived on the same island and had similar feeding habits then one or the other would be driven to extinction. (Lack 1983(1947)).

In the early 1970s Peter and Rosemary Grant of Princeton University began their own program of research on the Galapogas islands. Originally they set out to take some simple measurements over the course of a few years but, encouraged by the quality of the data they were able to obtain from the finches, they continued the program for over twenty years. (A detailed account of their research program is given in (Weiner 1995)) The beaks of the finches were the focus of their study. They presumed they would be able to record minor changes in the dimensions of the beaks over time and hoped to identify what selection pressures caused such changes. What they actually saw surprised them. The atmospheric conditions of the Galapogas are extremely variable, having long periods of drought at times and enormous volumes of rain at others and the Grants found that from year to year the dimensions of the finches' beaks actually varied enormously.

For instance in 1977 there was a terrible drought which brought about the downfall of most of the smaller birds of one particular population. The Grants observed that the reason for this was that the birds were forced to try and eat bigger and tougher seeds than they normally would and hence only those with the biggest and strongest beaks were able to feed efficiently. This trend towards larger and stronger beak size (and thus body size in general) was passed on to the next generation of birds. According to Jonathan Weiner's account what the Grants had witnessed was "evolution in action, in the dimensions of the birds beaks and in many other dimensions too. … Not only is Darwin's process in action among [the] finches, not only can natural selection lead to evolution among their flocks, but it leads there much more swiftly than Darwin supposed possible." (p.81) Weiner stresses this theme repeatedly in his account of the Grants' research, that the finches vary remarkably in short periods of time and that it is thus possible to see evolution occurring in human time scales.

In terms of the extrapolation of population genetics to macroevolution, however, this story suffers from the same problem as the previous ones, that the changes seen occurring amongst these finches are extremely small relative to the kinds of changes seen by paleontologists. Variation of an extreme nature in short periods of time has been observed and it does seem that natural selection is the force responsible but there was no

[50] Darwin visited the Galapogas islands and the diversification of the finches was, apparently, influential in the formation of his theory. The modern story has its origins with him - that from the single colonising species the other species evolved as they adapted to use different environmental opportunities. However it is modern studies of the Galapogas finches that concerns us here.

discernible speciation. Weiner's book is aimed at a popular audience and he is trying to make the research sound vibrant and dynamic, to hype it up, so as to appeal to a wide readership. One cannot be sure to what extent the Grants actually believe that they were seeing "evolution in action". However it must be said that there does seem to be a common perception amongst evolutionary biologists and particularly population geneticists that intra-specific variation is indeed a microcosm of evolution. This is shown not just by the story of the finches but also by that of the moths, the sickle-cells and the gulls, which are repeatedly held up as examples of evolution. However no more than variation is ever established (often very large amounts of variation to be sure). Hence the application of population genetics to microevolution is certainly vindicated but there is very little evidence for any extrapolation to macroevolution.

2.2: Prehistory.

2.2.1: Genealogy.

As discussed in the introduction, our story begins with the 'Modern Synthesis' in the 1930s and 1940s. To reiterate, in theoretical terms the Modern Synthesis was the marriage of Darwinian natural selection with the tenets of population genetics. In terms of the authority structure of the field of evolutionary science it meant that population genetics came to hold a dominant position, all other the sub-fields of evolutionary science (such as paleontology) placed in a position where they had to accept the tenets of population genetics as primary to all theorising about evolution.[51] George Simpson was the most prominent paleontologist of this period. It was his book *Tempo and Mode in Evolution* that brought paleontology within the Modern Synthesis. He established dozens of new research directions and probably deserves to be recognised as the founder of modern paleontology. However there were others that have been influential in a different fashion to Simpson - by virtue of what their graduate students went on to achieve.[52]

Norman Newell was one of these. (Details from (Boyd 1980).) Newell completed a Phd in geology in 1933 and spent his early career working at the Universities of Kansas and Wisconsin. In 1945 he obtained a professorship at Columbia University and a curatorship at the American Museum of Natural History. It seems that his great strength was his ability to organise research programs. Upon his appointments he established a training program in invertebrate paleontology using both institutions that produced more

[51] Not that this would really have had much influence on paleontological practice of the time, which would have remained pretty much unchanged. (collecting and cataloguing fossils, working out taxonomic structures, etc.) And, as discussed in Chapter 1, in terms of its own image as a professional science paleontology benefited from Simpson's demonstration that the data of paleontology can be seen to be fully consistent with the core statements of the Modern Synthesis.

[52] It seems that Simpson was not successful in bringing in a line of paleontologists to continue pursuing his interests. The anecdotal evidence is that he was a brilliant scientist but a difficult person to get along with. In an obituary published in *Evolution*, Gould said of him that "he was the most important paleontologist since Georges Cuvier" before going on to chronicle the extraordinary quantity of Simpson's achievements. However, says Gould, he "was not an easy man to like", could not "bear disagreement" and "took offence easily". (Gould 1985)

than forty postgraduate degrees over several decades. Apparently he valued "the success and stimulation of this program above all other experiences." At one stage he organised teams of students and colleagues to do a comparative study of modern reefs in the Bahamas with fossil reefs in Texas, in short order obtaining the funding, overcoming the logistical problems, organising publications and completing his own book on the subject.

The great strength of Newell's own paleontological work (he was active in both geology and paleontology) was his ability to combine biological and paleontological approaches. This approach to paleontological research was followed by many of Newell's students and seems to be gaining in importance (see Section 6.1.4). From Newell's career we can thus isolate two key achievements that helped push paleontology into professionalism. First was the graduate program he set up. Before this time paleontology was a subset of geology (and indeed in most institutions it still is). With Newell's program, however, young scientists had the opportunity to study paleontology in an environment devoted entirely to that discipline. Many of Newell's graduate students went on to play major roles in paleontology and in the development of punctuated equilibria in particular. In the 1950s he supervised Alan Cheetham, a most accomplished paleontologist and also one of punctuated equilibria's strongest supporters while in the 1960s he supervised both authors of punctuated equilibria, Stephen Gould and Niles Eldredge. He also supervised Bernhard Kummel who in turn supervised David Raup. Raup worked closely with Gould and Eldredge in the late 1960s and early 70s.

Second was his idea that paleontological studies should be informed by biology. Newell inspired his students to study paleontology as a branch of evolutionary science rather than as an exercise in cataloguing. Alan Cheetham, for instance, comments that it was at Newell's "suggestion that I took courses in genetics and biometrics" and that Newell's "influence on paleontology even exceeded that of Simpson in one respect: he had many more students". (Cheetham 1999d) David Raup comments that his supervisor, Bernhard Kummel, "had been trained by Norman Newell at the University of Wisconsin and was infused with new ambitions for paleontology: trying to make connections with other aspects of geology and modern biology … he pushed his students hard to strike out in new directions. Newell, of course, did much the same thing after he moved to Columbia. Under [Kummel's] influence I sort of 'minored' in genetics and evolutionary biology. Harvard was pretty conservative at the time and the program was not easy to arrange. But I took courses in population genetics and was mentored by Ernst Mayr."

Raup adds that by comparison the other centers for paleontological training at "Berkeley and Michigan … were locked in the old traditions – even to the point of avoiding any serious training in geology, let alone biology." (Raup 1999e) He identifies three areas in which Newell's own research also led the way in paleontology: "Study of marine environments (organisms and sediments) as a key to interpretation of the past" (Alan Cheetham followed this line of research - see Section 6.1.7,); "Promoting biometrics in the study of variation in morphology" (Biometry is basically the application of mathematics to biology. Newell thus took a set of biological techniques and applied them to paleontology); "Learning about and promoting ways of bridging the gap between paleontology and evolutionary and population biology. And, in general, encouraging synthesis and search for big patterns in the fossil record." (Raup 1999d)

In one major respect Newell differed from his academic descendants – he still saw macroevolution as an extrapolation of microevolution to the geological time-scale and

was thus committed to gradualism. His students were confronted with a "no change, no dissertation" dilemma. (Cheetham 1999b) That is only when morphological change was recorded over a time-span was the data considered significant. Eldredge, for instance, gave an extended account of his research as a graduate student in *Time Frames: The Rethinking of Darwinian Evolution and the Theory of Punctuated Equilibria*, commenting that:

> "If your choice is to look at evolution, and you've carefully picked out a trilobite species that meets all the criteria for a good example, and if your preliminary forays reveal a rather distressing sameness to the beasts from New York to Iowa, from the beginning of Hamilton time on up through its last gasp 8 million years later, a feeling of desperation is inevitable. For little or no change to be readily apparent over all that time and territory seemed then inconceivable – given the goals, the aspirations and, really, the basic underlying assumptions I brought to the study in the first place." ((Eldredge 1986), p.59)

Despite this it certainly seems that Newell gave his students a confidence in paleontology that was not extant before his time and thus paved the way for his students to challenge evolutionary orthodoxies. Eldredge identified the origins of punctuated equilibria with the time he spent as a graduate student working in a group with Gould, T. H. Waller and Harold Rollins. Waller apparently "set the pace" for the rest of them, showing that by choosing a well represented fossil species one could make a "detailed evolutionary analysis" and that the species concept was also valid in macroevolutionary time. Gould, wrote Eldredge, inspired them all to have the confidence to challenge orthodoxy: "In the `60s he [Gould] was already pursuing his multifarious interests in evolutionary biology and showing his fellow graduate students that it was altogether fitting and proper for younger members of the profession to think in theoretical terms, and to publish papers directly addressed to evolutionary theory." (p.59) In particular Gould published a paper in 1965 arguing that the geological concept of uniformitarianism (that all geological formations should be explainable by processes observable in the present) had been unconsciously and unnecessarily transferred to paleontology, where it became the dogma of gradualism. (Gould 1965)

Gould has referred to this formative period under Newell as a time when "a mini-revolution was brewing within American paleontology – a restructuring of its principal focus from biostratigraphic correlation in the service of geology (and the petroleum industry) to a concern with biological problems of evolution." He and Eldredge went to study with Norman Newell in the 1960s because he was a paleontologist with biological orientations and was "urging students to tackle evolutionary problems." However he experienced similar frustrations to Eldredge in that he held "a commitment to engage in the empirical study of evolution as illustrated by the fossil record" but that most lineages "showed stability … following geologically unresolvable origin." Gould saw this as an anomaly – "we were told that our primary data base contained virtually no examples of the phenomenon we wished to study." Gould was well primed to challenge scientific

orthodoxies. As a student his interests spread further than straight science – he studied the socio-philosophers T. S. Kuhn, N. R. Hanson, and P. Feyerabend and absorbed the general idea that scientific facts are often not as certain as they seem. In particular he detected what he believed to be a major bias affecting his own discipline – "I had, in short, and by these influences, recognized the powerful hold that gradualism, as ideology, had exerted within British and American natural sciences." (((Somit and Peterson 1992), pp.55-56)

2.2.2: The growth of invertebrate paleontology.

Modern paleontology contains three principal subdivisions: vertebrate paleontology; invertebrate paleontology; paleobotany. Of these it is vertebrate paleontology that has the highest profile in popular culture. People have become fascinated with dinosaurs and theories about their extinction. Professionals in advertising and marketing have used this fascination in their campaigns, further raising the profile of dinosaurs. People are also fascinated with the evolutionary history of hominids. The unearthing of hominid bones often makes the front page of newspapers, suggesting that our prehistoric origins hold great interest for the public at large.

However since the Modern Synthesis it is invertebrate paleontology that has come to numerically dominate the field. There are several reasons for this, not least of which is that invertebrate paleontology found application in the burgeoning petrol exploration industry which thus supplied a new source of funds. Vertebrate paleontology and paleobotany have no similar industrial applications and rely on philanthropic interest, popular museums and the academic tradition of 'knowledge for its own sake' to keep them going.

More pertinent to this thesis is the fact that invertebrate paleontology has come to dominate paleontological evolutionary theorising. Before the Modern Synthesis it was the vertebrate paleontologists who had the most to say about evolution. Vertebrate paleontology is allied with comparative anatomy, and it was the reconstructions of large animals and their phylogenetic relationships, illustrating the course of evolution, that was important. In the last forty years or so the emphasis has switched to analysis of macroevolutionary patterns and it is invertebrate paleontology that has the most to say about this. The explanation for this is simple. Invertebrate paleontologists began to introduce statistical techniques into paleontology in a large way and the criteria for data to be considered relevant thus became more demanding. To pass these kinds of statistical criteria one must obtain a certain quantity of data. Generally speaking vertebrate paleontologists do not have enough data to pass the statistical criteria and hence to make claims about long term trends. There simply aren't enough fossils. Invertebrate paleontologists, by contrast, often have enormous volumes of fossils to analyse, and it is thus possible for them to make claims about the nature of macroevolutionary trends.

Norman Newell was the first major influence on the growth of invertebrate paleontology, with his graduate program and large scale studies of fossil reefs. He recognised the potential of invertebrate paleontology for constructing macroevolutionary models and pushed his students to study widely, so as to be up to date with the latest from biology and geology. His career and its long term influence thus makes an interesting

contrast with that of his more famous contemporary, vertebrate paleontologist George Simpson. Simpson is widely regarded as the most influential paleontologist of the century, in that he brought paleontology into the Modern Synthesis, and yet his sub-discipline has had a relative decline as a source of evolutionary theorising

The use of computers has also been a major influence on the direction of paleontology. Computers allow scientists to perform rapid analyses on large amounts of data. They have facilitated the growth of invertebrate paleontology in that the large volumes of data available are able to be more easily scrutinised and manipulated. Essentially the large bones of vertebrate paleontology gave way to the large data sets of invertebrate paleontology. Almost all meaningful evolutionary theorising in paleontology now comes from invertebrate paleontologists and indeed most of the paleontologists involved in the debate over punctuated equilibria are specialists in invertebrate paleontology.

It should be noted that punctuated equilibria is not the only important piece of evolutionary theory to have emerged from invertebrate paleontology in the last thirty years. David Raup catalogues a variety of changes that caused paleontology to "leap into the twentieth century", such as "John Imbrie's introduction of biometrics, Newell et al.'s newly rigorous work on paleoecology, Martin Rudwick's so-called paradigm approach to functional morphology, and the influence of the [Modern Synthesis]." (Raup 1999b) The specifics of these research directions is not a concern of this thesis but it should be noted that they all emerged from invertebrate paleontology and include the application of biological techniques to paleontological data.

In the 1970s the fashion for applying statistical techniques to paleontological data really began to gain momentum. The so-called 'Chicago Mafia', a group which included Raup, John Sepkoski, Thomas J. Schopf, Daniel Simberloff, Niles Eldredge and Stephen Gould (not all of whom were actually centred in Chicago) published a series of articles based on stochastic models of evolutionary diversity. Some of these scientists, working at the Marine Biological Laboratory in Massachusetts, also began playing with random models of evolution (see, for instance, (Raup, Gould et al. 1973)). This group were committed to increasing the use of "quantitative methods" in paleontology and to forming "even closer ties with biology". Raup sees this as a very influential time in the development of modern paleontology. He believes that the development of a statistical-modelling approach to paleontological theorising was inevitable, that it was a movement waiting to happen. The fact that it fell to a group of paleontologists who were also committed to revamping the discipline was thus a mere quirk of history. ((Raup 1999b), (Raup 1999c))

In summary, the early 1970s was a time of great excitement for these outstanding young paleontologists. There was an openness to new research directions and an optimism that closer ties with biology would bring greater rewards than might previously have been expected. There was a questioning of traditional paleontological practice and a confidence amongst the new generation that they could change that practice for the better. This was the climate into which punctuated equilibria was born.

2.3: The 1970s.

2.3.1: Sociobiology.

Evolutionary science in the 1970s was marked by two major movements. The first of these was Darwinism extended to its outer limits: strict adaptationism; reduction of all evolutionary phenomena to selection at the genetic level; the application of the principals of the Modern Synthesis to human behaviour (sociobiology). The second movement was essentially the antithesis of the first. Its major tenets were the contentions that adaptation was over-emphasised, that sociobiology was in the service of powerful social groups and that reductionism, as applied by evolutionary biologists, had been over-extended. This second movement relates to the two major motivations of the dissenters from neo-Darwinism generall: the rejection of the notion that the only creative force in evolution is natural selection and the rejection of the reduction in practice of macroevolution to microevolution.[53]

The architects of the Modern Synthesis, for reasons already discussed, took a strictly adaptational perspective to their study of evolution. This remains true today – contemporary neo-Darwinians believe that adaptation is the predominant evolutionary process. Given the association of a belief in the predominance of natural selection and the density of adaptation it is perhaps simple to understand the dissension of the paleontologists - strict adaptationism is linked to the reduction in practice of macroevolution to microevolution. However this does not explain why scientists from other disciplines, such as geneticist Richard Lewontin and biologist Steven Rose, also dissented from strict adaptationism.

The anti-adaptationists of the 1970s were a loosely defined group in that there was no particular discipline that made up the majority of the ranks. Rather they can best be characterised as scientists who shared an interest in 'debunking the adaptation myth', in convincing others that adaptation should not be automatically invoked to explain all features of all animals. That such an unyieldingly adaptive attitude is prevalent amongst evolutionary biologists is itself debatable, though it seems fair to say that amongst non-scientists, that is in 'society at large', it is a common perception.[54]

It is perhaps simpler to delineate the anti-adaptationists by characterising their diametric opposition. Adaptationism has its purest incarnation in the research programme

[53] Punctuated equilibria has played a major role in the latter campaign and a minor but important role in the former.

[54] For instance the author of this thesis recently watched a National Geographic nature documentary on the hunting techniques of African predators – cheetah's, lions, wild dogs, etc. The diversity of strategies was impressive. In case after case the narrator of the documentary informed watchers that each animal's physique was perfectly adapted to its particular strategy – the cheetah's speed, the wild dogs stamina, etc. There was no mention of the possibility that the strategies employed by each kind of predator may instead have been a function of a limited physique instead – something like, for instance, 'The wild dogs do not have the speed of the cheetah, so instead they wear their prey down by pursuing them for long periods of time.'

usually entitled 'sociobiology'.[55] It is in some ways a continuation of a research tradition that predates Darwin, one characterised by an interest in explaining human and animal behaviour in terms of natural forces – thus it is one extremity of the 'nature v. nurture' debate.[56] The controversy arises mainly because of the manner in which this debate informs humans about themselves. Those on the 'nature' side of the debate argue that humans, being constructed by simple elements, are constrained to act in certain ways. Those on the 'nurture' side argue that environmental forces are more important – that the pattern of the structure and the fashion in which it is formed under environmental influences is more important.

For the purposes of this thesis the origin of sociobiology may be traced to the publication of Edward Wilson's books *Sociobiology: The New Synthesis* (Wilson 1975) and *On Human Nature* (Wilson 1978) and Richard Dawkins book *The Selfish Gene* (Dawkins 1976). The objective of sociobiology was to use population genetics to explain behaviour, both in animals and humans. They identified genes as the basic evolutionary individuals and asserted that genes are essentially 'selfish' in that they are only interested in replicating themselves.[57] Their major problem was to explain the existence of altruism. They did this by use of the concept of 'inclusive fitness', arguing that the apparent incongruity of 'selfish' genes and altruism is explained by the fact that the genes that code for such behaviour are often shared by the advantaged individuals.[58]

The anti-adaptationist movement of the 1970s, with its particular emphasis on debunking sociobiology, grew out of some of the rather more radical anti-authoritarian movements of the 1960s – groups such as 'Science for the People', which had its own eponymous journal.[59] Immediately after the publication of Wilson's *Sociobiology: The New Synthesis* a formal committee was established to tackle sociobiology, the 'Sociobiology Study Group', which later allied itself with the Science for the People group. ((Segerstrale 1986), p.53) They attacked sociobiology on two fronts, one epistemological and one social. Their epistemological argument against sociobiology was based on notions of evolutionary hierarchy, summed up by the following analogy: "Agata Mendel jokes that most contemporary molecular and developmental biologists reason like a child who, because turning the knob on the television makes the picture appear, concludes that the knob 'causes' or 'programs' the next, more absurd step of trying to understand the mechanism of television by analysing the knob."[60] ((Rose 1982b), p.73; paraphrased from (Mendel 1980)) They argued that the sociobiologists had taken reductionism too far and had thus lost sight of the 'big picture'. Punctuated equilibria, with its emphasis on the importance of multiple explanatory levels in evolutionary science, became an important part of this critique.

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[55] In the 1990s the research tradition of sociobiology has basically disappeared, to be replaced with 'evolutionary psychology'. There are differences between the two programs but they are relatively minor and for the purposes of this thesis it will be assumed that they are one research tradition.

[56] Metaphysically this is an aspect of the debate, as explicated by Gayon, over the existence of absolutely simple elements.

[57] I.e. only those genes that are good at being replicated survive through the generations.

[58] Space does not permit a full explication of 'inclusive fitness'. Readers unfamiliar with the concept are referred to (Dawkins 1976).

[59] For an account of the activities of this group see (Walsh 1976)

[60] Agata Mendel was a pseudonym for a group who published anti-sociobiology articles in French science journals.

However the major bone of contention for the dissenters was the social applications of sociobiology (and the entire research tradition of 'biological determinism' or strict adaptationism), which they associated with right-wing politics.[61] This lead some to attempt a Marxist deconstruction of evolutionary biology. In 1980 a conference, organised by Allan Muir, Martin Barker and Steven Rose, was held in at the University of Padua with just such a central theme. From this conference two volumes were produced with the imposing titles *Against Biological Determinism* (Rose 1982a) and *Towards a Liberatory Biology* (Rose 1982b). Apparently everyone at the conference was united in their "dissatisfaction with the prevailing neo-Darwinist paradigm and its reductionist ideology." ((Rose 1982a), p.5)

2.3.2: Wilson and Lewontin.

This rift among evolutionary scientists can be appreciated by consideration of the divergent careers of Edward Wilson and Richard Lewontin.[62] Wilson, an entomologist by specialisation, spent the early part of his research career using population genetics to analyse the behaviour of the social insects (bees, ants, termites, etc.). It was at Wilson's urging that Lewontin was appointed to the staff at Harvard in the early 1970s. Lewontin had a reputation as a brilliant young scientist but his Marxist leanings were well known and some at Harvard were reticent to hire him. Wilson, however, thought Lewontin's Marxist politics would not influence his scientific activities and lobbied for his appointment. ((Segerstrale 1986), p.63)

Wilson went on to become the architect of sociobiology, applying the population genetic techniques he had used on insects to other animals, including humans, in his book *Sociobiology: The New Synthesis* (Wilson 1975). Initially the book received "widespread publicity and positive reviews" ((Segerstrale 1986), p.53). The newly formed 'Sociobiology Study Group' responded with a scathing letter to the *New York Review of Books.* Interestingly they did not argue that the book was entirely erroneous, accepting most of Wilson's work as valid and focussing their criticism only on the first and last chapters – the ones that addressed human behaviour. Wilson, they argued, had tried to establish a logical connection between his ideas about animal behaviour and his ideas about human behaviour – "Wilson's claim for objectivity rests entirely upon the extent to which his last chapter follows from the fact and theory which came before." ((Caplan 1978)[63], p.261). They went on to list five ways in which they believed this extension invalid and suggested that Wilson's attempt to incorporate human behaviour in his thesis had socio-political rather than scientific motivations – "Wilson joins a long parade of

[61] It seems to be generally accepted that Darwin's idea of natural selection was a transfer from *laissez-faire* economics. There has been a very nice reflexivity between the ideology of Darwinism and that of 'free market' capitalism over the last 150 years. Politicians have used Darwinism to justify their economic practices on the basis that they are natural – survival of the fittest in a competitive market place gives efficient production, etc. But natural selection was based on economic principles in the first place. This is a fine example of what mathematicians call boot-strapping – pulling oneself up by ones own shoelaces.

[62] A detailed account of this rift can be found in (Segerstrale 1986). Much of the information presented here is taken from this article.

[63] Caplan's book reprints the Sociobiology Study Group's *New York Review of Books* letter, Wilson's reply in the same journal and many other early exchanges from the sociobiology debate.

biological determinists whose work has served to buttress the institutions of their society by exonerating them from responsibility for social problems." (p.264) Amongst those to put their name on the letter were many of Wilson's colleagues, including Richard Lewontin. Their relationship soon degenerated to the point where they would no longer speak to each other, despite sharing office space in the same building.

Segerstrale contends that, contrary to the reporting of the time, the dispute between Wilson and Lewontin did not originate exclusively from their political differences. Rather, she contends, the clash stemmed from divergences in "their larger agendas", that these agendas "involved a coupling of scientific and moral interests", and that given their divergent agendas a clash between these two was inevitable. Segerstrale documents Wilson's upbringing as a fundamentalist Christian in the Southern United States and his later conversion to evolutionism. This, she contends, explains his evolutionary zeal, his attempt to bring human morals and ethics within the evolutionary fold: "Wilson's zeal in making sociobiology a truly predictive science, encompassing all of social behaviour, was intimately tied to an old desire of his: to prove the (Christian) theologians wrong." To achieve this Wilson had to tie his statements about the origins of human behaviour, and in particular altruistic behaviour, as closely as possible to the 'hard' science of population genetics. ((Segerstrale 1986), pp.54-59)

An anti-theological attitude is common amongst sociobiologists. Richard Dawkins is also an outspoken atheist. In *The Selfish Gene* he extended his concept of genetic selection to culture by proposing the idea of 'memes', units that are replicated and selected in culture in a fashion analogous to that of genes in nature (examples of memes are songs, ideas, fashions, building techniques). The idea is that those memes which prove popular will multiply and come to dominate and those that are unpopular are destined for obscurity. Dawkins contended that cultural evolution can thus be reduced to the natural (cultural) selection of memes.

The main example that Dawkins chose to elucidate his idea was religion: "Consider the idea of God. We do not know how it arose in the meme pool. Probably it originated many times by independent 'mutation'. … The survival value of the god meme in the meme pool results from its great psychological appeal. It provides a superficially plausible answer to deep and troubling questions about existence. It suggests that injustices in this world may be rectified in the next. The 'everlasting arms' hold out a cushion against our own inadequacies which, like a doctor's placebo, is none the less effective for being imaginary." He also chose religion as the subject when discussing the construction of co-adapted meme-complexes, citing hell fire and faith (in the sense of "blind trust in the absence of evidence") as examples of two memes that are part of the larger religion meme. Dawkins went on to ridicule Christian faith even further: "The meme for blind faith secures its own perpetuation by the simple unconscious expedient of discouraging rational inquiry." By incorporating religion into his thesis Dawkins took a position of superiority over believers. They may believe in God, but he knows why they believe in God, and it has nothing to do with God's existence.[64] ((Dawkins 1976), pp.207-213)

[64] It is interesting, then, to see what Dawkins offered as a substitute. His outlook seems rather bleak - all organisms are simply vehicles for gene replication except humans who are also vehicles for meme replication (human cultures are thus meme pools). However he did offer some scant hope: "… even if we look on the dark side and assume that individual man is fundamentally selfish, our conscious foresight …

According to Segerstrale, Lewontin's quarrel with Wilson can best be understood in terms of two agendas, one epistemological and one social but both informed by his Marxist beliefs. On one hand "Lewontin's philosophical preoccupation with Marxism is strongly linked to a more general critical meta-scientific interest of his: the *correct* depiction of reality in theories and models". That is, for Lewontin the principals of testability and parsimony are not sufficient criteria to judge the soundness of scientific ideas. Rather a theory should be "a true account of underlying processes in the real (i.e. material) world." He preferred overly complex but accurate theory over theory that was simple but could be over-generalised - hence his anti-reductionism and his opposition to the 'adaptationist program', which he believes is based on "non permissible generalizations about the natural world." Lewontin also held strong ethical and moral beliefs about the social actions of science. He was a leading member of the 'Science for the People' group and in the early 1970s "had taken upon himself [an agenda] to reveal "racist" research". Unluckily for Wilson the publication of his treatise on sociobiology coincided with a time when debate about racism in science was still raging from the IQ controversies of a few years earlier. Thus Wilson found himself in conflict with both of Lewontin's fundamental agendas. ((Segerstrale 1986), pp.59-63)

2.3.3: Sociobiology, adaptationism and punctuated equilibria.

The twin agendas that motivated Lewontin's anti-adaptationism provide a good exemplar of the typical dissenter from modern Darwinism. Two elements are almost always present, intertwined scientific/epistemological opposition to strict adaptationism and concerns for the social impact of science. It is easy to see how punctuated equilibria naturally became a part of the anti-adaptationist movement. At the epistemological level punctuated equilibria disputes the reduction of evolutionary theory to the level of the individual whilst on the social level the authors of punctuated equilibria, Eldredge and Gould, may be described in their politics as 'left-leaning' with especial concern for the social impact of science. Both Eldredge and Gould have produced large volumes of literature re the former issue whilst Gould has been most vocal on the latter issue, with publications such as *The Mismeasure of Man* (Gould 1981a), his historical account of racist applications of biology in America.

In 1980 Randall Albury produced a sociological analysis of sociobiology (Albury 1980). Observing that sociobiology had "grown and flourished" since the publication of Wilson's 1975 book, he provided two very different possible accounts for this success. On one side is what he called the "rationalist" view, that sociobiology was "intellectually sound" as a logical extension of neo-Darwinism and that its success was due to its "intellectual promise" as a source of successful research ideas. The other account, which Albury called "reductionist", is that sociobiology was successful because it served

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could save us from the worst selfish excesses of the blind replicators. We have at least the mental equipment to foster our long-term selfish interests rather than merely our short-term selfish interests. We can see the long-term benefits of participating in a 'conspiracy of doves', and we can sit down together to discuss ways of making the conspiracy work. … We are built as gene machines and cultured as meme machines, but we alone have the power to turn against our creators. We, alone on earth, can rebel against the tyranny of the selfish replicators." (p.215)

"dominant class interests in U.S. society." He cited a number of examples which provided the basis for this view: As the women's movement struggled for an equal rights amendment to the U.S. constitution "sociobiology claimed that men are innately dominant while women are innately docile and domestic"; when "ethnic minorities pressed their demands for social and economic equality, sociobiology maintained that xenophobia is a genetically endowed component of human nature"; and when the U.S. government wanted "a revival of military assertiveness after the relative quiescence of the post-Vietnam period" sociobiology proclaimed warfare to be innate to our biology. (pp.122-123)[65]

As one might imagine the anti-adaptationists subscribed to the latter view of sociobiology – that it served the interests of dominant social groups. The list of anti-sociobiology literature is extensive - probably the most complete statement is to be found in the book *Not In Our Genes* (Lewontin, Rose et al. 1984), which contains articles by many of the leading dissenters. They attacked sociobiology on two fronts. The first was similar to that described by Albury above, in that they documented ways in which 'biological determinism'[66] had served the social interests of dominant groups to the detriment of less powerful groups. The second attempted to debase the scientific foundation of sociobiology – they charged that it is impossible to isolate genes that code for any particular behavior and that the entire programme, being based on pure supposition, was thus unscientific.[67]

In the preface to *Not in Our Genes* the authors stated their motivations, placing their political inclinations on the table for all to see: "We [the authors] share a commitment to the prospect of the creation of a more socially just – a socialist – society. And we recognize that a critical science is an integral part of the struggle to create that society, just as we also believe that the social function of much of today's science is to hinder the creation of that society by acting to preserve the interests of the dominant class, gender, and race." ((Lewontin, Rose et al. 1984), pp.ix-x) Two doctrines were identified as underwriting biology's part in maintaining the dominant class interests: 'Reductionism', where "compositional units of a whole are ontologically prior to the whole"; and 'Biological Determinism', the notion that human behaviour is "governed by

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[65] Albury, citing Bourdieu, noted that a more apt analysis of sociobiology "incorporates the most important aspects of both positions", that in fact the ideology was 'doubly determined' by external influences and by the 'specific logic of the field of production'. He then went on to provide just such an analysis. He observed that, internally, sociobiology offered practitioners "three strong incentives" in: "the definition of a unique product", examples of its production and the "promise of expanded production in the future"; the assurance that the product "can be subject to intense monopolization"; the creation of a market with the demonstration that sociobiology "has scientific application outside the charmed circle of its origin". Externally sociobiology marketed itself as having important applications in social planning, thus assuring itself of research grants, etc. This external support enhanced sociobiology's competitive position but, as Albury observed, the practitioners were also anxious to be seen as following "the internal rules of the scientific community", else their peers would not have accorded them the status they needed for an extended reign. (pp.123-127)

[66] The term 'biological determinism' referred to the tradition of reducing behaviour to biology. In the past abominable deeds have been justified by 'biological determinism', including the genocide of the Nazis. The authors of *Not In Our Genes* claimed that sociobiology was the modern embodiment of this tradition and thus sought to link sociobiology with social actions from the past which were clearly abhorrent.

[67] Once again we see that typical dissenters from strict adaptationism (biological determinism, sociobiology, etc) have twin, coupled agendas, one epistemological and one social.

a chain of determinants that runs from the gene to the individual to the sum of the behaviors of all individuals." According to the authors these philosophical doctrines were the basis upon which capitalist societies justify themselves (that is, capitalism was held to be inevitable). This, according to the authors, was especially true of the 'New Right', a group characterised as holding a philosophy in which the rights of the individual are seen as ontologically prior to that of the "collectivity". (pp.5-6)

The concern of the present thesis with respect to the attack on strict adaptationism and its purported applications to society at large is its relationship to punctuated equilibria. Generally speaking it is easy to see that punctuated equilibria, with its emphasis on the importance of a hierarchical evolutionary perspective, is quite the antithesis of the strict reductionism of Wilson and Dawkins. One would not say that this, however, was the major motivation for the creation of punctuated equilibria, which was more to do with the status of paleontology in the field of evolutionary science. However it should be noted that Stephen Gould has been one of the most prominent and energetic campaigners against strict adaptationism, or what he calls 'pan-adaptationism'. He has published prolifically on the topic, from short essays in *Natural History* magazine, such as his article 'Tires to Sandals', to his history of the misuses of biology in the United States, the book *The Mismeasure of Man* ((Gould 1981b), (Gould 1981a)).

The most influential of these anti-adaptationist publications amongst evolutionary scientists is his joint article with Richard Lewontin 'The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme' (Gould and Lewontin 1979). Their article was based on the metaphor of a 'spandrel', which is a tapering triangular space formed when two arches meet at right angles. In many cathedrals the spandrels are ornately decorated and one could be excused for thinking their function was aesthetic, that they had been placed there in order to provide a surface for a fresco. This, however, would be an inversion of explanation. The spandrels are primarily an engineering by-product – they are necessary when one mounts a dome on arches meeting at right angles. The fact that they make a fine space for frescoes, etc., is secondary. Gould and Lewontin charged that many evolutionary scientists make just such an inversion of explanation when they analyse adaptive features of organisms. Some evolutionary scientists assume, apparently, that the feature exists because of its function rather than considering the possibility that the feature may exist for other non-adaptive reasons and that it was only then turned to its present function. They argued that in many cases the evolution of functional features are more a case of making do with what one already has than developing what one specifically needs.

Generally speaking then, punctuated equilibria can be associated with two movements in evolutionary science. First and foremost punctuated equilibria is a major part of the attempt by paleontologists to challenge the hegemony of population genetics in the field of evolutionary science. Secondly punctuated equilibria has been a minor player in a more general critique of neo-Darwinism – the anti-adaptationist movement. Punctuated equilibria lent itself naturally to use in this campaign as it supports the notion that natural selection at the level of the individual organism or at the level of the gene cannot provide a sufficient model of evolution. And, as noted above, many of the punctuationists had individual epistemological and ethical interests in attacking strict adaptationism.

It should also be noted that the difference between the punctuationist perspective on evolutionary theory and that of the syntheticists had more to do with how the tempo of evolution relates to adaptation than to questions of tempo itself. Consider, for instance this discussion of horse evolution from the 1975 edition of John Maynard Smith's book *The Theory of Evolution*, bearing in mind that at he wrote the book punctuated equilibria was not a well known theory and that whilst he may have heard of it he would not have taken it into account:

> "The interest in this story lies in the fact that the changes did not occur gradually and continuously. Three functionally distinct types of foot, the three toed padded foot, the three toed springing foot and the one toed springing foot, succeeded one another, each persisting for long periods with little change, and the transitions between them occurred in single lines of descent. Each type is probably an improvement, in a galloping mammal, on its predecessor. The rapidity of the transitions between them, however, suggests that intermediate types of mechanism would have a lower efficiency; consequently selection would act so as to preserve an existing mechanism, and once some threshold has been passed, rapidly to perfect a new one." ((Maynard Smith 1975), p.272)

In his analysis there is stasis and accelerated evolution at times of change - superficially reminiscent of punctuated equilibria. There is, however, one glaring difference between his analysis and a punctuational one – he believed that the changes occurred in a single lineage. This belief is underwritten by the assumption that each type is an improvement on its predecessor. Therein lies the major difference between a syntheticist and a punctuationist perspective. Whilst Maynard Smith accepted varying rates of evolution, he also believed that the long term trends in evolution are adaptive and are caused by natural selection. He saw evolution as a process of improvement in design. Punctuationists believed that when changes occur they may be adaptive in a local sense (and in this sense under the auspices of natural selection) but that they are random with respect to long term evolutionary trends. There is no improvement in adaptation, simply change.

2.3.4: Punctuated equilibria in the 1970s.

The overall political climate into which punctuated equilibria was born, and the influence that this had on its development, can now be understood. The early 1970s was a time when (in Western societies) generations clashed, a time when the wisdom of incumbent authorities and the ruling classes were questioned. There were riots in American universities and clashes with police, the Vietnam war and the protests against it, Jemmy Hendrix, Janis Joplin and LSD. One can imagine that amongst young scientists the general excitement about these challenges to established wisdom would have carried

over into their work. Evolutionary science was also, at the time, the scene of contrasting and clashing world-views. On one hand there was the burgeoning sociobiology research programme, which saw established wisdom pushed to its furthest extent and on the other left-wing movements such as ‘Science for the People’ which were dedicated to exposing apparent social misuses of science (such as ‘biologically determinist' sociobiology). The theory of punctuated equilibria was thus formulated at a time when authority and established credos were being questioned, in society generally, in science generally and in evolutionary science in particular.

Eldredge’s 1971 punctuated equilibria article, however, contained no strong suggestions of revolution. (Eldredge 1971) Its form was that of a typical scientific article and was published in the technical and rather conservative journal *Evolution*. The language was dry, there were no superfluous adjectives or adverbs and no hint as to how the author’s ideas were formed. Eldredge spoke entirely in the passive voice and simply pointed out that the prevailing modes of interpretation in paleontology, which emphasised gradualism, were in conflict with the model of speciation accepted as predominant by most biologists, allopatric speciation. He then presented data from his own research to illustrate his claims and provided graphs to show how his saltation model of evolutionary change compared with the standard phyletic model. As yet the term ‘punctuated equilibria’ had not been coined. Nor had the term ‘stasis’ - Eldredge merely suggested that an “implicit consequence of this [saltation] model … is the assumption that little or no morphological change occurs within a species within its stratigraphic interval of occurrence.” (p.159)

Eldredge did not claim any revolutionary consequences for his ‘saltation model’. There is only the merest hint of a challenge to established credos when he suggested that the emphasis on gradualism and hence “a strictly phyletic model of species transformation” had dominated “paleontological thought” (p.166). Eldredge’s application of allopatric speciation to paleontological data in this article was not the challenge to neo-Darwinism that punctuated equilibria was later to become. Rather he was merely pointing out that paleontology’s view of speciation was outdated and that some anomalous data might be reconciled by consideration of the consequences of allopatric speciation for evolution in geological time.

It was the 1972 article co-authored with Stephen Gould that set the scene for much of the later debate (Eldredge and Gould 1972). This article announced that ‘punctuated equilibria’ was the harbinger of a revolution in evolutionary science, the idea being that via punctuated equilibria paleontologists would gain a more authoritative voice and would thus achieve a more equitable relationship with their biological colleagues. The challenge, then, was to the authority structure of evolutionary science.

Eldredge and Gould felt that paleontologists had been scouring the fossil record for over a century trying to find Darwin’s “insensibly graded series” without any real success ((Eldredge 1986), p.27-8). Examples of such series actually seemed to be rare in the fossil record whilst there were many examples of species remaining much the same over periods of time. As is well known, this disparity between data and theory was traditionally blamed on the imperfection of the fossil record, the data being reinterpreted according to gradualistic models. Some paleontologists, apparently, were even thankful for the imperfection of the fossil record, as else they would not be able to delimit species. ((Eldredge 1986) , p.69; (Eldredge and Gould 1972), p.90) Eldredge and Gould felt it had

gone on long enough, believing that Darwin had introduced phyletic gradualism into evolutionary theory by translating "Victorian society into biology, where it need not reside" ((Gould and Eldredge 1977), p.145). It was time, they insisted, to take a new look at the fossils and to take the data for what it was, not as an imperfect record of a preconceived notion.

While punctuated equilibria may well have been the brainchild of Eldredge, Gould's influence in transforming it from a technical idea of interest only to paleontologists, to a cogent criticism of neo-Darwinism and a strong challenge to the authority structure of evolutionary science should not be underestimated. Gould's early research was centred on analysis of form and diversity in Bermudan land snails and betrayed little evolutionary zeal.[68] However he had already demonstrated a strong desire to question traditional wisdom in the field of evolutionary science - witness his 1965 article questioning the doctrine of 'uniformitarianism' in geology and paleontology (Gould 1965) – and was (is) an extremely prolific writer and skilful rhetorician [69] Eldredge is reported to have said that they deliberately wrote the 1972 article in a confrontational style in order to provoke discussion on the inherent gradualistic bias in evolutionary thought ((Willis 1989), p.269). Given Gould's propensity for rhetoric it can be assumed that the idea of recasting punctuated equilibria as a revolutionary idea was mainly his.

As Latour observes, the history of scientific ideas usually uses a model of diffusion. That is, after an idea (a black box, in Latour's terms) has gained some measure of acceptance, most retrospective analyses of why the idea was successful give all credit to the originator of the idea and ignore the people who acted to promote and develop it. In Latour's words: "Forgotten are the many people who carry [the idea] from hand to hand, the crowds of acting entities that shape the fact and are shaped by them, the complex negotiations …" The question becomes 'who thought of it first?' and is "taken as seriously as that of discovering the legitimate heir of an empire."[70] So, according to this model of diffusion the originator plucks the idea from thin air (that is, the fact/idea existed already and just waited to be discovered) and after that the idea, by virtue of its own qualities, propagates itself. Latour believes that this diffusion model is a fiction ("By itself it [a black box] has no *inertia*") and counsels the student of science history and sociology to follow the course of a black box's development via the people who developed it ("*Understanding* what facts and machines are is the same task as understanding who the people are.". ((Latour 1987), pp.132-140) In the case of punctuated equilibria, then, Eldredge and Gould should be given equal credit. Eldredge may have thought of the theory first, but it was Gould who transformed it from a minor correction of paleontological theory to a major criticism of neo-Darwinism.

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[68] A short article published in 1970 presented some of the data he had accumulated and his interpretation of that data, which he saw as fluctuations in response to climatic oscillations. There was no a hint of an attempt to see evolutionary change in the data but neither was there any hint of revolutionary notions about the nature of evolution. (Gould 1970)

[69] In Jan 1974, for instance, he began writing monthly essays for *Natural History* magazine and as of 1999 had not missed contributing to a single issue. His list of publications, even excluding these essays runs into the hundreds.

[70] This occurs even when the originator had no influence in their own time (Gregor Mendel is a classic example of this).

2.3.5: Early reactions - Gingerich and Hecht, a contrast of interests.

During its formative period (up to the early 1980s) punctuated equilibria did not attract substantial attention from non-paleontological scientists and within paleontology itself many of the early citations were regarding allopatric speciation rather than punctuated equilibria – not many paleontologists were actually testing the model or attempting to use it. (see Section 3.4) It can be said that Eldredge and Gould were successful in one of their aims, to bring paleontology up to date with biological thinking on speciation, but that their chief goal, to bring about a revolution in paleontological thought, was still some way away.

The most prominent critic of punctuated equilibria in the early to mid 1970s was Phillip Gingerich, a specialist in mammalian fossils. He was not, however, a deliberate antagonist of punctuated equilibria. Whilst he eventually found against punctuated equilibria in his analyses his general attitude to the theory was positive - he saw punctuated equilibria as an interesting model to test and set about doing so. The lack of antagonism between Gingerich and the proponents of punctuated equilibria is illustrated by the fact that amongst the scientists he thanks for assistance at the end of his first article about punctuated equilibria is Niles Eldredge. (Gingerich 1974) The opposition between Gingerich and the punctuationists may be classed as one of friendly rivalry rather than conflict.

Gingerich's first publication concerning punctuated equilibria was a short (three pages) *Nature* article in which he tested the theory with data from the mammalian lineage *Hyopsodus.* He recognised the criteria which Eldredge and Gould had set for a valid test and claimed that the *Hyopsodus* lineage fulfilled the requirements: "The punctuated equilibrium model can only be tested by a relatively complete, stratigraphically controlled fossil record such as that of *Hyopsodus*." He then stated that superficially the *Hyopsodus* lineage "appeared" to conform to punctuated equilibria, and was for this reason "chosen to test the model." He then claimed that contrary to Eldredge and Gould's claims when a "large number of stratigraphic levels" were studied "neither long periods of morphological equilibrium, nor rapid speciation events" became apparent. (pp.108-109)

In this first article Gingerich thus created a 'fact' (that the *Hyopsodus* lineage displays phyletic gradualism) that underwent a Latourian 'trial of strength'. Initially it was within opposition territory – it seemed to have a punctuated pattern. But then, when subjected to Gingerich's detailed and precise analysis, its 'true' nature shone through. Gingerich then referred the reader to a number of other studies of both vertebrates and invertebrates that, he claimed, "exhibit phyletic gradualism". His conclusion, not surprisingly, was that "Darwin's view that species evolved gradually" is correct, that "interspecies transitions are rare in the fossil record [because], as Darwin proposed, of the incomplete nature of most stratigraphical sections" and that punctuated equilibria "remains to be substantiated by a detailed stratigraphical study within a single geological formation." (p.109)

In 1976 Gingerich published a much longer article on the subject (twenty-eight pages). (Gingerich 1976) This time he performed a punctuated equilibria v phyletic gradualism test in four mammalian lineages, *Hyopsodus*, *Haplomylus*, *Pelycodus* and *Pleisiadapis*. The rhetorical style of this article was similar to the one he used in 1974

although the argument is longer and somewhat more refined. In particular Gingerich attempted to impose new criteria by which punctuated equilibria should be judged: "Although gradual, the observed rates of divergence are sufficiently rapid that an appearance of abrupt change would be registered if (1) there were significant gaps in the fossil record, (2) stratigraphic sampling was not sufficiently refined or (3) a typological species concept was applied." (p.1) These criteria are actually negative rather than positive ones[71] – that is they are conditions that need to be ruled out before punctuated equilibria can be inferred.

With the imposition of these new criteria Gingerich rejected the logic of Eldredge and Gould's argument. Eldredge and Gould had asserted that when gradualism and punctuationism are equally probable patterns in the data paleontologists should choose punctuationism because it concurs with modern biological thinking on the nature of speciation. Gingerich asserted that gradual change is prevalent and that any claims for punctuation would theretofore need careful accounting.[72] The discussion between Gingerich and Eldredge and Gould can thus be seen in the light of Bourdieu's struggle for authority, in that each side attempted to define the valid criteria by which judgement should be made.[73]

In his publications Gingerich displayed an interesting set of somewhat conflicting interests. On one side he seemed to believe that phyletic gradualism was prevalent. He thus wanted to cast doubt on the ideas of Eldredge and Gould and to impose his own values. On the other side he approved of their attempt to make paleontology central to evolutionary science. For instance at one stage he debased the logical construction of their argument with a simple modalisation: "Eldredge and Gould (1972, p.94) outline in an *apparently* logical series of steps …" (my italics). However he credited them with providing "new impetus … for detailed studies" and stressed the significance of these studies: "Few problems are of more fundamental importance to our understanding of evolution than an exhaustive testing of these two models, models that can only be tested by detailed studies of the fossil record utilizing sound methods of stratigraphical paleontology." He even narrowed the limits of his own claims by stating that his conclusions were only valid within a certain geological, temporal and systemic range. (p.20)[74]

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[71] Formally speaking, they are 'necessary' rather than 'sufficient' conditions.

[72] This may seem confusing to some readers. Basically the difference in their views may be summed up thus: If stasis is prevalent then a sudden change from one species to another (within a lineage) in the fossil record is most likely to be a punctuation, as it is unlikely that a period of gradual change suddenly occurred just when their was a break in the fossilisation process; If gradual change in species is prevalent then any breaks in the record will necessarily show a punctuation as species will keep changing during a period when no fossils are inscribed.

[73] It needs to be made clear that this struggle was internal to paleontology, that when it came to the status of paleontology within evolutionary science Gingerich was on the same team as the punctuationists. Gingerich concurred with Eldredge and Gould with respect to their general directive of using the fossil record to make assertions about macroevolutionary patterns even if he did not agree that punctuated equilibria is predominant. This point is explicated below.

[74] He offered two reasons for this. First there is the possibility "that the tempo of evolution in the marine setting [which are Eldredge and Gould's specialities] differs from that of the continental setting". Second that the geological period he studied was a time of "explosive initial radiation" in many mammal groups and that "more mature radiations might be expected to be more stable" (p.20)

In some ways, then, Gingerich was more of an ally than a foe of punctuated equilibria. He did not agree with the means of Eldredge and Gould (a punctuated interpretation of the fossil record) but he did want to achieve the same end (a rise in the status of paleontology). In particular it should be observed that Gingerich did not attempt to deconstruct the rhetoric of Eldredge and Gould's 1972 article to any great extent. The modalisation of the logic of Eldredge and Gould's argument explicated above is in fact the only instance of Gingerich attempting such a deconstruction.

By contrast, in another early exchange of the punctuated equilibria debate (this time between Eldredge and Gould and the biologist Max Hecht) deconstruction of rhetoric was central to the critic's argument (Hecht, Gould et al. 1974). In his 'Statement and Critique' Hecht agreed with Eldredge and Gould that paleontologists generally hold "naive concepts … with respect to the interpretation of the data from the fossil record." However he debased Eldredge and Gould's interpretation of phyletic gradualism, asserting that they had "set up phyletic gradualism as a straw man only to be knocked down" and that their portrayal of it was "oversimplified". He then reconstructed phyletic gradualism, transforming it into 'phyletic evolution' or 'phyletic transformation' which, apparently is a more subtle model and reframed the question that Eldredge and Gould had created (punctuated equilibria or phyletic gradualism?) into a question of "the relative importance of phyletic transformation and of speciation".[75] He also questioned the notion that paleontologists can study speciation at all, claiming that the speciation process, as "demonstrated by neozoological studies and by biological experimentation" has "no obvious morphological aspect" and hence is invisible in paleontological data. This last claim is a nice example of the use of debasement in scientific argument. Hecht attempted to remove the scientific basis of Eldredge and Gould's claims about speciation by denying that they have any valid criteria to even recognise speciation when it happens. (pp.295-303)

In their 'Reply' Eldredge and Gould used appeals to the experience of their paleontological colleagues to rebut Hecht. They denied that phyletic gradualism is a 'straw man' ("we simply refer the reader to any recent issue of the *Journal of Paleontology*"). They agreed that paleontologists may not be able to recognise sibling species but charged that he ignored stasis (the main evidence for which was an appeal to paleontological experience).[76] They denied that they had ignored the possibility of phyletic transformation, agreeing that it does occur, but doubted "that such regimes could persist over thousands of millions of years, through thousands and thousands of generations, without interruption by some more plausible event …" (pp.303-305).

These two examples of criticism of punctuated equilibria provide a good comparison of the difference between the strategies of paleontological critics and those of biological critics. In general, paleontological critics may have disagreed with a punctuated interpretation of large scale evolutionary patterns but they were in accord with Eldredge and Gould when it came to the importance of the questions asked about evolution and paleontological authority to answer these questions (i.e. the nature of speciation). Biological critics, by contrast, questioned the very validity of the

[75] Phyletic evolution is transformation within a particular species over time without speciation. No assumptions are made about the rate of change, which could be gradual of punctuated. However there are no punctuated speciation events.

[76] Sibling species are distinct populations whose morphology seems identical but are unable to interbreed.

paleontological voice. Gingerich, we may recall, wrote that the questions Eldredge and Gould asked were of "fundamental importance" for understanding evolution, whereas Hecht denied that paleontologists could even discuss speciation.

Thus, around punctuated equilibria two separate struggles for authority were beginning to take place, one internal to paleontology and one between paleontology and population biology. Within paleontology some scientists, such as Gingerich, were dissenting from the punctuated view of evolution but were allied with Eldredge and Gould with respect to paleontology's validity to speak about macroevolution in theoretical terms. They demurred re the punctuated model of evolutionary change, holding that phyletic gradualism (or phyletic transformation or phyletic evolution) was still an important process but concurred when it came to the more general claims about paleontology's authority to have the last word on macroevolutionary patterns. External to paleontology however, some biologists were beginning to object to the wider claims of the punctuationists – that macroevolution could not be reduced to microevolution and hence that biology was limited in what it could say about macroevolution. The differing strategies, of course, reflected the differing interests held by the individual scientists. Paleontologists such as Gingerich were committed to gradualism but were as eager as Eldredge and Gould to see a more authoritative paleontology. Biologists on the other hand saw punctuated equilibria as an attempt to debase their authority and reacted accordingly.

2.3.6: Gould's Ontogeny and Phylogeny.

In 1977 Gould published a major monograph entitled *Ontogeny and Phylogeny.*[77] (Gould 1977b) In it he addressed what he believed to be a neglected but important area of inquiry for evolutionary science – how the study of development informs the study of evolution. In this pursuit Gould was inspired by the approach of continental European scientists, who had continued to emphasise the importance of developmental biology to the study of evolution whilst their colleagues in Britain and the United States had focussed on the genetics of populations.

The first half of the book provided a history of developmental biology. Gould thought it important to relate the reasons for the subject's fall from grace, for only then could evolutionary scientists contemplate it in objective terms. In the early 1900s, it seems, the relationship between ontogeny and phylogeny was an important subject in evolutionary science. In particular 'Haeckel's biogenetic law', that ontogeny recapitulates phylogeny[78], was a widely accepted principle. However with the development of Mendelian genetics into the 1920s it became an unfashionable research programme: "Haeckel's biogenetic law was so extreme, and its collapse so spectacular, that the entire subject became taboo." Gould based his petition for a reconsideration of the subject on an appeal to the experience of his colleagues – he began the book by recounting the anecdotal evidence of colleagues admitting in hushed tones that the subject may indeed have some importance. (pp.1-2)

[77] Ontogeny is the course of development of an organisms life. Phylogeny is evolutionary history.
[78] That the course of development of individual organisms (particularly their embryonic development) mirrors their evolutionary history.

In summary, *Ontogeny and Phylogeny* was one long argument for the importance of heterochrony in evolutionary studies.[79] Here and in many other publications in the years following, Gould argued that evolution is channelled in certain directions by the constraints of development. (see, for instance (Gould 1979a) or (Gould 1980a)) As a consequence of this, he asserted, the power of natural selection to shape evolution is reduced – natural selection is restricted to choosing between predetermined pathways and is not the omnipotent evolutionary force characterised by the Modern Synthesis. Gould's theses re development thus became a critique of natural selection on the periphery of the punctuationist research programme.

2.3.7: Steven Stanley and species selection.

In the mid 1970s a strong ally for Eldredge and Gould emerged in paleontologist Steven Stanley, of John Hopkins University in Maryland. He had already demonstrated a strong commitment to the revitalisation of paleontology - with David Raup he had co-authored a new textbook, *Principles of Paleontology* that focussed on theoretical approaches to interpretation of the fossil record and was conspicuously lacking in descriptions of actual fossils.[80] (Raup and Stanley 1971) Indeed after Eldredge and Gould, Stanley has probably been the most influential punctuationist, having made two major entries into the debate. The first of these was his 1975 article 'A Theory of Evolution above the Species Level' in which he proposed the theory of species selection ((Stanley 1975b), the second was his punctuationist manifesto, the book *Macroevolution: Pattern and Process.*

The basic idea of species selection was that species can be selected in macroevolutionary time in a fashion similar to the way that organisms are selected in microevolutionary time. Recalling that one of the major aims of dissenters from neo-Darwinism has been to negate the primacy of natural selection in evolutionary explanations one can see immediately that species selection was a rather direct assault, in that it is an attempt to replace natural selection in macroevolutionary applications. Stanley made this very clear in the opening (abstract) to his article, stating that "natural selection operated so slowly within established species that it cannot account for the major features of evolution", that evolutionary change "is concentrated in speciation events" and that the "direction of transpecific evolution is determined by a process of species selection". (p.646) Species selection was thus of the heuristic periphery of the punctuationist research programme.

Hypothetically speaking species selection is independent of punctuated equilibria. However the strength of its impact is diluted without the assumption that evolutionary change is concentrated at speciation events – if most evolutionary change occurs by phyletic transformation the effect of species selection is drowned out. Stanley thus spent over half the article describing some 'Critical Tests' of punctuated versus gradual evolution, concluding that "the rectangular [punctuated] model passes each test, and the gradualistic model fails as a dominant pattern of change."

[79] Heterochrony is "changes in relative time of appearance and rate of development for characters already present in ancestors." (p.1)
[80] This was a considerable break with paleontological textbook tradition. (Prothero 1992)

Natural selection is based on the presence of three principal properties of organisms: the selected individuals are stable entities (relative to the relevant time-scales); the variation upon which selection acts is random; the individuals reproduce with integrity of form (relative to extant variation). Stanley's main argument for the existence of a new regime of selection was that these three properties are also present in species. First, citing Mayr as well as Eldredge and Gould, he asserted that in the main species are stable, that "homeostatic mechanisms oppose wholesale restructuring of the genotype in large, well-established, populations." Then he argued that the variation upon which species selection acts is random because "speciation is to a large extent random", because speciation occurs in small isolated populations, because it "is impossible to predict at what time or what environment [such isolation] will occur" and because the sample of individuals that become isolated will be taken at random. That species reproduce with relative integrity is not mentioned and apparently taken as a given. (pp.646-648)

Having established the existence of species selection Stanley moved on to claims about its significance. He took an extremely strong line, not only issuing a challenge to the authority of biology over macroevolution but also asserting that all important evolutionary processes occur at the macroevolutionary level and that microevolutionary effects provide little more than grist for the mill of higher level processes. Interspersed in the text are hints at what is to come: "Macroevolution is decoupled from microevolution, and we must envision the process governing it as being analogous to natural selection but operating at a higher level of biological organization."; "Species selection, which must largely determine the overall course of evolution, …"; "The randomness of speciation generally disallows long-term phyletic trends in evolution." Then, in his final paragraph, Stanley issued the strongest possible challenge: "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 the 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 turn not to population genetic studies of established species, but to studies of speciation and extinction in order to decipher the higher-level process that governs the general course of evolution." (p.648-650)

Stanley followed up with another article that same year, attempting to demonstrate the problem solving potential of species selection. (Stanley 1975a) Specifically he applied the idea to the vexing question of why sexual reproduction is almost completely predominant among higher organisms. This phenomenon had traditionally been explained by a 'good for the species' type argument. In the 1960s, however, there came to be a new emphasis on the individual as the only possible target for selection and such arguments became unpopular. Most phenomena that had been explained by 'good for the species' type arguments (such as altruistic behaviour) were instead explained by the concept of inclusive fitness. Sexual reproduction, however, was resistant to explanation by inclusive fitness and had become something of an anomaly.

In attempting to resolve the problem of sexual reproduction, then, Stanley was trying to win recognition for his theory, to show that his product was a valuable commodity. The existence of sexual reproduction was one of the outstanding problems of evolutionary science and if species selection were shown to solve it then it would have

become a theory of indubitable importance. Also, it should be noted that in terms of the struggle for authority this application of his theory is an attempt to invert the traditional direction of explanation in evolutionary science. The normal direction was biology applied to macroevolutionary phenomena but here was an attempt to show that phenomena observable in biological time-scales can be explained by macroevolutionary processes.

2.3.8: Stanley's *Macroevolution: Pattern and Process.*

In 1979 Stanley published his punctuationist manifesto, *Macroevolution: Pattern and Process*. (Stanley 1979) This 300 page volume was one long argument in favour of the entire punctuational research programme, core and periphery. It began with an historical introduction, moved through evidence in favour of punctuated equilibria, discussed the possible causes of punctuations and stasis, and finished with the apparent consequences of the punctuational model, such as species selection. Its aim was to provide both a resource book for practising paleontologists and a textbook for advanced students.[81]

In the preface Stanley made the aim of the book very clear. First he noted that in the past paleontology had played second fiddle to biology: "It has long been fashionable in paleontology to pay homage to the actualistic idea that the present is the key to the past". He then made an appeal to the experience of his paleontological colleagues, attempting to identify with them: "Like many other young paleontologists, I embarked on a career with this idea in mind and … put the belief into practice by undertaking a dissertation on living animals." With this identification in his pocket he described how he turned the tables: "… during the past few years I have found myself aiming more and more in the direction of bringing fossil data to bear on biologic questions – in particular, questions relating to the process of evolution." He finished this rhetorical *coup de gras* with the claim that his personal revolution is actually part of a wider movement: "Certainly, I am not alone in this posture." The reader is thus given a choice-that-is-no-choice by Stanley – either stay amongst the old school and be a junior partner to biology or join the movement. (p.ix)

It is not necessary to give a detailed explication of Stanley's book here, suffice to say that he reiterated all the major claims and assertions of the punctuationists discussed so far. For instance he asserted that traditionally the fossil record was considered "woefully inadequate" but that it is actually of "sufficiently high quality to allow us" to practice analysis at the level of the species, and that such kinds of analysis show "that many ideas now enjoying widespread support amongst biologists are in need of re-examination." (p.1) There is the claim that the architects of the Modern Synthesis were responsible for the traditional view of the fossil record, that they ignored the sudden origins and stability of species in the fossil record, choosing instead to emphasise phyletic gradualism. (pp.19-22) There is acknowledgment that phyletic evolution does account for some evolutionary change with a qualifying statement ("such evolution seldom produces major morphologic transitions." (p.37)) Finally came the declaration that the processes of macroevolution are essentially decoupled from microevolution (p.187). By producing

[81] The role of textbooks in scientific revolutions is crucial. No revolution is successful until the next generation are convinced of its value.

such a large, detailed and comprehensive statement of the punctuationist position Stanley substantially upped the ante. The challenge was thus put to evolutionary biologists to either accept paleontologists as an equal authority on evolution or to attempt a deconstruction of their arguments.

2.3.9: Paleontology revitalised.

From the mid to late 1970s there was evidence that the punctuationists were beginning to achieve their principal goal – which was to make paleontology a more theoretically minded discipline, a discipline with the authority to make assertions about the nature of evolution and to thus raise its status within the field of evolutionary science. As of 1979 punctuated equilibria had still not attracted much attention outside of paleontology and it appeared that biologists were not overly concerned about a few paleontologists making claims that attempted to impinge on the authority of their disciplines. Within paleontology, however, citations of Eldredge and Gould's 1972 article were on the rise, and most of these citations were positive. There were also a number of other events demonstrative of the changes taking place in paleontology.

In 1975 Ralph Johnson and Thomas Schopf founded the journal *Paleobiology.* [82] Articles published in *Paleobiology* had to be of theoretical interest – descriptive articles were directed to the *Journal of Paleontology*. In a sense the founding of this journal was a major step in the establishment of an independent theoretical paleontology in that it allowed paleontologists to publish articles about evolution without being subject to the judgements of evolutionary biologists. The paleontological journal *Lethaia*, founded in 1968, soon joined *Paleobiology* in this approach.[83] By the mid-1970s meetings of the Paleontological Society had also come to be dominated by generalised discussions of theory – proposals to discuss particular specialties were rejected. (Prothero 1992)

In 1977 paleontologist Anthony Hallam brought together articles by many of the prominent paleontologists of the time in a book called *Patterns of Evolution, As Illustrated by the Fossil Record*. (Hallam 1977) Amongst the authors were many that have already featured in this history – Eldredge, Gingerich, Gould, Raup, Schopf and Stanley. As suggested by the title, the essays concentrated on how paleontology informed perspectives of evolution rather than the other way around, although there was also emphasis on bringing paleontology up to date with biology. Gould was asked to write an historical introduction and Schopf a concluding chapter. The remaining authors (15 in all) were asked to write general accounts of the evolutionary patterns displayed by large taxonomic groups (eg. Gingerich on mammals, Eldredge on trilobites, Schopf on bryozoa). The intention of the book was to provide a role model for paleontological evolutionary perspectives in a similar fashion to that of George Simpson forty years earlier. The essays produced, apart from the one by Gould, were technical, written in typical scientific style[84] and broad in scope, attempting to consider many different outlooks.

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[82] Recall that Schopf also created *Models in Paleobiology*, the book that carried Eldredge and Gould's 1972 article.

[83] In the mid-1980s another theoretically disposed paleontological journal was founded – *Palaios.*

[84] Passive voice, no adjectives, etc.

Hallam's preface gives a good guide to the tone of the rest of the essays in the book. First he noted that before the then recent explosion of interest in evolutionary theory most paleontologists were more concerned about geology than evolution. He identified Simpson as the major exception to this, but then observed that it had been "almost a quarter of a century … since Simpson's second book appeared" and declared that "the time is ripe for a modern evaluation of what the fossil record has to reveal about evolution." Hallam thus placed the book as a direct descendant of the tradition of Simpson whilst also hinting that the new methods described in the book would surpass those of Simpson. Hallam also made a break with traditional paleontology, first by noting that it "has been customary to be somewhat apologetic about the fossil record", then by proclaiming that "the time has surely come for us to emphasize the more positive aspects." He summarised the new boundaries that 'modern' paleontologists were attempting to draw within evolutionary science: "elucidation of evolutionary *mechanisms* must remain the province of geneticists and ecologists, but these scientists are denied the valuable time dimension which allows us to investigate evolutionary *patterns* in a comprehensive and meaningful way." (p.v, his italics) It is also worth noting that throughout the two page preface Hallam consistently used the words 'we' and 'us' when referring to paleontologists in general. The (paleontological) reader is thus automatically brought into the 'modern' paleontological fraternity of which Hallam is a member.

Gould was asked by Hallam to write a history of paleontological attitudes towards evolution, to be used as an introduction to the book. Ever the inventive writer, Gould used a rather unorthodox approach and came up with 'Eternal Metaphors of Paleontology' (pp.1-26). Instead of writing a simple chronological history Gould asserted that there are three basic questions that have informed paleontological evolutionary perspectives throughout history and proceeded to elucidate the different fashions in which these questions have been addressed over time: Does evolution have directional properties?; What is the cause of evolutionary change?; What is the tempo of evolutionary change?[85] Gould contended that the answers to these questions have always taken one of two diametrically opposite forms (respectively: steady state or directional; environmental or internal; gradual or punctuational).

Gould's historical account of these themes is not relevant to this thesis. What is relevant, however, is that at the end of the chapter he took the opportunity to expound upon his own (contemporary) agenda – punctuated equilibria and notions of evolutionary hierarchy. First he gave a summary of how punctuated equilibria addresses the question of tempo and then contended that punctuated equilibria in combination with a hierarchical perspective can provide resolution to the other two questions also. In particular he argued that natural selection "is undeniably steady-statist and environmentalist in ecological [microevolutionary] time" but that once one "discards the shackles of phyletic gradualism as an explanation for 'trends', we see that the operation of natural selection in evolutionary [macroevolutionary] time can yield direction".[86] His

[85] Note that I have rephrased the questions into modern terminology. Gould asserted that his three questions informed inquiry into life's history well before any concept of organic evolution emerged and the history he recounted predates Darwin.

[86] Three notes on Gould's use of rhetoric here. First, phyletic gradualism as characterised by Gould is the population genetical extrapolation to macroevolution. The use of the word "shackles" here thus implies restraint of paleontological thought by indoctrination from population geneticists. Second, his appropriation of the word 'evolutionary'. Normally in evolutionary science the term "microevolutionary time" is used for

argument, in simple terms, was that natural selection can only cause adaptation to local environments and that since environments fluctuate randomly over time it cannot produce directional change. Evolutionary trends, however, can still transpire because of the differential success of species and the cause of these trends could also be regarded as internal because those species that follow a path of increased "biomechanical efficiency" are more likely to persist than those that acquire "limiting morphological specialization" and "an engineer might predict [their] path on structural principles alone." (pp.22-23)

Gould then went on to a discussion of Stanley's 'species selection'. He concurred with Stanley over the importance of the phenomenon and claimed precedence, providing a quote from his and Eldredge's 1972 article where they explicated species selection but chose not to name it. However he did not welcome the name that Stanley chose because of its "fundamentally non-Darwinian nature". Surely, he stated, "the differential success of species is as Darwinian a process as their origin." He then went on to suggest that it be called instead "Wright's rule" laying claim to a prestigious and most orthodox Darwinian ally.[87] This disagreement between Gould and Stanley points to a difference in their preferred tactics. Stanley is quite happy to be thought of as non-Darwinian. His tactics are basically full frontal attack. Gould's tactics by contrast are more subtle. He prefers to appropriate Darwinism for himself, redefining its boundaries so that they encompass his interests. (pp.23-24)

Gould concluded the chapter by discussing the importance of an independent macroevolution for paleontology. He first noted that 'Wright's rule' decouples macroevolution from microevolution whilst "[u]nder phyletic gradualism, trends are merely extensions of directional selection within local populations" and that macroevolution is thus mere extrapolation. He implored paleontologists to campaign for independence: "There can scarcely be a more important task for palaeontologists than defining the ways in which macro-evolution depends upon processes not observed in ecological time." (p.24)

Eldredge's chapter ('Trilobites and Evolutionary Patterns') focussed on his speciality, the trilobites. The scientific details of this chapter need not be related here but his historical account of the relationship between paleontology and theories of evolution is interesting. His basic thesis in regard to this was that a "conceptual bias" had meant that "palaeontology has to date contributed almost nothing to evolutionary theory." And what was the form of this conceptual bias? In essence that paleontologists had accepted the population genetic view of evolution: "evolution is defined as change in gene content and their phenotypic expression." However, said Eldredge, "there is patently another way

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smaller time scales and the term "macroevolutionary time" is used for larger time scales. Gould instead chose to use the terms "ecological time" and "evolutionary time" instead. This implies that only the large time scales are relevant to evolution with the smaller ones having only ecological significance. In this subtle fashion Gould redefined evolution as macroevolution alone, thus laying a paleontological claim to authority over evolution *in toto*. Thirdly his use of the word 'undeniably' when stating that natural selection is a steady state/environmental phenomenon, inducing the reader to skim over the claim without thinking about whether they actually agree with it.

[87] Sewall Wright, according to Gould, laid the foundations for species selection with his 'shifting balance' theory.

of looking" at evolution – to "assume that populations and species are real entities … and not merely segments of lineages arbitrarily subdivided …" (pp.306-307)[88]

Of the fifteen chapters not by Eldredge or Gould seven cited their 1972 article. Of these seven citations, two were by close colleagues of Eldredge and Gould – Raup and Stanley. Another was by the amiable foe Gingerich.[89] The remaining four citations were essentially positive and there were strong signs that Eldredge and Gould's rhetoric was beginning to have an influence.[90] In the final summary chapter Schopf evaluated the position taken by each of the essays on the opposing themes explicated by Gould in the introduction. (pp.545-561) In regard to the tempo of evolution he found that 12 of the essays found for punctuational change and 4 against. However in none of the chapters was punctuated equilibria central to the analysis. This is qualified by the fact that the articles were intended to be broad in scope, to not focus on any particular issue.

It can be concluded that as of 1977 punctuated equilibria had become an important aspect of paleontological perspectives on the tempo of evolution in macroevolutionary time but that it had not become central to many paleontological research programmes. However the wider aims of the punctuationist revolution were beginning to be realised. The fact that all these authors came together to write a manifesto for paleontological evolutionary perspectives is ample evidence of this. Amongst the authors there was also as much concern for how paleontology informs the Darwinian evolutionary perspective as the other way round. They clearly felt confident that they had the authority to make authoritative statements about evolutionary theory. It should also be recalled that all of the subtle tactics and swift manoeuvres presented by Gould in the opening chapter were accepted as representing the attitudes of the rest of the authors, and this in a book that purported to be the most important paleontological publication on the topic of evolution for almost forty years.

The authors represented in the book were not outsiders. Rather they were amongst the cream of the profession. It was these professionals, at the top of their discipline, who lead the revolt against the authority structure of evolutionary science. Not many of them would actually think of themselves as revolutionaries, but the fact is that by simply doing their science in typical scientific fashion, by pursuing their own scientific interests, they were actually involved in a change of order in evolutionary science. As Bourdieu observes, in established scientific fields the option of revolution is available only to those

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[88] It is interesting that Simpson himself reviewed the book. (Simpson 1978) He found little to object to, placing every chapter, including Gould's and Eldredge's as well within the boundaries of the Modern Synthesis. For instance he says of Eldredge's chapter that apart from "a few esoteric terms, what he has to say is quite "neo-Darwinian" (syntheticist)." (p.78) However he took strong exception to Eldredge's assertion that until recent times paleontology had contributed almost nothing the knowledge of evolution. This is not surprising considering that Simpson's scientific reputation was built on his contribution to the Modern Synthesis. Simpson did not cite himself as a counter-example to Eldredge's claim however, choosing instead to cite *Patterns of Evolution* itself.

[89] Further evidence of this amiability is given by the fact that Eldredge favourably cited one of Gingerich's articles alongside his and Gould's 1972 as examples "carefully delimited studies of judiciously chosen material" that lead to "studies of within and among population variation, as well as speciation itself." (p.306)

[90] Robert Carroll, for instance, wrote "Eldredge and Gould (1972) have recently emphasized how one's phylogenetic conceptions are influenced by prior assumptions regarding the probable mode or pattern of evolution. The concepts of phylogenetic gradualism, in particular, have tended to exaggerate the incompleteness of the fossil record." (p.427)

richest in social capital (as they are the only ones with the necessary means) and the course of revolutions is via the established protocols. (see Section 1.2.1)

Chapter 3

Constructing the revolution.

(A rhetorical analysis of 'Punctuated Equilibria: An Alternative to Phyletic Gradualism.', followed by a citation analysis of same.)

3.1: The relationship between rhetoric and scientific facts.

The *Australian Pocket Oxford Dictionary* offers two definitions for the word 'rhetoric': the art of speaking or writing effectively; artificial or inflated or exaggerated language. Scientists have traditionally shunned rhetoric, the definition they associate with it being the second of those listed above. "The facts speak for themselves" – that is, scientific article are supposed to simply present objective facts and hence there should be no need for rhetoric The scientist is merely a spokesperson for nature, facts are merely waiting to be 'discovered'. Science, within this narrative structure, exists independently of the scientist, (a scientist being defined as someone who does science).

It is possible to invert this structure and define science as what scientists do – *to define science socially rather than materially*. With this definition the nature of scientific facts is altered. They are not waiting to be discovered but instead must be created by the scientist. Hence the facts do not speak for themselves. The scientist is not a mere spokesperson for the facts, he or she is the constructor, the inventor of those facts. This does not make facts any less real or certain. If I invent a better mousetrap, it exists. It is just that it is seen as something that is created rather than discovered.

The usual medium for the distribution of scientific facts is the 'paper', an article published in a journal.[91] Scientists create facts in their laboratory and transport them to other scientists' laboratories via these 'papers'. During this transportation process a fact exists in the text and, of course, the way it is presented in the text will affect its status. The inventor of a fact has a vested interest in seeing others accept it and will thus attempt to write the 'paper' in a persuasive fashion. In science the more objective a fact is, the less the subject of opinion, the more certain it is. Therefore scientist X will present the fact in a form that he or she knows other scientists will accept – as if it were an objective fact. It can thus be seen that rhetoric is just as important to scientific texts as to any other form of writing (rhetoric as in the first rather than the second definition above).

Most scientific articles use the passive voice to convey objectivity. For example, a scientist might write 'it was observed that', not 'we observed that'. This gives the impression that the observation would have been the same regardless of who the observer was. Having established objectivity, the status of a particular scientist's fact or scientist's claim is determined initially by the presentation it is given by that scientist and then by

[91] Latour and Woolgar actually prefer to see science as a discipline whose main objective is to produce such articles. A laboratory is in this sense a factory for the production of scientific articles. See (Latour and Woolgar 1986).

how it is treated by other scientists, particularly in the literature.[92] A fact becomes strong if it is accepted by other scientists and is made even stronger if it is used to build other facts. On the other side of the coin, if a claim is criticised by other scientists, or even worse ignored, it will not be a fact at all.

3.2: The book.

Eldredge and Gould's 'Punctuated Equilibrium: An Alternative to Phyletic Gradualism' was published in *Models in Paleobiology* ((Schopf 1972))[93]. This book was a collection of articles derived from papers given at the annual meeting of the Paleontological Society, and the Geological Society held in Washington D. C. on November 2, 1971. The intended audience for the book was other paleontologists and indeed the article did not receive much attention outside paleontology until the late 1970s.[94]

Traditionally, paleontologists had not been too concerned with theoretical issues[95], and this relegated paleontology to a lowly status within evolutionary science. Paleontologists were considered to be more akin to stamp collectors than scientists, merely collecting and classifying fossils, documenting the history of evolution without concern for 'deeper' issues like mechanisms and causes. The how and why of evolution were left to other sub-fields of evolutionary science. *Models in Paleobiology* was symbolic of a change in the way that paleontologists thought about their discipline, while also being a harbinger of that change.[96] One simply has to look at the title of the book to comprehend this change. The word 'model' implies theoretical contemplation. The second key word in the title, 'paleobiology', is an even stronger symbol of this change. 'Paleobiology', compared with 'paleontology', implies active, dynamic science – *real biology* - with modelling, hypothesising and theoretical debate[97].

In his introduction the editor, Thomas Schopf, explicitly stated his motivation for gathering together this group of articles. He related an anecdote in which he had a conversation with a graduate student. The student, it seems, was in a research program

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[92] Latour and Woolgar formulated a classification system for the status of scientific facts, which I give here for ease of reference: *Type 1* statements are conjectures or speculations, *type 2* are tentative suggestions, perhaps pointing to areas requiring further investigation, *type 3* are qualified statements (e.g. 'it is generally assumed that …"), *type 4* are unqualified statements of fact that still require explanation, and *type 5* are statements requiring no explanation – assumed facts that all good scientists should know.((Latour and Woolgar 1986), pp.75-90)

[93] This book, and particularly Eldredge and Gould's article, will be referred to repeatedly throughout this chapter. Hence, for the rest of this chapter it will be cited with only a page number and Eldredge and Gould's article will be referred to simply as 'the article'.

[94] The 'attention' the article received will be discussed extensively in other sections. For now the reader will have to bear with me.

[95] George Simpson, who played an important role in the evolutionary synthesis of the forties, was probably the first exception to this.

[96] Gould later described this movement as a "mini-revolution … a restructuring of [paleontology's] principal focus from biostratigraphic correlation in the service of geology … to a concern with biological problems of evolution." ('Punctuated equilibrium in fact and theory', in (Somit and Peterson 1992), p.55)

[97] Paleobiology was a word created to delineate theoretical discussion about paleontological issues from traditional paleontological pursuits.

that involved describing a group of fossils. There was an "assumption", wrote Schopf, that "because the description had not previously been made, it was worth doing." This reminded Schopf of other similar conversations and made him wonder why this form of descriptive study was so popular. He decided it was because the student and others in the same situation were "unaware of the various alternative strategies of research in invertebrate paleontology" and resolved to remedy the situation. (p.3)

Schopf urged paleontologists to break away from their traditional methodology, asserting that they needed to move from "general survey to analytical inductive inference." This assertion, he wrote "may be uncomfortable words to some of us." "But," he went on, "the issue as to what is the best research strategy does not go away because our traditions support one particular viewpoint." Schopf continued on to say that "paleontology has collected much of its data and basic theses" and hence that paleontologists "should turn to broader horizons and interpretive themes." The models in the book were intended to be read as "suggestions" for "fellow workers." Schopf stated that he knew of no other "comparable book in the field" and hoped that it would "provide focus for the analytical approach in paleobiology." The commitment of the authors in the book was "to a reinvigoration of paleontology," a commitment demonstrated by the fact that both the authors and the publisher forewent any royalties from the book in order to keep the price down, making it available to "the people we want to reach most – the working paleontologist and his students." Any profits from the book were directed to the Paleontological Society. (pp.3-6)

One can see, then, that paleontologists in the early 1970s, or at least those represented in *Models in Paleobiology*, were very keen to change the status of their discipline. It should be noted that in his introduction Schopf spoke mostly in the active plural voice, using the words "we" and "our" to mean all the authors in the book. For instance: "… we offer these models …"; "We wanted to write a book …"; " … we know of no … comparable book …"; " … our first commitment is to a reinvigoration …" (pp.4-6). This portrayed a certain solidarity among the authors. They were committed to furthering the paleontological cause and hoped the reader would become inspired to do likewise.

A brief examination of the other articles in the book will also help to frame the setting in which Eldredge and Gould's article was published. Apart from Schopf's introduction and Eldredge and Gould's article, there were eight other contributions. Six of them had the word "model" in the title (eg. "Models in Phylogeny"), the other two beginning their title with the word "approaches" (eg. "Approaches to Morphologic Analysis), suggesting that they were offering new research agendas. A survey of the introductions and conclusions of the eight articles also yields many key words and sentences suggestive of new research directions:

- "Approaches to the study of morphology by paleontologists are presently undergoing rapid development. New approaches … new techniques and analytical methods … old approaches are being reviewed and integrated with modern biology" (p.29)
- "Few studies have been specifically designed to study the fundamental factors … Few attempts have been made at proposing and testing models …" (p.48)

- “Especially in need of being carried out are studies that explain the process … hopefully theses results will … lead to comprehensive models … so that an explanation in terms of natural selection is also forthcoming.” (p.60)
- “… information obtainable from fossil assemblages can be analyzed in these terms to produce insights unobtainable in other ways.” (p.63)
- “ … offers much promise for the paleoecologist.” (p.80)
- “We propose to … test the hypotheses …” (p.117)
- “… phylogeny will continue to challenge our ingenuity.” (p.145)
- “ … new approach to problems …” (p.161)
- “ … a number of theoretical aspects remain to be developed …” (p.190)
- “We do not need to wait for all the taxa in the fossil record to be described … in order to proceed with interpreting.” (p.215)

Eldredge and Gould’s article can also be read as a spur to paleontologists. As will be discussed at length later, it exhorted them to raise the status of their own discipline. It attempted this in three ways. First by proposing a new theory that was primarily concerned with the data of paleontology - with a hypothesis to test paleontologists become investigators and analysts rather than mere collectors and classifiers. Second it described a historical and philosophical perspective in which paleontologists have been duped into being the errand runners for other evolutionary scientists then told them that they should break out on their own. Third it identified areas in which paleontologists were behind the times in terms of the theory behind their practice and urged them to catch up.

3.3: The article.

3.3.1: Use of philosophy.

‘Punctuated Equilibria: An Alternative to Phyletic Gradualism’ is an atypical scientific paper in that it draws on material from the humanities. However it is typical of Gould who, whilst conceding that punctuated equilibria was essentially Eldredge’s idea, has professed to coining the term ‘punctuated equilibrium’ and writing most of the article (Gould 1991). He later professed his belief in breaking down “falsely restrictive intellectual boundaries”, avowing that he “dream[s] of integrated knowledge”. He regretted the “petty and parochial boundaries” that both the arts and the sciences have constructed” – “the impenetrable and sterile language of so much scholarship in the humanities, the dry, impersonal and barbarous passive voice of scientific prose.” He believed he could contribute to a more integrated worldview by bringing “the data and arguments of the humanities, not as a window dressing for vain show, but as an intrinsic and central part of a scientific case …” (‘Fulfilling the spandrels of world and mind’, in (Selzer 1993), p.322). In particular Gould had always maintained strong interest in the history and philosophy of science. He had read works by T. S. Kuhn, N. R. Hanson and P, Feyerabend in the 1960s, and credited them with having given him the awareness to

recognise the ideological hold of gradualism over paleontology.((Somit and Peterson 1992), p.56)

The employment of philosophy begins in the very first paragraph, which is the first of a 4 section list that summarises the article: "The expectations of theory color perception to such a degree that new notions seldom arise from facts collected under the influence of old pictures of the world. New pictures must cast their influence before facts can be seen in different perspective." (p.83). At this stage the reader is not given any clues as to where Eldredge and Gould got this statement from. They do not source the statement, presenting it as if it were an accepted fact[98] - it is given in the passive voice, the voice of objectivity and there is no modalisation of the statement, no 'we believe that' or 'recent philosophers of science have found that'.[99] This statement and others like it served Eldredge and Gould well throughout the article, priming the reader for a confrontation with new ideas about old data. They wanted the reader to agree that a new way of thinking might indeed be necessary, before the new way of thinking is presented. The reader, they hoped, would thus become more amenable to Eldredge and Gould's claims. Eldredge and Gould thus reconstructed material from the philosophy of science to suit their purpose. They composed a sociophilosophical statement to fit the aim of their article - to convince paleontologists that their new idea, the theory of punctuated equilibria, is better than the one they hope to replace, phyletic gradualism – and have presented it as if it were a strongly accepted fact.

The first section proper was devoted to a deconstruction of inductivism. Eldredge and Gould opened the section with a quote from Peter Medawar that "unbiased observation is a myth". They then discussed how Isaac Newton's remark – "I frame no hypotheses" - has been misinterpreted as an inductivist plea, when really he only wanted to "eschew idle speculation and untestable opinion." (They quote two sources, Hanson and Koyré for this reading) In Newton and Medawar, then, Eldredge and Gould gathered two highly respected allies. This was their prelude to a frontal assault on inductivism. Calling on the authority of other disciplines, they stated that "most philosophers would brand the inductivist credo as naive and untenable …". They listed two arguments for this claim. First, scientists "do not encounter facts as *data* (literally "given") discovered objectively" but rather "[a]ll observation is colored by theory and expectation." They cited two sources for this statement: Vernon, a psychologist; and Feyerabend, a philosopher who they described as having a "radical view … that theories force observation into preset channels.". Second, theory does not arise from the "patient accumulation of facts. Rather, we observe in order to test hypotheses and examine their consequences." This time they cited Hanson, a philosopher and historian of science.(pp.84-85)

It appears then, from the second of their two arguments, that what Eldredge and Gould were proposing was to replace inductivism with Popperian falsificationism. Observations are for testing theories. How one is supposed to do this, however, is

[98] In terms of Latour and Woolgar's classification system (see footnote 2) it is a *type 4* fact - an accepted fact requiring no reference to a source but not so obvious as to not require explanation.

[99] One suspects that what they are referring to here is the notion of the theory-ladenness of observation, which is a much more subtle concept than as presented by Eldredge and Gould. It is by no means an 'accepted fact' amongst those who like to watch the way that scientists work and indeed is the topic of ongoing debate.

problematic since observations are biased by theories. The seemed not to have grasped the subtle but crucial point about the dynamics of theory and observation – that they affect each other. Next Eldredge and Gould discussed how inductivism "continues to control the methodology and ethic of practicing scientists …" (p.85). They provided examples of this "control", from Darwin last century to the contemporary geologist Leopold. They then go on to link inductivism with phyletic gradualism, and with the idea that one cannot refute a theory internally.[100]

3.3.2: The dictatorship.

One of the most important constructions in Eldredge and Gould's article was the image of inductivism and phyletic gradualism as co-conspirators in a dictatorship that had cast some kind of spell of influence over paleontology. Inductivism and phyletic gradualism became animated entities in their own right: "It holds that new species are …"; "Under its influence …" (p.84). In both cases the "it" was phyletic gradualism. The image of a dictatorship was created with some robust language:

- To credit accomplishments to "patient induction" is a "delusion" (p.85).
- Inductivism "forces us into a vicious circle" while a "theory" (by implication phyletic gradualism) "compels us to see the world in its light" (p.86).
- The "influence" (of phyletic gradualism) is so "tenacious" because paleontologists think they "see objectively", not recognising its "guiding sway" (p.86).
- "It colors our language. We are compelled to talk of "morphological breaks" in order to be understood.".
- "It prescribes the cases that are worthy of study. … there is something insidious here: … the picture itself excludes an investigation of the very cases that could place it in jeopardy" (p.90).

In these statements one could visualise the dictatorship in action. Its agents were metaphorical thought police, compelling paleontologists to think in a certain way, convincing them that they did so of their own free will. And like a dictatorship, it forced its own language on the people, decided what activities they may undertake and did not allow any activities that might undermine its power.

Eldredge and Gould did not blame individual scientists for the dictatorship. Rather they used the work of other scientists as examples of how the dictatorship had controlled thought. They started with Darwin, who "in traditional obeisance to inductivist tenets" wrote in his autobiography that he had collected facts without any theory.[101] They then moved to a contemporary figure - the geologist Leopold who claimed, apparently

[100] That is, it is not possible to refute a theory simply by collecting data whilst working within its parameters. One must have a new picture in mind to re-order the data.

[101] Eldredge and Gould also mentioned that elsewhere Darwin took a completely contradictory line. He compared collecting facts without theory to counting pebbles in a gravel pit. To Eldredge and Gould this is symbolic of the dilemma facing scientists, that in "unguarded moments" they "have correctly attributed their success to skill in hypothesizing and power in imagination" whilst "in the delusion of conscious reflection, they have usually ascribed their accomplishments to patient induction." (p.85)

that he could "describe and analyze the aesthetics of rivers" without personal bias by defining impartial measures, gathering data and then analysing it using statistical methods. It was no accident, ironicised Eldredge and Gould, that the system he came up with for aesthetic measurement threw up Hells Canyon of the Snake River as number one, as at the time he was opposed to a proposal to dam Hells Canyon. (pp.85-86)

Eldredge and Gould claimed that examples of phyletic gradualism are rare in the fossil record, that it is actually full of discontinuities. What paleontologists had done in the face of these discontinuities, they asserted, had been to invoke the imperfection of the fossil record to explain the discontinuities then fill in the gaps with dashed lines. Generally, they contended, there had been no logical extrapolation from the facts to the conclusion, with phyletic gradualism being simply foisted upon the data. As on example of this they used a 1951 study of coral by Sylvester-Bradley.[102] They did not claim that the analysis was necessarily incorrect, stating that the species may well have "evolved as claimed." Instead they wrote that they "merely wish to show how the *a priori* picture of phyletic gradualism has imposed itself upon limited data." (p.97, their italics) Eldredge and Gould insisted they were not trying to disprove the findings of Sylvester-Bradley. Rather they simply wanted to show how the thought processes of the paleontologists were controlled by phyletic gradualism.

Another "example of *a priori* beliefs in phyletic gradualism", which they described as "extreme", was the work of Brace (1967) on human evolution. Brace, apparently, had interpreted human evolution as a "gradual, progressive, unilineal process". Once again Eldredge and Gould were not claiming that Brace's interpretation was incorrect. What was "seriously wrong" with Brace's view, they argued, was that his interpretation was inconsistent with "modern biological thought". This lead the reader to another of the manifestations of the dictatorship of phyletic gradualism – that it had caused paleontologists to fall behind the times in terms of biological theory. (pp.97-98, their italics)

3.3.3: Paleontologists under the dictatorship and the call to arms.

The most obvious form of resistance to the tyranny of a dictatorship is, of course revolution. However, the people must first be convinced that they are being oppressed by the dictatorship, otherwise they will not feel any need to rebel. Eldredge and Gould attempted to convince paleontologists that they had been oppressed by phyletic gradualism in two ways. First, paleontologists had spent over a century looking for gradual evolutionary change in the fossil record because Darwin told them to. This, they claimed, was a wild goose chase – a fruitless search that was wasting paleontologists' time. Secondly, phyletic gradualism had caused paleontology to fall behind the times. Eldredge and Gould declared that their new vision would give paleontologists the opportunity to catch up with modern biology and become respected members of the scientific community.

In the introductory summary to the article Eldredge and Gould state that if their new model of evolution is correct, "the great expectation of insensibly graded fossil

[102] Sylvester-Bradley's study was itself a reinterpretation of an earlier study by Carruthers (1910).

series is a chimera." [103] Darwin, it seems, set paleontologists the task of finding gradualism in the fossil record as he saw this as the only way to silence his critics. "The task that Darwin set has guided *our* studies of evolution to this day" (my italics).[104] The search for these gradual fossil series had become no more than an historical artefact. The modern synthesis, they noted, had silenced the mutationists and paleontologists were thus searching for proof of something that had already been demonstrated. (pp.84-87)

Darwin's "insistence on insensibly graded series" was compounded by his confusion over the process of speciation (apparently he was "muddled"). They stated that there are two ways that new species can possibly arise – transformation or splitting of a population The second of these is the only process that can increase diversity and hence it must occur to some degree. According to Eldredge and Gould, however, Darwin emphasised the first process, and when he did discuss the second, he "continued to look through the glasses of transformation: he saw splitting … proceeding slowly and gradually". "Our present texts have not abandoned this view … although modern biology has", they wrote.[105] (pp.87-89)

The narrative framework within which their new theory was now fully unveiled: Under phyletic gradualism's grip paleontologists had continued to search for gradualism in the fossil record not realising that they had been trying to demonstrate a thesis (transformation of entire populations, or 'phyletic evolution') that modern biology had long abandoned. They now made appeals to the human agency of paleontologists: the "rarity of transitional series has remained our persistent bugbear"; "We have all heard the traditional response [to discontinuities in the fossil record] so often that it has become a catechism that brooks no analysis: the fossil record is extremely imperfect." (p.90)[106] Eldredge and Gould were calling upon their shared experiences with other paleontologists – the frustration of looking for a particular form of data (gradual) that is extremely hard to find, the years of being told that the data they collect is imperfect. Later they stated that if it were accepted that many of the apparent imperfections of the fossil record are actually "the way in which evolution occurs" it would "release us from a self-imposed status of inferiority among the evolutionary sciences." (p.96)

Eldredge and Gould again called upon the authority of Feyerabend: "The traditional approach to morphological breaks merely underscores what Feyerabend meant in comparing theories to party lines, for it renders the picture of phyletic gradualism unfalsifiable." As before they were reconstructing the philosophy of science to suit their purpose. Feyerabend was not concerned with which theories are and which aren't falsifiable. To criticises a theory for being unfalsifiable is to call on Popper's philosophy, not Feyerabend's. Still, it is a very effective criticism – in the scientific community, unfalsifiable is akin to being unscientific.[107]

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[103] At this stage in the article, their presentation of punctuated equilibria is modalised by an "if", which says that it is not a very strong fact. As the article progresses however, it becomes more certain. Indeed eventually the reader is forced to either agree with Eldredge and Gould or to oppose the findings of modern biology, which is not much of a choice.

[104] To emphasise that here Eldredge and Gould purported to speak for all paleontologists.)

[105] Once again, the "our" in the last statement is all paleontologists.

[106] Once again the "we" and the "our" is all paleontologists.

[107] Popper's philosophy of science is easily the best known in scientific communities. In fact for scientists, it has become the definition of science – scientific theories are falsifiable, theories from other disciplines

They provided two examples of paleontologists citing the imperfection of the fossil record The first was Eaton's (1970) declaration that it was fortunate that the fossil record is imperfect, as it allows paleontologists to delimit species. They were "amused by the absurdity" of this claim. Their discussion of Neef (1970) was equally as damning. Apparently his data provided no criteria with which to choose between phyletic gradualism and saltative evolution so he simply chose the former. They also stated that they had "encountered no dearth of examples" and cited Neef "nearly at random", thus implying that the practice had thoroughly permeated the methodology of paleontology. Even worse was to come. Phyletic gradualism was also corrupting the minds of the young. Calling on the authority of Thomas Kuhn, who had "stressed the impact" of textbooks on budding scientists, they charged that the "pervasive influence" of phyletic gradualism was to be found in the textbooks that mould the thought of the "new professionals." (pp.90-91)

3.3.4: The edifice and the dichotomy

To have a revolution one must create solidarity amongst the people one is trying to rally. That is, one must create an 'us' and a 'them', a dichotomy, and the oppressed must be left in no doubt as to whom they should blame and whom they should side with. The tactics used by Eldredge and Gould to create the 'them' has already been discussed. The 'them' in this case did not have a face. Rather it was a reified object called 'phyletic gradualism'. This object was cast as a dictator whose influence had an iron grip on the thought of paleontologists. Individual scientists were not to blame for the predicament – it was the theory itself that was oppressive. The 'us' that Eldredge and Gould created, by contrast, had a very human face. It was the fraternity of paleontologists.

The construction of the 'us' in the dichotomy can be seen through the use of the words 'we' and 'our'. Eldredge and Gould used the words to side with the reader, to identify with them. This analysis will focus on the word 'we' which was used 80 times in the article. The word was used to delineate different objects at different points in the article. Three categories were defined to classify these varying registers:

we_1 - Eldredge and Gould;
we_2 - all paleontologists;
we_3 - all paleontologists who are sensible and agree with Eldredge and Gould.[108]

I found there to be 44 of type we_1, 24 of type we_2 and 11 of type we_3.[109] In most cases the categorisation was simple (e.g. we_1: "In this paper we shall argue: …"). However there was a significant number of occasions when categorisation was not clear cut. It was often difficult to decide between we_2 and we_3. This was not surprising as there is only a subtle distinction between the two. What was unexpected was that at other times

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are not. Even before Popper scientific papers were written to give the impression that the author proposed a hypotheses then set out to test it.

[108] I must give credit to Greg Myers, whose classification system I followed closely. ('Making Enemies: How Gould and Lewontin Criticize.', in (Selzer 1993), pp.256-275)

[109] There was one 'we' in a quote from Darwin.

it was even difficult to decide between we_1 and the other two 'we's. This points to a rhetorical tactic used by the authors to blur the boundaries between themselves and the readers. As the different registers merged into one another the authors and the readers became one, united in a common cause.

The use of we_1 throughout the article is remarkable for the amount of times it is used. Usually in a scientific article the passive voice is prevalent - the active voice being reserved for speculative statements. (e.g. 'It was observed that X became Z. We think factor Y may be the cause, but further research is required.') Eldredge and Gould, however, preferred to give their assertions a more human face. Consider the following excerpts: "We believe that an inadequate picture has been guiding … We hold that its influence … We contend that a notion developed elsewhere…" (p.86). They could well have written: 'An inadequate picture has been guiding … Its influence …. A notion developed elsewhere …". The statements have more certainty cast in the second format. This certainty would, however, have been at the expense of identification with the reader.[110]

The we_2 and we_3 registers were also used to create identification with the reader. Eldredge and Gould did not did not want the reader to feel that the authors were talking down to him or her. Rather they wanted the reader to know that they too, had been oppressed by the doctrine of phyletic gradualism, that they too felt the pain of being second class scientific citizens. We_2 and we_3 were frequently used to this end. Consider this example, in which we_2 was employed: because of phyletic gradualism, "[*w*]*e* are compelled to talk of …" (p.90, my italics). In the passive voice this statement would have read 'They are compelled to talk of …', creating a distance between authors and reader. Through the use of we_2 and we_3 the reader was left in no doubt that Eldredge and Gould were on the same side as themselves.

The distinction between we_2 and we_3 was a subtle one, Eldredge and Gould moving nimbly between the two. The effect of this was that the reader remained unaware that they have moved from a position where they had only paleontology in common with Eldredge and Gould to one where they also agreed with their ideas. In one paragraph, for instance, they wrote: "If *we* doubt phyletic gradualism, *we* should not seek to 'disprove it in the rocks'. *We* should bring a new picture from elsewhere …" (p91, my italics.). I put the first 'we' in category 2 and the second and third in category 3. Whether one agrees with these classifications or not it is clear that there was a move from where 'we' simply referred to all paleontologists to one where there was an implication that the reader should be sensible and agree with Eldredge and Gould's ideas.

At times, as I have already mentioned, there was only the finest distinction between we_1 and the other two 'we's. Consider for instance this excerpt, from the section where Eldredge and Gould discussed the apparent imperfection of the fossil record and how paleontologists had traditionally used it to cast doubt on their own data: "*We* have encountered no dearth of examples …" (p.90, my italics). Reading it the first time one automatically assumes that it refers to Eldredge and Gould. However with some thought one soon realises that as well as referring to the research that the authors did for the article it is an appeal to the experience of paleontologists, and hence can be read as a 'we' of type 2. The three 'we's are interspersed fairly evenly throughout the article,[111] except

[110] As we shall see later, though, in one crucial section Eldredge and Gould do switch to the passive voice.
[111] Except in the section written in the passive voice.

perhaps that as the article progresses we_3 begins to supersede we_2, and there are numerous instances where more than one 'we' was used in the same paragraph. All in all the reader was left with the feeling that there is a unity of identification between the authors and other paleontologists, the three 'we's merging together in solidarity to raise paleontologists from the more.

So here is the dichotomy: on one hand we have the reified object of phyletic gradualism and on the other we have the union of paleontologists that Eldredge and Gould were attempting to create. Phyletic gradualism is no person or group of people, yet it was a dictator that controlled the way that paleontologists thought, forcing them to undervalue their own worth, doubt their own data and be left behind as the rest of biology progressed to new ways of thinking. The 'us' and 'them' scenario was thus created, the scene ripe for revolution. However there was still one ingredient missing from the revolutionary recipe - the people needed to be convinced not just that they were oppressed but also that there was something better on offer.

3.3.5: Latourian black boxes and logical consequences.

It was in this ripe-for-revolution context that Eldredge and Gould presented their new explanatory model for the patterns that paleontologists observe in the fossil record. The delivery of this new model made quite a contrast with their historical analysis of the state of contemporary paleontology. They turned to a more orthodox scientific presentation, submitting their model/theory, punctuated equilibria[112], as a logical consequence of modern biological theory. We have already seen how Eldredge and Gould established that the old theory, phyletic gradualism, had caused paleontology to fall behind the times. The reader, they hoped, would thus be faced with the following decision: 'Do I stick with phyletic gradualism and remain the laughing stock of the biological community, or do I accept Eldredge and Gould's theory, catch up with modern biology and achieve a higher scientific status?'

To be precise, Eldredge and Gould presented punctuated equilibria as a logical consequence of Mayr's theory of allopatric speciation.[113] They framed Mayr's theory as a structure that cannot be questioned – a Latourian 'black box'[114] - then claimed that

[112] One must say that this is a rather catchy name – indeed one may call it a buzzword.

[113] It should be noted that both Mayr and his theory of allopatric speciation hold high status positions in evolutionary science.

[114] To Latour a 'black box' is a scientific structure that needs no justifications and cannot be questioned. They occur both in the physical and the conceptual world. For instance the computer I am using to write this text is one such 'black box'. I do not need to question its inner workings and most of the time I can safely assume that it is doing what I intend it to do. A good example of a theoretical 'black box' is the helical structure of DNA. Scientists can simply refer to it – there will be no dissent regarding its structure. The 'black box' is a concept that I find most invaluable when analysing scientific literature. If a scientist frames their claims as a logical consequence of black boxes, it makes it hard for others to question their findings. Dissenters, the scientist hopes, cannot question their claims unless they are prepared to also question the 'black box' that the claim is built on and thus go against the consensus of the particular disciplinary community. There is a loophole, however - a dissenter can instead question the validity of the logical implication leading from the black box to the new claim. Hence we can see the importance of rhetoric to scientists. Anyone can claim that their theory is a logical consequence of a black box, but it is

punctuated equilibria follows automatically from it. They hoped that the reader would be given a choice either to accept their theory or to disagree with Mayr. In the opening summary of the article, for instance, Eldredge and Gould stated that the "theory of allopatric speciation … suggests a different interpretation of paleontological data." (p.84). One must note the immediate reification of the theory - it was the theory that was making the statement, not Mayr or Eldredge and Gould. At this stage, though, it was a rather soft claim - it merely "suggests". Later on, as we shall see, the statement became much stronger.

Eldredge and Gould began the discussion of their new ideas with a section titled "An Irony" (pp.92-93). The "biological species concept", they wrote, "was a major triumph of the synthetic theory", the irony being that instead of trying to extract "its insights about evolutionary processes, we [paleontologists] sought only its prescriptions for classification.". In this section they implied that paleontologists had missed the boat when it came to species. They had focussed on the question of the "nature of paleontological species", which is a "theoretical debate unsurpassed in the annals of paleontology for its ponderous emptiness." Instead, they suggested, the biospecies concept "abounds with implications for the operations of evolutionary processes." Eldredge and Gould's theory was, of course, one of those implications. This two page discussion of the biospecies concept was, on one level, largely superfluous to Eldredge and Gould's argument. It did not add to the logical strength of their argument. What it did do was to create an atmosphere of excitement about their research. In contrast to the "ponderous", "futile" and "narrow" discussions that occurred in the past, their new way of looking at biospecies "*abounds* with implications" (my italics).

Eldredge and Gould's model is presented in a section entitled "Implications of allopatric speciation for the fossil record." (p.93) The word "implication", intimating a logical progression, is a hint of what is to come – a logical deduction. Deduction is the strongest form of argument. If the premises are true and the logic is sound the conclusion must also be true. To construct a deductive argument one must do two things – create undeniable premises then show that one's conclusion follows unquestionably from those premises. The gist of Eldredge and Gould's argument was that the theory of allopatric speciation implies that speciation is a rare event that occurs rapidly (in geological time-scales) and that in between speciation events species are relatively stable entities. This, they proposed explained the nature of the fossil record – transitional fossils were rare because the fossil record is too coarse a filter to pick them up and hence the search for 'insensibly graded series' was a wild goose chase.

The premise of Eldredge and Gould's argument was thus the theory of allopatric speciation. This theory was, they said, "for the vast majority of biologists, *the* theory of speciation." (their italics) The reader could not oppose Eldredge and Gould's premise without also opposing the opinion of most of their disciplinary colleagues. Eldredge and Gould then discussed the 'consequences' of the allopatric theory for paleontology. The words 'consequence' and 'implication' are used profusely throughout the section, implying logical progression. Apart from the heading there is "we discuss … the implications of the allopatric theory for interpreting the fossil record"; "As a consequence

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how tight their logical argument is that will decide whether they can convince the readers. See (Latour 1987).

of the allopatric theory …"; "Another consequence of the theory of allopatric processes …"; "These simple consequences of the allopatric theory …" (pp.94-95).

Another tactic that Eldredge and Gould used to imply logical progression was numbered lists. A numbered four part list outlined "the tenets and predictions of allopatric speciation". The "four statements" outlined in this list "entail two important consequences: …", another numbered (two part) list following. The two "important consequences" were that speciation events will not be recorded in the fossil record and that many "breaks in the fossil record are real." (p.96) These lists were presented in contrast to two lists of the same format given earlier in the article, which demonstrated the logical consequences of phyletic gradualism. Four statements summarised the "tenets" of phyletic gradualism, and two "consequences" followed: that the fossil record "should consist of … insensibly graded intermediate forms …" and that breaks in the fossil record were due to imperfections. (p.89)

Both these twin lists were deductive arguments. Eldredge and Gould hoped that their logic was strong enough that if any reader wanted to disagree with the conclusions they would also have had to doubt the premise. They had already made it untenable for paleontologists to accept the deductive conclusions of phyletic gradualism and disagree with the premise of allopatric speciation. The reader was thus compelled to accept the deductive conclusions of allopatric speciation – which are in fact Eldredge and Gould's claims - and discard the premise of phyletic gradualism.

3.3.6: The passive voice.

After a short section in which Eldredge and Gould demonstrated how other paleontologists had been influenced by phyletic gradualism,[115] the authors provided some examples from their own research which they had interpreted using their model. At the beginning they professed to "admit" their own "bias" toward punctuated equilibria and reminded the reader that "the data of paleontology cannot decide which picture is more adequate" but that "punctuated equilibria is more in accord with the process of speciation as understood by modern evolutionists." (pp.98-99)

Before moving on to their detailed examples, however, they stated that: "We could cite any number of reported sequences that fare better under notions of allopatric speciation … This is surely true for all or part of the three warhorses of English [paleontological] literature: …" (p.99). They then summarised these three famous fossil sequences could be reinterpreted with punctuated equilibria. This seems rather contradictory; having admitted their bias, and very magnanimously stated that paleontological data could not discern which model is the better one, in the very next paragraph it was implied that there are copious numbers of fossil series that "fare better" with their model.

Next came eight pages of technical writing in which Eldredge and Gould applied the punctuated equilibria model to some fossil examples from their own research. Here they made a sudden switch to the passive voice. The word 'we' disappeared entirely. There was not a single page in the nineteen previous to this section or the eight that followed where the word 'we' did not appear. Also, the language became very 'scientific'

[115] Discussed earlier – see section 3.3.2.

– dry, precise, full of paleontological jargon. In other words, for the duration of this section in which they introduced the theory of punctuated equilibria Eldredge and Gould switched to the language of an average paleontological article. When Eldredge and Gould discussed the work of other scientists the active voice was used and the language was not technical. In those cases they were not trying to do a 'scientific' analysis of the work but were merely demonstrating the influence of phyletic gradualism. There is thus a sharp contrast the rhetoric they used when discussing others and their own research.

The passive voice is the voice of objectivity, so Eldredge and Gould's use of it when presenting their theory was perhaps not so strange - after all, it is the standard way that scientists communicate. The question is, why did they admit their "bias" before getting technical? Why did they say that "the data … cannot decide"? To answer this question, one must take an overview of the article. The previous nineteen pages were devoted to a very personal, humanistic account of the state of modern paleontology. So, before getting to the technical detail, Eldredge and Gould eased the reader into it, and identify with them by saying, in effect, 'Hey, we're just as biased as anyone and we know that data can be read this way or that way depending on how you look at it, but if we do try and be objective we'll see that punctuated equilibria is really just a better model.'

And indeed this is the conclusion that they came to in this section. Utilising a "*more literal* reading of the fossil record" they found "*rapid* evolutionary events punctuating a history of stasis" (their italics).[116] Their model , they reiterated, "merely represents the application to the fossil record of the dominant theory of speciation in modern evolutionary thought." And, contrary to their earlier statement that fossil data cannot help to decide which model is the better one, they stated that the "consequences" of allopatric speciation (i.e. punctuated equilibria) are "more nearly demonstrated than those of phyletic gradualism by the fossil record of the vast majority of Metazoa." (p.108)

3.3.7: The birth of species selection.

In a section entitled "Some Extrapolations to Macroevolution" (p108-112) Eldredge and Gould suggested some further applications of punctuated equilibria. I do not intend to analyse the rhetoric of this section except to say that it has a similar structure to those sections already discussed. There is an identification of their ideas with those of modern biology, there is a reference to the "unconscious" action of phyletic gradualism, there is a claim that punctuated equilibria explains naturally phenomena that are "anomalous" under phyletic gradualism.

What I do want to note from this section is the discussion of high level ordering which went under the heading "*Trends*". Here they proposed that many of the trends seen over long periods of time in the fossil record that were previously explained by phyletic gradualism could now be explained as some sort of ordering at the species level. They specifically avoided suggesting that it was a new form of selection: "We postulate no

[116] It is important to note here that for Eldredge and Gould the 'stasis' or equilibrium, part of punctuated equilibrium was just as important as the speciation, or punctuation, part. If there were no stasis, then their opponents could have respond that punctuated equilibria was nothing more than a claim that evolution can proceed at differing rates. Their 'stasis' of species thus delimited punctuated equilibria from gradualism by facilitating a different perspective on the nature of species. More on this later.

'new' type of selection.", knowing that to do so would probably estrange all the readers that they had captured so far. What they hoped to achieve was a transfer of authority - to take phenomena that were previously explained in the realm of other sub-disciplines of evolutionary science and place them in the hands of paleontologists (specifically the apparent directional trends of evolution). As we shall see they were to some extent successful in this regard as the vague concept they outlined here became a well known theory, most often called 'species selection'.[117]

3.3.8: Questions.

This article marked the beginning of an often heated debate that has now spanned almost thirty years. The bulk of this thesis follows the course of this debate over time, tracing the trajectory of Eldredge and Gould's theory. A particular scientist's claims live or die not by data *per se*, but by the treatment they receive from other scientists. Thus the first questions to ask are about the status of punctuated equilibria as a theory: Did it become accepted fact?; Did the article achieve its aim of raising the status of paleontology? There are also other questions that inform this thesis that are perhaps not as apparent and are definitely more difficult to answer: Why has this idea (punctuated equilibria) been the subject of debate for so long?; Why have so many seemed to be so riled by it? It appears there are issues arising from punctuated equilibria that are perhaps more contentious than the ordering of paleontological data.

To sum up this analysis, Eldredge and Gould's 1972 article was more than a proposal for a new theory about the nature of paleontological data. Rather they attempted to construct a revolution. Revolutions are about changing status quo power structures in favour of a particular, usually oppressed, group of people, and this is exactly what they aspired to do. They attempted to create solidarity amongst paleontologists, describing how they had, as a group, been subjugated by particular views on the nature of evolution and fossil data. They framed their new theory as a logical consequence of modern biology, urging paleontologists to accept punctuated equilibria and thus join them in a new way of thinking that would raise the status of their discipline. They gave the reader a choice between staying with the status quo, remaining the laughing stock of science and behind the times in terms of biological thought, or allying with them to become a member of an active, dynamic and respected scientific discipline that was at the cutting edge of evolutionary thought.

[117] As we shall also see, their claims in this area became much stronger later on as they tackled the hegemony of natural selection, making assertions that species are indeed valid units of selection in geological time just as organisms are in generational time.

3.4: Citation analysis.

In science the status of any particular theory is determined by how it is treated by other scientists. Thus one way to assess the status of a particular theory is to examine how it has been treated in the scientific literature. A citation analysis is often a good way to achieve such an assessment, especially in cases where one or two key articles have come to symbolise the particular theory. This is the case with punctuated equilibria.[118]

Strictly speaking Eldredge's 1971 'The Allopatric Model and Phylogeny in Paleozoic Invertebrates' marked the beginning of punctuated equilibria. (Eldredge 1971) However it was Eldredge and Gould's "Punctuated Equilibria: An Alternative to Phyletic Gradualism' that posed punctuated equilibria as a challenge to the Modern Synthesis and set the tone for the debate that followed. (Eldredge and Gould 1972) The 1971 article may have been the beginning of punctuated equilibria the theory but the 1972 article marked the beginning of punctuationism the research programme. Indeed more often than not when punctuated equilibria is referred to in scientific literature it is the latter that is cited. Hence the 1972 article was chosen for citation analysis.

3.4.1: The data.

The citation analysis was based on data procured from the *Scientific Citation Index* (SCI)[119]. (Various 1998) The research proceeded as follows:

- The total number of articles citing Eldredge and Gould's 1972 article (henceforth referred to as EG72) was tallied for each year from 1973 to 1997. Results are given in Table 1 and Graph 1.[120]
- Three disciplinary groups were defined - paleontology and geology; biology and other evolutionary sciences; general science – and the citations for each year were classified accordingly. Classification was determined by journal. For instance if an article was published in *American Geologist* it went in the first group, if it was in *Evolution* it went in the second and if it was in *Nature* it went in the third.[121] Results are given in Table 2 and Graph 2.

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[118] This is not the first time a citation analysis has been used to assess the status of punctuated equilibria. The philosopher Michael Ruse has also done so in *Mystery of Mysteries: Is Evolution a Social Construction?* (Ruse 1999) His results will be discussed later.

[119] The SCI is an annual publication that records which scientific articles and books have been cited by which scientific journal articles in that particular year. Cited articles are listed in alphabetical order of the first named authors, under which a list of all articles that cited the particular article in the particular year is provided. For example, let us say that we anted to know who, in 1998, had cited John Smith's 1997 article 'X:', published in journal *Y*. We would then get the SCI for 1998 look up "Smith, John, 1997, … etc" below which we would find a list of all the articles that had cited this Smith's article that year.

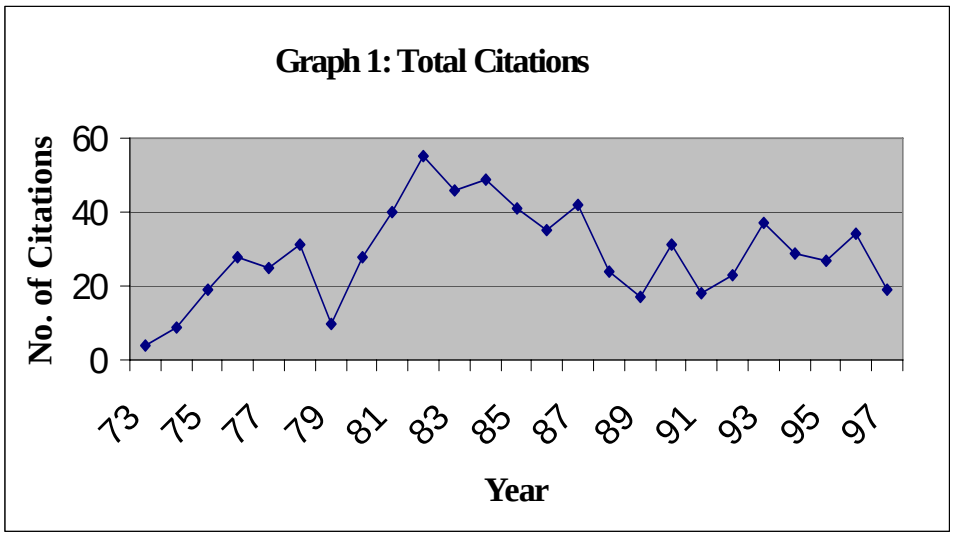
[120] Note that since 1985 each year's edition of the SCI contains citing articles from that year and from late in the previous year. For this category the tally was taken according to actual year that citing article was published. For the other categories, however, citations were recorded according to year of listing in SCI.

[121] This method of classification is possibly misleading in that the journal type does not always reflect the discipline of the author – it is quite common, for example, for a paleontologist to publish in the journal

- Approximately one third of citing articles were randomly chosen.[122] These articles were then reviewed to determine the context of the citation of EG72. Citations were ranked in terms of the following classifications: Strongly positive (SP), Mildly positive (MP); Neutral (N); Mildly Negative (MN); Strongly Negative (SN). Note was also taken as to whether punctuated equilibria was central to the article, either as the subject or the basis of analysis or to whether it was simply mentioned in passing. The results are presented in Tables 3, 4 and 5, and Graphs 3 and 4.

Table 1: No of Citations Per Year

Year	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97
No.	4	9	19	28	25	31	10	28	40	55	46	49	41	35	42	24	17	31	18	23	37	29	27	34	19



As one can see from the graph, the total number of articles citing EG72 rose steadily, peaking in 1982 (with a downturn in 1979). After the mid 1980s the average number of citing articles fell somewhat. However interest remained strong up to the end of the review period.[123]

Nature. Thus, strictly speaking the data represents which types of journal published authors that were interested in punctuated equilibria rather than which types of author were interested in punctuated equilibria. However two facts balance this misgiving. Firstly one can assume a strong correspondence between author and journal. Secondly as a measure of the type of audience interest rather than author-interest the correspondence is even stronger – for example if a biology journal chose to publish an article about punctuated equilibria by a paleontologist then it can be assumed that the editors of the journal believed it would be of interest to their (presumably) biologist subscribers.

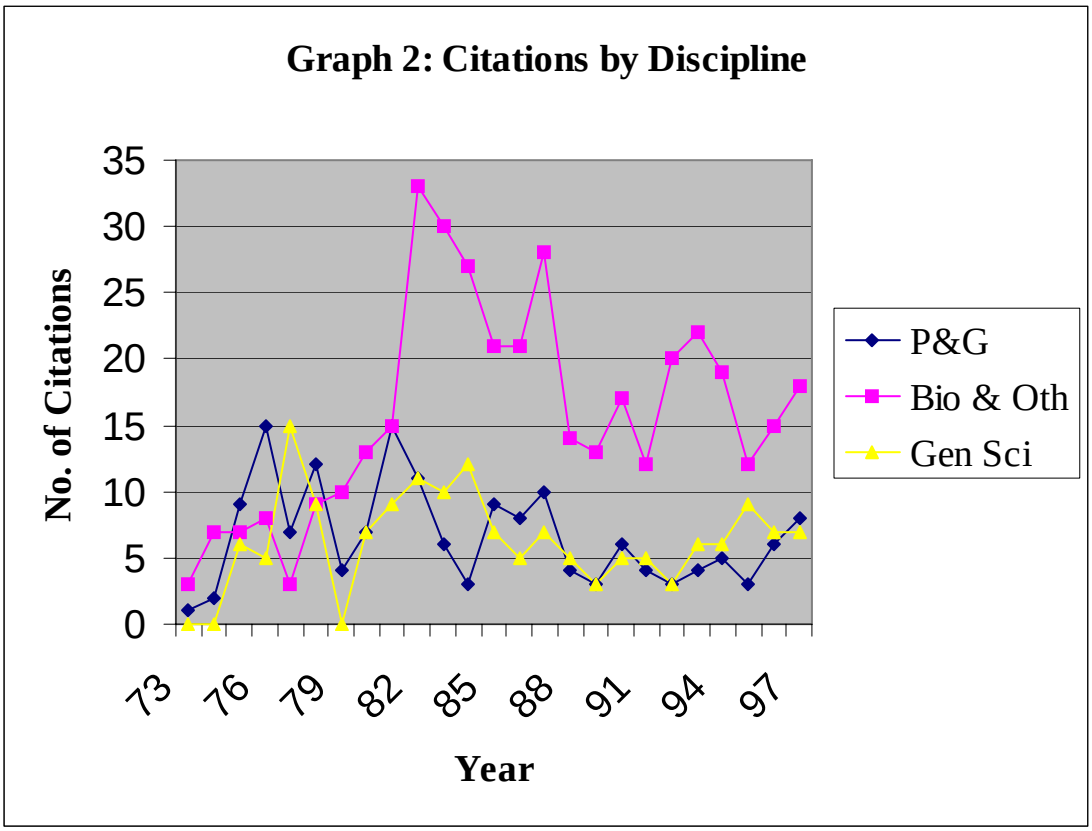
[122] The regime for selection of articles to examine proceeded thus. For 1973 all four articles were examined. For 1974, 1978 and 1981 the first then every third article as listed in the SCI was chosen. For all other years the first then every fourth was chosen. In a few cases the articles chosen by this procedure were unable to be examined either because they were published solely in another language or they were published in journals not held by any accessible library. In those cases the next article listed was chosen.

[123] Ruse believes the totals (of articles citing EG72 and a few other punctuated equilibria articles) are "respectable figures" although he qualifies this by comparing them to the totals for some other famous

Table 2: Citations by Discipline

('Pal&Geo' = Paleontology and Geology; 'Bio&Oth' = Biology and Other Evolutionary Sciences; 'GenSci' = General Science)

Year	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97
Pal&Geo	1	2	9	15	7	12	4	7	15	11	6	3	9	8	10	4	3	6	4	3	4	5	3	6	8
Bio&Oth	3	7	7	8	3	9	10	13	15	33	30	27	21	21	28	14	13	17	12	20	22	19	12	15	18
GenSci	0	0	6	5	15	9	0	7	9	11	10	12	7	5	7	5	3	5	5	3	6	6	9	7	7



As one can see from the graph, interest in punctuated equilibria was fairly constant over the entire period in both the *Paleontology and Geography* and the *General Science* categories. However in the *Biology and Other Evolutionary Sciences* category the number of citations was also fairly constant until the early 1980s, when there was a sudden explosion of interest. After the mid 1980s interest declined until 1990, after which it remained fairly constant.

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publications, such as Macarthur and Wilson's *The Theory of Island Biogeography* (MacArthur and Wilson 1967) which totalled 2600 citations over the period from 1967 to 1995. I must say that I believe this comparison to be unfair, given that the principal market for Macarthur and Wilson's ideas (evolutionary biologists) is much larger than Eldredge and Gould's (paleontologists). Ruse's analysis, and my opinion of it, are discussed more thoroughly below.

Citation Assessments

('No.Rev.' = Number Reviewed; SP = Strongly Positive; MP = Mildly Positive; N = Neutral; MN = Mildly Negative; SN = Strongly Negative)

Table 3: Citation Assessment Totals

(The ratios of reviewed articles to total citations in each group of years are not equal. For instance the 27 articles reviewed in the period 1973-77 represents 32% of the 85 citation whilst the 46 articles reviewed in the period 1978-82 represents 28% of the 184 citations. Comparison between year groups with citation totals is thus not possible with this data. The percentage analyses which do make comparison between year groups meaningful are presented in tables 4 and 5 and graphs 3 and 4. Table 3 is provided for reference only.)

Years	**No. Rev.**	**SP**	**MP**	**N**	**MN**	**SN**
73-77	27	6	14	1	4	2
78-82	46	12	13	8	8	5
83-87	50	14	14	10	7	5
88-92	30	3	14	8	4	1
93-97	35	12	13	9	1	0
Total	188	47	68	36	24	13

Table 4: Citation Assessment Percentages

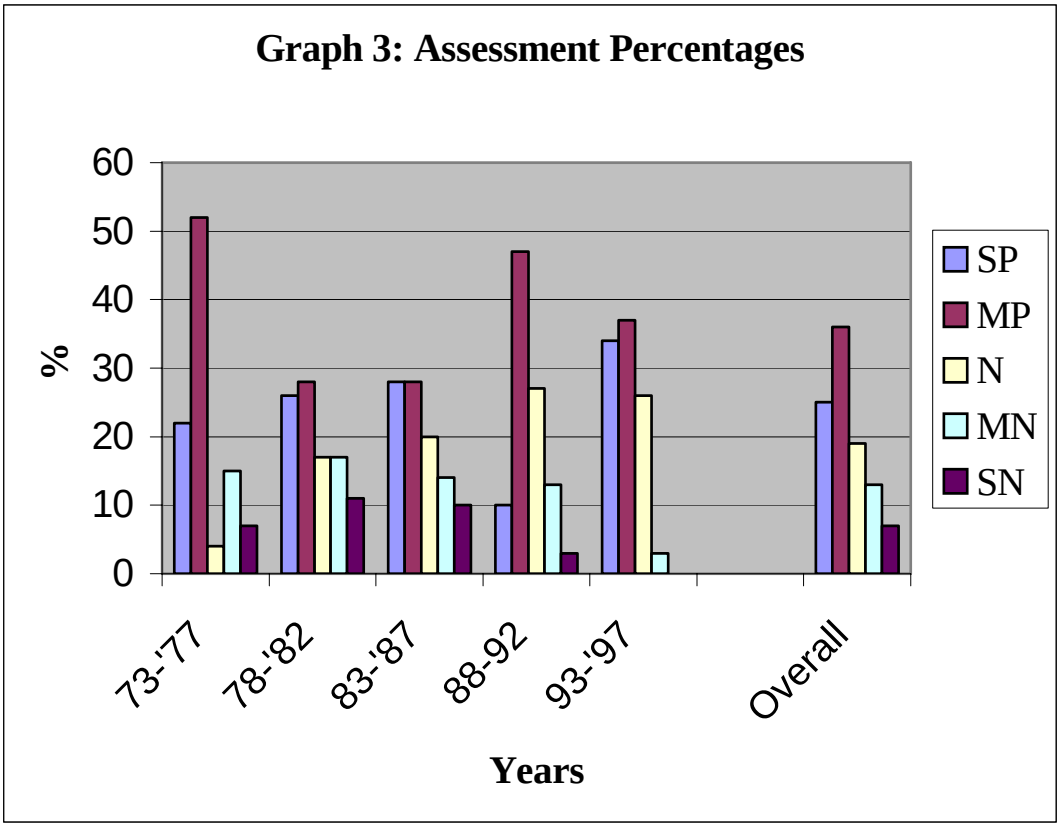
(A bar chart of the data from table 4 is presented in graph 3)

Years	**SP%**	**MP%**	**N%**	**MN%**	**SN%**
73-77	22	52	4	15	7
78-82	26	28	17	17	11
83-87	28	28	20	14	10
88-92	10	47	27	13	3
93-97	34	37	26	3	0
Total	25	36	19	13	7

Table 5: Coarse Grained Assessment Percentages

(A bar chart of the data from table 5 is presented in graph 4)

Years	**Positive%**	**Neutral%**	**Negative%**
73-77	74	4	22
78-82	54	17	28
83-87	56	20	24
88-92	57	27	16
93-97	71	26	4
Total	61	19	20


Graph 3: Assessment Percentages
60
50
40
30
20
10
0
%
SP
MP
N
MN
SN
73-'77
78-'82
83-'87
88-92
93-'97
Overall
Years

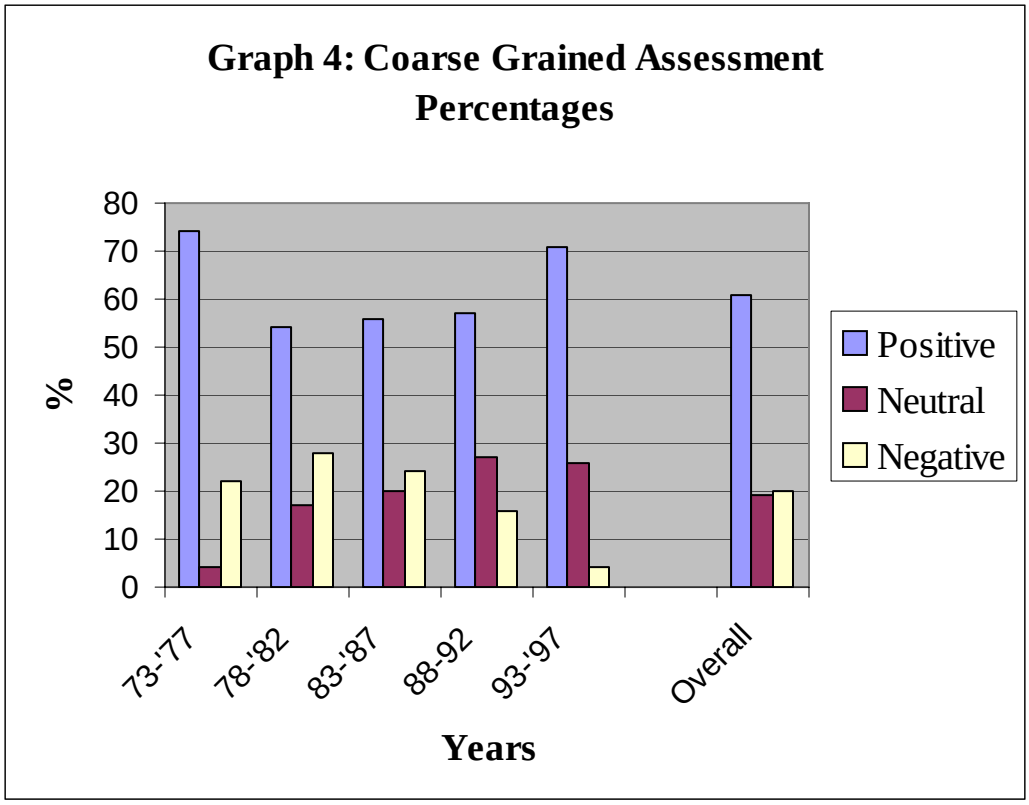

Graph 4: Coarse Grained Assessment Percentages
80
70
60
50
40
30
20
10
0
%
Positive
Neutral
Negative
73-'77
78-'82
83-'87
88-92
93-'97
Overall
Years

Table 6: How Central Was Punctuated Equilibria?

(Articles were considered 'Central' either when punctuated equilibria was the subject of analysis in the paper or it was a crucial aspect of the logical structure of the paper. Comparison is made with the citation assessment totals as there seemed to be a strong correlation between centrality of punctuated equilibria and strength of response.)

	Total	**SP**	**MP**	**N**	**MN**	**SN**
No.	188	47	68	36	24	13
Central	65	39	14	4	2	6
%Central	35%	60%	21%	11%	8%	46%

3.4.2: Some examples to help make sense of the data.

Classifying the citations into pro and con categories was, of course, a somewhat subjective exercise. However every attempt was made to be consistent in the application of classifying criteria. The following examples will give the reader some idea of how classification was achieved. It will also, it is hoped, provide further meaning for the tables and graphs above, in that the reader will have a better idea of what the numbers represent.

Immediately clear from the examples is the fact that punctuated equilibria has been cited a wide-range of contexts. This shows that it is not an overly technical theory, useable only by specialists. Rather it is a theory that is readily understood by anyone with a basic comprehension of evolutionary theory, has interested a wide range of scientists and has a wide range of possible applications.[124] This made it difficult to rank the citations into simple pro and con categories.

Despite the wide range of perspectives encountered it was possible to ascertain certain themes in the citations. Probably the most important of these was that authors who had made punctuated equilibria central to their article (either as the subject of analysis or the basis of further analysis) were generally polarised in their opinion about the value of punctuated equilibria, usually being either resolutely for it or vehemently against it. Another important trend was the *lack* of consistency in the appraisals of punctuated equilibria. Every scientist, it seems, was applying their own personal set of criteria. Argument was as much about which criteria should be applied to the data as about the significance of data itself. Bourdieu's 'anarchic criss-crossing on individual strategies' was apparent.

Papers in which the scientists not only found against punctuated equilibria in their data but also attempted to debase the theory were categorised as ***strongly negative*** (SN). In the first two examples below the scientists implied that punctuated fossil patterns are, as Darwin believed, an artefact of the fossilisation process. In the third example the scientist dissented against the punctuationist's attempts to decouple macroevolution from microevolution and denied that biological and paleontological data were in any way at odds with each other. In the fourth example the scientist reasserted that speciation was an

[124] This is not to say that the theory is simple to test for in fossil data however. Indeed verification and/or refutation of punctuated equilibria in particular sets of data has turned out to be a complex and subtle exercise requiring a long research programme – see Section 6.1.4.

adaptive process, denying the punctuationist assertion that it is essentially random. Punctuated equilibria was the principal focus of two of the four articles discussed. This ratio (half) is representative of the category- that is, nearly half of the authors who were strongly negative about punctuated equilibria had set out to write specifically about it (six of the thirteen articles reviewed, to be precise).

1. (Gingerich 1974) Gingerich explicitly set out to test punctuated equilibria. He detected no examples of either stasis or punctuated speciation events – rather he found that all evolution occurred gradually. He asserted that gaps in the record were, "as Darwin proposed", because of imperfections in the fossil record. Summing up he concluded that the fossil record of *Hyposodus* justified "Darwin's view that species evolved gradually."
2. (Malmgren and Kennet 1981) Micropaleontologists Malmgren and Kennet also set out to test punctuated equilibria. They concluded thus: "The trends of this lineage are one of the clearest examples of gradualism in any group of fossils. It is probably not a coincidence that such a bioseries is so well represented in a sequence containing few breaks in sedimentation, relatively high stratigraphic resolution and abundant microfossil assemblages." In short, they asserted that the reason a punctuated pattern did not appear in their data was that there were no gaps in the record (that is, no breaks in the sedimentation process). The insinuation was thus that punctuated equilibria only appears where the fossil record has been corrupted by fluctuating sedimentation.
3. (Chaline 1987) Punctuated equilibria was not the sole focus of this 70 page article. However Chaline clearly held some strong opinions abut the theory – he particularly disliked the idea of decoupling macroevolution from microevolution. In his conclusion he wrote: "Arvicolid data are in complete disagreement with the punctuated equilibria model. This misleading model, based on an unfortunate confusion between modes and processes, has launched a false controversy, setting biological against paleontological data, when in fact they are complementary."
4. (Nevo 1991) Once again punctuated equilibria was not the sole focus of this 120 page article. Nevo examined recent fossil data and contemporary populations for his study, attempting to gain the widest possible view of the evolution of the mole rats. Regarding punctuated equilibria he was very negative, asserting that all speciation events were gradual and adaptive. For instance: "The *establishment* of a species was certainly *adaptive* and *gradual* in population genetic terms and even *geologically* was not a burst."

The category ***mildly negative*** (MN) was reserved for articles whose authors either: Disputed one or two aspects of punctuated equilibria without attempting to debase the entire program; Found that punctuated equilibria was not applicable to a particular field of study but did not contest its applicability elsewhere; Or thought that punctuated equilibria was an important idea and acknowledged that the punctuationists had made some valid claims but thought that it was not a challenge to neo-Darwinism or the Modern Synthesis. Note that in none of the four examples below was punctuated equilibria the principal focus. This was standard for this category – the authors had not set out to test for punctuated equilibria but rather had found that some aspect of their

research repudiated some aspect of punctuated equilibria (punctuated equilibria was deemed central to only two of the twenty-four 'mildly negative' articles).

1. (Hopsoo and Radinsky 1980) This article was a review of current practice in vertebrate paleontology. As far as punctuated equilibria was concerned, the authors found that it had limited applicability to vertebrate paleontology: "The question of punctuated equilibrium versus phyletic gradualism as the dominant mode of evolution remains controversial, but it seems to us to be an untestable question." This is not a surprising finding as, generally speaking, vertebrate paleontologists do not deal with a sufficient density of fossils to make assertions about rates of change.
2. (Huxley 1981) Huxley stated that he thought punctuated equilibria was an interesting proposal that required "numerous and detailed investigations in uninterrupted sedimentary sequences" However he also asserted that it had always been part of Darwinism. Huxley insisted that Darwin had known about stasis and had predicted that many speciation events would, due to migration, appear as discontinuities in the fossil record. The only difference was that it was now possible to study these phenomena "in a degree of detail that was not accessible at Darwin's time."
3. (Orzack 1985) As of 1985 Orzack was a population geneticist at the Museum of Comparative Zoology, Harvard (Gould, of course, is a stalwart of the same institution). In this paper he did not challenge the authority of the punctuationists to make assertions about macroevolutionary patterns and discussed the phenomenon of stasis from a population genetic perspective. He did, however, dispute their authority to make assertions about the cause of microevolutionary processes. In particular he maintained that stasis could not be caused by genetic homeostasis or developmental constraints: **"**One point of this paper is that there is no reason to believe that stability is an inherent property of development … any stasis found during the history of a species cannot be attributed in general to the force of homeostasis."
4. (Bock 1992) Bock agreed with the punctuationists that reproductive isolation generally occurs allopatrically. However he disputed the idea that it was associated with morphological change. He thus concluded that the punctuationists could not ascribe breaks in the fossil record to speciation and that they would have to identify some other process.

Articles that reported their findings to be inconclusive with respect to punctuated equilibria or cited Eldredge and Gould for some peripheral reason were categorised as ***neutral*** (N). Punctuated equilibria was generally not the sole focus of the articles in this category (regarding the former reason for citation of EG72, the authors had simply looked for punctuated equilibria in their data as an afterthought). Only four of the thirty-six 'neutral' articles classed had punctuated equilibria as the central focus The example below was chosen as both reasons for citing EG72 are present.[125]

[125] It was not necessary to provide several examples as I have for the other categories as there was not as much variation in the types of responses. Indeed it would have been a rather repetitive exercise.

- (Anderson and Evenson 1978) The authors cited Eldredge and Gould for the theory of allopatric speciation.[126] They attempted to do a punctuated equilibria/phyletic gradualism test but found that their data was inconclusive in this respect. Punctuated equilibria was not the sole focus of the article.

The category ***mildly positive*** (MP) accrued the largest tally of articles. A diverse range of scientists displayed an attitude of acceptance to punctuated equilibria so a general attitude of acceptance thus became the qualifying criteria for the category. This was the same for the 'strongly positive' (SP) category - delineation between SP and MP was determined by the extent to which the authors actually used punctuated equilibria or simply by the tone of the article. A large number of examples have been presented in order to illustrate the wide range of perspectives. In them the authors: Professed preference for the allopatric speciation model and equated punctuated equilibria with the application of allopatric speciation to the fossil record (Examples 1&2); Credited Eldredge and Gould with having revitalised paleontology (3&6); Accepted stasis as predominant in the fossil record but were unsure about punctuated speciation (4); Accepted punctuated speciation as predominant in the fossil record but were unsure about stasis (5); Reported punctuated equilibria as a widely accepted macroevolutionary pattern (7); Questioned past opposition to punctuated equilibria in a particular discipline (8); Accepted that macroevolution and microevolution are effectively independent areas of investigation (9).

Punctuated equilibria was the principal focus of only two of the nine articles discussed below (examples 4 and 5). This ratio is representative of the category (punctuated equilibria was deemed central to fourteen of the sixty-eight 'mildly positive' articles). Those articles that focussed specifically on punctuated equilibria and whose authors demonstrated a positive attitude towards it were classed as 'strongly positive'. In examples 4 and 5 the authors focussed on punctuated equilibria and accepted some parts of punctuated equilibria but were unsure about other parts (hence they were classified MP rather than SP).

1. (Cracraft 1974) As its title suggests, this paper provided a summary of prevailing paleontological techniques for interpreting macroevolutionary data. Punctuated equilibria was thus only one of the ideas discussed. In his discussion of punctuated equilibria Cracraft interpreted the theory as allopatric speciation applied to the fossil record and agreed with Eldredge and Gould that such a model was to be preferred over phyletic gradualism. For instance, he wrote that Eldredge and Gould had "discussed in some detail the reasons for preferring an allopatric speciation model rather than one of phyletic gradualism."
2. (Rightmire 1978) Rightmire accepted that Eldredge and Gould were correct in asserting allopatric speciation to be the prevalent form of speciation. He also equated punctuated equilibria with the application of allopatric speciation to the fossil record, as did Cracraft. There was, however, no attempt to actually test punctuated equilibria itself.

[126] They did not, however, equate punctuated equilibria with allopatric speciation as many of the authors in the MP and SP categories did. Rather they simply noted that Eldredge and Gould had listed the reasons for preferring the allopatric model over other models of speciation.

3. (Fagerstrom 1978) Fagerstrom credited Eldredge and Gould with having rejuvenated paleontology: “The decade of the 1970s has witnessed an exciting revival of interest in evolutionary theory among paleontologists due largely to the stimulus provided by Eldredge(1971) and Eldredge and Gould(1972).” His own studies, he said, “provide good support for the punctuated equilibrium model.” However he qualified his findings, conceding that there were some “weaknesses” due to inconclusive data.
4. (Rightmire 1981) This time Rightmire set out to test punctuated equilibria against the human fossil record. He was positive about stasis, stating that *Homo erectus* was an “apparently stable taxon, exhibiting little morphological change throughout most of its long history.” However he was not so sure about the possibility of punctuated (allopatric) speciation, saying that there was a “possibility” that the transition was “spread over a large geographic range.”
5. (Schopf 1981) Schopf wrote that the idea that “speciation is geologically rapid” was established beyond reasonable doubt and that investigations should thus focus on stasis. The rest of the article discussed different possible ways of testing stasis against fossil data.
6. (Bell and Legendre 1987) Bell and Legendre credited punctuated equilibria with having produced a resurgence in paleontology, asserting that it had “stimulated interest” in finding new approaches to the analysis of fossil data. They credited Eldredge and Gould with having inspired their research even though punctuated equilibria was not strictly relevant to it.
7. (Gingerich 1993) This article was a discussion of different approaches to the analysis of fossil data. Punctuated equilibria was thus not the principal focus. However in one section Gingerich chose to use a particular example, “ the transition from *H. grangeri* to *H. aemular*” because it displayed “a ‘punctuated equilibrium’ pattern of stasis and change (Eldredge and Gould 1972).” Earlier in his career Gingerich was a staunch opponent of punctuated equilibria (see Section 2.3.5 and ‘strongly negative’ example 1). By 1993 however, he was ready to admit that punctuated equilibria had been accepted by paleontologists as a common macroevolutionary pattern: “Paleontologists seem generally to agree that evolution takes place gradually on a scale of generations while exhibiting, in many cases, a punctuated equilibria patterns of stasis and change on a scale of geological ages, epochs, periods and eras. Gradual evolution and punctuated evolution are not alternatives but descriptions of evolution on different time scales.”
8. (Norris, Corfield et al. 1996) These micropaleontologists noted that traditionally their colleagues had been opposed to punctuated equilibria because of “gradual morphologic trends” in the data. They questioned this viewpoint, contending that such trends were not necessarily related to speciation processes.
9. (Gilbert, Opitz et al. 1996) Whilst stating that punctuated equilibrium had “remained a controversial theory” these biologists asserted that it had brought to light the inadequacy of microevolution to explain macroevolution, especially “the failure of microevolutionary biology to distinguish between punctuated equilibrium and phyletic gradualism … when applied to macroevolution …”.

Articles in which the authors either accepted punctuated equilibria without misgiving and used it as the basis for some sort of analysis or tested for punctuated

equilibria in their data and found unreservedly in favour of it were categorised as ***strongly positive***. In two of the examples below (3&5) punctuated equilibria was the principal focus of analysis. In a further two examples (1&4) punctuated equilibria was simply assumed to be true and used as the basis for further analysis. In the fifth example (2) punctuated equilibria was not strictly necessary to the logical structure of the argument. However the author credited punctuated equilibria with having created a climate of excitement about evolutionary theorising in paleontology and with having directly inspired her research. In four of the five examples punctuated equilibria was central to the analysis (either as the subject or the basis) which is typical for the SP category (punctuated equilibria was central to thirty-nine of the forty-seven).

1. (Raup 1978) Punctuated equilibria was assumed to be the predominant macroevolutionary pattern and underpinned the logical structure of the paper.
2. (Vrba 1980) Vrba credited punctuated equilibria with having rejuvenated paleontology. It had, she wrote, "elicited a particularly lively response" amongst her colleagues which had resulted in "a revitalization of evolutionary thinking among paleontologists as well as further afield." She reported that as a result of punctuated equilibria many paleontologists were "having a fresh look at what their data could mean." She credited punctuated equilibria with having inspired her research despite the fact that it was not strictly based on the theory
3. (Stidd 1981) Stidd expressed complete agreement with Eldredge and Gould's (reconstructed) history of paleontology. He declared that in his own sub-discipline (paleobotany) practitioners had "been guided by a theory of evolution" that dated back to Darwin but that he wished to "consider the evolution of medullosans from a punctuational perspective along with a few embellishments."
4. (Arnold and Fristrup 1982) Arnold and Fristrup asserted that evolutionary theory was in some way deficient, that its various parts were disarticulated and that "the development of a unified theory of evolution demands the recognition and incorporation of hierarchical structure as a conceptual foundation." They then spent the rest of the article elaborating this theme. The logical structure of their argument was underpinned by the assumption that punctuated equilibria is predominant in the fossil record. They also argued for species selection, saying that species have properties called "branching" and "persistence" which make them candidates for selection. They summed up their argument with the contention that "recursive and hierarchical application of the logic embodied in the theory of natural selection" is "necessary to explain fully the processes of change within the domain of biology."
5. (Elena, Cooper et al. 1996) These population biologists found evidence for punctuated equilibria in their laboratory after observing the changes in an *E. coli* population over 3000 generations. Essentially what they reported seeing was that whilst genetic mutations were common most were not beneficial and died out, leaving the population unchanged. Occasionally however beneficial mutations would occur which would rapidly sweep through the population. They concluded that their "data clearly demonstrate a pattern of punctuated evolution" and suggested that "the selective sweep of beneficial alleles through a population might explain some cases of punctuate evolution in the fossil record." They declared that their experiment demonstrated that "punctuated evolution can occur in bacterial populations as a

consequence of the two most elementary population genetic processes: mutation and natural selection."

3.4.3: Discussion of data.

Over the review period (1973-1997) Eldredge and Gould's 1972 paper was cited 721 times. This is a large number of citations for a single article, especially when the relatively small size of the author's discipline (paleontology) is taken into consideration. The number of citations climbed steadily throughout the 1970s, reaching a peak in the early to mid 1980s. Indeed during the period 1981-1987 the number of annual citations averaged 44. After 1987 the number of annual citations did drop somewhat. However it has remained steady, averaging approximately 26 citations per year and falling below 20 only twice. (See Table 1 and Graph 1). In general, interest in punctuated equilibria has been spread evenly across three broadly defined fields: paleontology and geology; biology and other evolutionary sciences; general science. The only exception to this was the period 1981-1987 when the number of citations in the second listed category increased dramatically. (See Table 2 and Graph 2)

Generally speaking the data and graphs are consistent with a theory that has held a strong interest amongst a broad group of scientists across a long period of time. They are also consistent with one of the major assertions of this thesis - that the controversy over punctuated equilibria is primarily a disciplinary dispute about authority over evolutionary theory. The claim that the primary division is one of discipline is shown by the fact that during punctuated equilibria's most controversial period, the early to mid 1980s, the rise in the total number of annual citations was caused not by an increase in interest from the theory's home discipline (paleontology) or by an across the board increase but by an increase in interest from the discipline that stood to suffer most if its assertions were accepted (biology).

The punctuationists needed controversy in order to have their challenges taken seriously. Whilst mainstream evolutionary scientists ignored them they remained on the fringes of respectable science. To have a controversy one needs to define an opposition - two factions are required for a fight, an argument, a dispute or even a discussion In the early days (the 1970s) the biologists showed little interest in punctuated equilibria. Despite the best efforts of the punctuationists to incite discussion and argument the controversy remained small. In the early 1980s (for several reasons that are discussed in Chapter 5) many more biologists felt compelled to reply to the punctuationists' assertions. The controversy thus had a corresponding increase in size.

A total of 188 articles were chosen for review in the 'citation assessment'.[127] Punctuated equilibria was considered central, as either a crucial part of the basis of or as the subject of analysis, to 65 of these 188 articles (35%). One of the most interesting aspects of this analysis was that the 65 articles in which punctuated equilibria was central were not spread evenly across the assessment categories. Rather they were bunched up at either end, with over 73% occurring in the *strongly positive* or *strongly negative*

[127] This represents just over a quarter of the total number of citations (721).

category.[128] This indicates that those who were most involved in punctuated equilibria (using it, trying to verify it or trying to disprove it) were the ones that felt most strongly about it and thus discussed it in the strongest terms. Those on the periphery of the debate, who mentioned it only in passing, were likely to be more moderate in their appraisal of it. Perhaps this is not so surprising, perhaps it is true of most controversial scientific theories. The point to be made remains the same though – that those scientists who were "in the trenches", who were actually involved in either testing or attempting to use punctuated equilibria, felt that there was a lot at stake in the debate.

Another strong theme emerging from the 'citation assessment' data is that, overall, the response to punctuated equilibria has been extremely positive. In general the positive citations totally outnumber the number of negative responses. Tables 4 and 5 display this trend quite clearly. Punctuated equilibria has, generally speaking, been a well-received theory in evolutionary science. However this is not to say that negative responses to punctuated equilibria have occurred in insignificant numbers. Indeed up until 1987 the negative citations of punctuated equilibria averaged about a quarter of the total. After 1987, however, the number of negative citations gradually decreased, dropping off to almost zero in the late 1990s. This trend, in combination with the fact that the total number of citations has not decreased substantially, is consistent with my assertion that punctuated equilibria's place in evolutionary science, as an important paleontological theory with possible applications in other evolutionary sub-disciplines, has been accepted by all but the most hardened syntheticists (This claim is tendered in Chapter 6).

Close examination of the examples in Section 3.4.2 reveals further evidence that by the 1990s resistance to punctuated equilibria had decreased markedly. If we compare, for instance, the response of (Norris, Corfield et al. 1996) to that of (Malmgren and Kennet 1981) we can see that at least some micropaleontologists had warmed to the theory. In punctuated equilibria's early years it was difficult to find biologists who were positive about the theory but by the 1990s most biological citations were either MP or SP (see (Gilbert, Opitz et al. 1996) and (Elena, Cooper et al. 1996) above for instance). And by the 1990s even one of punctuated equilibria's most staunch early critics, Phillip Gingerich, had conceded that most paleontologists thought punctuated equilibria to be prevalent in the fossil record (compare (Gingerich 1974) to (Gingerich 1993) in above examples).

The citation assessments also revealed evidence that Eldredge and Gould's attempts at Latourian 'black box stacking' seemed to have had the desired effect. Recall that in their 1972 article punctuated equilibria was presented as a logical consequence of Ernst Mayr's theory of allopatric speciation, which itself was presented as an object whose integrity cannot be questioned (a Latourian 'black box'). In the early years of punctuated equilibria (1972 – early 1980s) paleontologists quite routinely cited Eldredge and Gould for allopatric speciation and identified the theory with punctuated equilibria.[129] This association with allopatric speciation added immeasurable strength and prestige to punctuated equilibria in those crucial formative times. However this is not to

[128] There were only 6 punctuated equilibria-was-central articles in the SN category. However this represents almost half the total number of articles in the SN category.

[129] In later years it has been more common for paleontologists to simply refer to the theory of allopatric speciation without citation.

say that the association is purely the result of rhetorical construction – that the association is without scientific merit. Rather Eldredge and Gould were the first paleontologists to attempt to apply allopatric speciation to the fossil record and they deserve recognition for this.

3.4.4: Ruse's citation analysis.

In his book *Mystery of Mysteries: Is Evolution a Social Construction?* the philosopher Michael Ruse presented a citation analysis of some of Stephen Gould's publications, in the context of a chapter about Gould's scientific career ((Ruse 1999), pp.135-152). The aim of the citation analysis was to assess how much influence Gould has had in evolutionary science. His focus was thus slightly different to mine but not surprisingly, considering that Gould has been one of punctuated equilibria's principal defenders, there is considerable overlap in our studies. Hence his findings need to be discussed.

Before beginning this discussion it should be made clear that Ruse displayed a certain personal antagonism towards Gould. On the first page of the chapter, for instance, he produced a little anecdote about a dinner he had with Gould and some others. Apparently the group sung some hymns and Gould's voice was loudest. This was, according to Ruse, symbolic of the wider state of affairs: "But then, no voice is ever louder than that of Steve Gould, which is a major reason why he is the best-known evolutionist in America today." (p.135) In another section Ruse reported that scientists are "frequently scathing" in their comments about Gould, "especially about the way he blends professional and popular". This was especially true, apparently, of those "trying to provide and promote a fully functioning professional evolutionism." Ruse provided anecdotal evidence for this assertion quoting "Laurence Slobodkin, founder of a department of evolution at the State University of New York", who criticised Gould for being too verbose and not using the passive voice in his articles: "Slobodkin … moans that Gould 'violates certain rules of etiquette,' failing to work for 'clarity in the duel sense of expository simplicity and in making oneself transparent so that the empirical world is visible through the text but the peculiarities of the author are invisible'. (Slobodkin 1988)" Ruse then tells us that in Eldredge and Gould's 1972 punctuated equilibria article Gould "added all the flamboyant material about revolutionary change" and "bullied the editor" into accepting it as it was. (p.147) Overall, then, it was Ruse's contention that Gould's scientific ideas are vacuous and that he is only well known because he is outspoken and has the writing skills to back it up.

Ruse's first citation analysis was a comparison of the total citations between two of Gould's scientific publications and two of his 'popular' publications. (Respectively (Gould 1966) and (Gould 1977b) versus (Gould 1977a) and (Gould 1981a)) The detail of this survey is not relevant to our consideration of punctuated equilibria. Suffice to say that the total citations of the scientific publications outweigh the total citations of the popular publications by almost ten to one. Ruse concluded from this that "the professional scientific community makes much more use of Gould's professional writings that it does of his popular writings" and that Gould's popular writings are thus of little influence. (p.148) Frankly this first analysis seems rather absurd. There is no reason why

Gould's popular writings should be cited in scientific articles. They may be about science but they are not scientific articles. Counts of scientific citations for non-scientific articles cannot measure their influence. Gould's books are certainly widely read – most of them make the best seller lists. And within the scientific community it is also certainly true that his 'popular' books are widely read by scientists. How influential they have been on scientists' attitudes about science remains to be seen. Perhaps a survey of how many scientists read Gould's popular books might be more appropriate.

The second citation analysis presented is a simple count of the number of times four punctuationist articles ((Eldredge and Gould 1972), (Gould and Eldredge 1977), (Gould 1980b) and (Gould 1982b)) had been cited between 1970 and 1994, with subtotals given for five year intervals (i.e.70-74, 75-79, …). For the record the 1972 article had a total of 643 citations, the 1977 article 435 citations, the 1980 article 160 citations and the 1982 article 73 citations. Ruse conceded that these "are respectable figures". He qualified this, however, by commenting that "punctuated equilibria theory seems not to be in the category of MacArthur and Wilson's island biogeography or Wilson's sociobiology, and less than Gould's own *Ontogeny and Phylogeny*, for that matter …" (p.150) I do not believe these to be fair comparisons as the principal market for all three of the aforementioned theories/books are much larger than for punctuated equilibria.

The third of Ruse's citation analyses took a closer look at citations of Gould and references to punctuated equilibria in two journals – *Paleobiology* and *Evolution.* Ruse surveyed the period 1975-1994 and found that 35 percent of articles in *Paleobiology* had cited something by Gould but "only 13 percent refer to punctuated equilibria" and 9.8 percent of articles in *Evolution* had cited something by Gould but only 2.1 percent had referred to punctuated equilibria. Ruse also attempted to categorise the articles that referred to punctuated equilibria into positive, negative and neutral. He found that "a mere 4 percent" (of the entire total) of *Paleobiology* articles responded favourably to punctuated equilibria and a "mere 0.4 percent" of *Evolution* articles responded favourably to punctuated equilibria. There is no indication as to what criteria Ruse used for these assessments. Ruse concluded that "punctuated equilibria is not a great professional success" and that "over time, in both *Paleobiology* and *Evolution*, favourable interest in Gould's work … is declining." (p.151)

If Ruse's data is compared with my own it can be seen that the totals for the numbers of citations pretty well match. However agreement ends there. In the second analysis Ruse's comparisons of the total number of citations of punctuated equilibria with theories from other disciplines are, as I have already stated, not valid. In the third analysis we can trust that his total numbers are accurate but he did not comment on how significant these numbers were beyond use of the adjectives 'only' and 'mere' and gave no indication as to what a 'favourable response' actually was. Ruse made no attempt to ascertain how many of the articles were actually using punctuated equilibria in some central way. His personal bias against Gould was apparent throughout the chapter and he was predisposed to a negative appraisal of the professional success of punctuated equilibria.

Chapter 4.

Maintaining the revolution.

(Rhetorical analyses of Eldredge and Gould's 1977, 1986 and 1993 punctuated equilibria articles.)

4.1: 1977 - a new dichotomy.

In 1977 Gould and Eldredge published their second joint article on punctuated equilibria – 'Punctuated equilibria: the tempo and mode of evolution reconsidered' (Gould and Eldredge 1977).[130] The title of the article was perhaps a little misleading, in that they did not really 'reconsider' their position on the 'tempo and mode of evolution' at all - rather, they reinforced the position they had taken five years earlier. Gould and Eldredge gave their paper the structure of a review, providing a survey of recent research into punctuated equilibria.[131] It was not, however, a typical scientific review. Traditionally such articles endeavour to present a summary of contemporary research on important topics without partisan comment, and this cannot be said of Gould and Eldredge's paper. The 1972 article, apart from introducing the theory of punctuated equilibria, had one overriding agenda – to rid paleontology of the 'dogma' of phyletic gradualism and in the process to raise the status of paleontology. The 1977 article continued this campaign.

Between 1972 and 1977 the terrain of the battle between punctuated equilibria and gradualism[132] had, according to Gould and Eldredge, changed considerably. Punctuated equilibria, they declared, had become the orthodox view amongst paleontologists and had also gained some measure of acceptance amongst other evolutionary scientists. The focus of their criticism also changed. In 1972 the opponent was phyletic gradualism itself, which was presented as a reified object that had been influencing the practice of paleontologists to their detriment. The authors did not exclude themselves from the domain of phyletic gradualism's influence, and did not identify particular scientists as having views opposing their own. I suggested that Gould and Eldredge took this tack in order not to unduly upset their colleagues, to identify with them and hence to make their appeal as wide as possible.

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[130] For the rest of this chapter this article will be referred to by page number only.

[131] Superficially the paper is indeed a typical review article: no new ideas were introduced; many paleontologists had been stimulated by the 1972 article to put punctuated equilibria to the test and the bulk of the 1977 article was devoted to a discussion of the pertinent literature; 'species selection' was also discussed, an idea which had been only briefly mentioned in the 1972 article (and at that time did not have a name) but which was now, largely through the work of Steven Stanley, a fully fledged theory (see Section 2.3.7).

[132] In much of the 1977 article, Gould and Eldredge dropped the first word from 'phyletic gradualism' and referred simply to 'gradualism'. I will follow this change of terminology in my analysis.

In the 1977 article, however, they gave their opposition a human face, portraying proponents of phyletic gradualism as the old guard, conservatively holding out against the new order. Particular scientists were explicitly identified in this respect, Gould and Eldredge criticising them on the basis that their views were biased and old-fashioned. It is here that the major shift in the rhetoric of their argument is seen. In 1972, they asserted that phyletic gradualism was influencing the views of paleontologists whereas in 1977 they charged particular paleontologists with holding a bias towards gradualism. One need go no further that the abstract to see an example of this: "We argue that virtually none of the examples brought forward to refute our model can stand as support for phyletic gradualism; many are so weak and ambiguous that they only reflect the persistent *bias for gradualism* still deeply embedded in paleontological thought." (p.115, my italics). In 1972, phyletic gradualism was 'compelling' paleontologists to see data in a particular way. In 1977, there is, instead, a '*bias for gradualism*'.[133]

Gould and Eldredge thus changed the structure of the dichotomy they had created in their initial punctuated equilibria article. In 1972, the dichotomy had paleontologists on one side and (a reified) phyletic gradualism on the other. In 1977, there were punctuationists on one side and gradualists on the other. Gould and Eldredge's opponents were now people. Having established the dichotomy they proceeded to denounce the practice of the proponents of gradualism and to exalt the practice of the proponents of punctuated equilibria.

4.1.1: D & R (debasement and reconstruction).

In section 1.3 the *debasement* and *reconstruction* method of analysing scientific criticism was introduced. To reiterate the postulate is that all scientific criticism takes one or both these forms, where to 'debase' is to invalidate the basis of another scientist's statement/s and to 'reconstruct' is to use another scientists work to one's own end by removing an object or objects (either data or statement/s) from their original context and reformulating them so that they uphold one's own statements.[134] Debasement is thus a challenge to the methodology of an opponent (e.g. a claim that data was not collected properly) and reconstruction is a claim about the interpretation of data, that the data doesn't say what the opponent says it does and that it actually says something else. These two separate modes of criticism are sometimes found in isolation. Often, however, they are used in unison and together they form a strategy that can be summarised by the following statement: 'You didn't do the experiment properly so you're data is no good and despite that the data supports my view and not yours anyway.".

The combined strategy, in which both debasement and reconstruction are employed, was one that Gould and Eldredge use repeatedly in their 1977 article. The combined strategy was also used in the 1972 article but was less significant to the thrust

[133] Gould and Eldredge used the word 'bias' frequently throughout the article. They made use of it's subtle ambiguity, at times using it to mean human prejudice and at other times using it to mean a predisposition of particular kinds of data towards gradualistic conclusions. At times it is impossible to decide which definition was intended, the overall effect being that the two definitions become merged into one, human prejudice becoming associated with the practice of gradualism.

[134] It should be noted that the word debase is here used in a very different sense to its usual definition (to humiliate and degrade).

of the argument. In that case they were more interested in challenging phyletic gradualism as an object than dealing with particular scientists who were proponents of phyletic gradualism - they did not challenge the conclusions of those who had found gradualism in paleontological data, but rather wanted to illustrate how phyletic gradualism had directed paleontologists towards particular conclusions. In 1977, however, they took issue directly with paleontologists who had claimed to have found gradualism in their data, repeatedly criticising the methodology of the 'gradualists', thus invalidating the data collected by them, and claiming that, properly interpreted, the data supports punctuated equilibria and not gradualism anyway.

In science a change in theory in a particular discipline is invariably accompanied by a change in the methodology of the affected discipline. The new theory and methodology generally come as a parcel – usually it is not possible to identify which arrived first. Proponents of the new programme will judge the claims of the old by the new methodology.[135] Gould and Eldredge's 1977 article was no exception. Apart from claiming that the findings of their opponents were biased towards gradualism they also criticised the methods of data collection used by them (debasement). They presented the methodology of their opponents as a narrow mode of analysis in contrast to those who found punctuated equilibria, who were presented as having taken a wider, more complete view. Thus when gradualists collect data they merely collect fossils from one vertical section of strata and only look at one species through that section, whereas the new methodology of punctuated equilibria called for paleontologists to look for fossils across the geographical range of a species and across all species in a fauna. Gould and Eldredge thus claimed that the methodology of the gradualists was linked to the a priori bias that affected their interpretations, in that they 'went looking' for gradualism in the fossil record.

New systems of interpretation also came with a new programme, old and new data alike being reinterpreted according to the new theory.[136] Once again, Gould and Eldredge's 1977 article is no exception. Repeatedly they asserted that their opponents data actually supports punctuated equilibria and not gradualism (reconstruction). A comparison of the treatment of their opponents with that of their allies reveals a certain asymmetry in their approach. Discussion of the literature of their opponents was saturated with commentary. The articles were not just presented and summarised. Rather they were examined, dissected and scrutinised in great detail. By contrast, and perhaps not surprisingly, when they discussed the literature of their allies (i.e. paleontologists who found punctuated equilibria) they summarise the data and findings almost without comment (letting 'the facts speak for themselves'). They thus applied different standards of assessment to other scientists' work depending on whether they were friend or foe. (Not that this is an unusual thing for a scientists – or anyone- to do.)

[135] I will call the union of theory and methodology of a particular view a 'programme' or 'research programme'.

[136] The aggregation of the methodology and systems of interpretation associated with a programme will henceforth be referred to as the *practice* of that programme.

4.1.2: Criticism and affirmation.

In a section titled "Testing Punctuated Equilibria" (pp.120-139) Gould and Eldredge appraised much of the literature spawned by their 1972 article. They went to great lengths to dissect the literature of their opponents, whom they grouped under the name 'gradualists'. Their appraisal of the work of the 'gradualists' had two general themes. First came criticism of the methodology of the gradualists on the grounds that it was too narrow, that their methodology had been superseded by the more holistic methodology of punctuated equilibria. The second criticism was that their opponents interpretations of data were biased by their presupposition that evolution is a gradual process. All in all Gould and Eldredge constructed an image of gradualists as being old-fashioned, conservative stalwarts, who refused to use the new-fangled methods and whose prejudice prevented them from seeing the punctuational light. A detailed examination of the text reveals precisely how they manufactured this image.

There were three sub-sections of criticism of articles claiming to have found gradualism, and hence counter-examples to punctuated equilibria, in paleontological data. The first sub-section was titled '*Invalid claims of gradualism made at the wrong scale*.' It is important to take note that the scale was "wrong", and the claims therefore "invalid", only in the methodology of the new theory and not the old. Gould and Eldredge stated that punctuated equilibria was a "theory about speciation" and must be tested "by considering tempos of change in species and in the process of speciation during geological time." (p121)

Hecht had offered three counter-examples to punctuated equilibria – *Drosophilia* populations in the laboratory, the development of domestic animals and plants, and the polar bear. Gould and Eldredge criticised him for using too small a scale (debasement), then reconstructed his counter-examples so that they instead became affirming cases. In respect of the first two they stated that the rates of change cited by Hecht "would propel a peripheral isolate to full speciation in a geological instant", and in respect of the latter they state that "we could scarcely ask for a better case of rapid, allopatric speciation." (p.121)

They next discussed the use of scales that were too large. Apparently, sequences of species showing unidirectional trends were often cited as proof of phyletic gradualism in the fossil record. Gould and Eldredge stated that of course such trends occur – it is a matter of simple probability. However, they said, these sequences had nothing to do with punctuated equilibria, "for the crucial data lie unreported in the blank spaces between successive species." They then continued on to totally debase the argument: "The remarkable fact that such blatantly inadequate data have been so widely accepted as convincing proof of gradualism only reinforces our claim that gradualism has always rested on prior prejudice rather than paleontological data." (p.122)

They analysed several examples of paleontologists using this kind of macroscopic argument to support gradualism. In each case they criticised the paleontologists for using data too coarse for the test. The reader was thus led to the conclusion that, considering the inconclusive nature of the data, these paleontologists must have found for gradualism because of personal bias. In one case Gould and Eldredge made this point explicitly: "… as a lovely illustration of a priori bias, we cite Drooger's way of telling …". (p.122)

The next sub-section was titled "*Invalid claims of gradualism based on inadequate data.*" Once again it should be noted that the data were 'inadequate' only in the methodology of the new theory. Gould and Eldredge asserted that data collected in the traditional manner was ambiguous, and hence "exclusively gradualistic interpretations can only arise from fervent desire." (p.121). The reader was thus presented with an image of traditionalist stalwarts doing their utmost to find gradualism in paleontological data.

They single out two articles for particular attention in this section. Makurath and Anderson, they wrote, "search valiantly for gradualism" in a Devonian brachiopod lineage. They made two measurements ("spondylium width" and "beak length") on the fossils, which were taken from three different "samples" (strata in the rocks). They then tried two different methods of analysis on the data, neither of which, apparently, showed any gradualism. A third method was applied to part of the data, and they claimed to have found gradual change there. However, said Gould and Eldredge, they wrote off the rest of the data because of sampling errors, "presumably because they [the data] confute the gradualistic interpretation." The debasement of Makurath and Anderson's interpretations was completed with criticism of their methods of data collection: "But what are we to make of such limited and ambiguous information? The authors present only three samples with no control of geographic variation (beyond a dubious agglomeration of distant collections into a single sample)." (p.123)

The second article singled out for criticism, by Klapper and Johnson, came in for similar treatment. Gould and Eldredge described the data used as "scrappy" and stated that "it is hard to see how anyone could derive with confidence the gradualistic interpretation of Fig. 2 – unless one were predisposed to gradualism from the start." (the figure referred to is reproduced from Klapper and Johnson's article) They then "quote verbatim the only cited evidence for gradual transition" in Klapper and Johnson's article, where, apparently, there was only a single specimen that was transitional between the two species they were examining. "No further comment" was Gould and Eldredge's statement after this quote (the irony casts doubt on Klapper and Johnson's interpretation. Gould and Eldredge are implying that the fact that only a single transitional specimen was found is supportive of the hypothesis of rapid peripheral speciation). Klapper and Johnson, who were examining fossils in Nevada also hypothesised that the ancestor of one of the species they were examining was from Australia, as this gave a better fit to their (gradualistic) conclusions. Gould and Eldredge continued their ironic theme – "Our model cannot be falsified by citing the very evidence it predicts, and then choosing gradualistic explanation based on hypothetical ancestors half a world away." They summed up this section by saying that "falsifications of punctuated equilibria … [rely on] … the gradualistic interpretations they claim to test." (p.125)

The third sub-section of criticism, which was by far the longest, was titled "*Potentially valid (but mostly unproven) cases of gradualism.*" (p.125) The fact that the articles discussed in this section came in for the most comprehensive treatment was because they were more difficult to debase and reconstruct, presumably owing to the fact that they were 'potentially valid'. However, considering that the articles were 'mostly unproven', it is not surprising that Gould and Eldredge were able to continue their critical agenda with only a little extra effort.

There were actually three articles that came in for special attention in this sub-section. The first, by Kellog, is an examination of a continuous fossil sequence of a

particular species. Kellog, it seems, found a unidirectional trend toward increased size in the sequence. Gould and Eldredge were very magnanimous in their treatment of Kellog's research. They "applaud this excellent study, with its careful collections and presentation of copious data", "cheerfully admit their own prejudices" but "find it hard" to see Kellog's data as anything but three "periods of stasis interrupted by very rapid rates of change." Gould and Eldredge then demonstrated how Kellog's data could be reconstructed so as to support an interpretation of punctuated equilibria rather than gradualism. (p.127)

Gould and Eldredge also debased Kellog's data via criticism of her methodology. They cast her "preference" for an explanation of the apparent trend of increasing size due to natural selection as dubious in that "she has no control on geographic variation", and hence "successive immigration of normal geographic variants responding to changing local environments." is a more likely explanation Also, her choice of species to analyse was apparently biased in that it was the one where she had noted a change in form over the stratigraphic range. This breaks one of the tenets of the new methodology – "Unbiased tests of gradualism must study all adequately preserved species in faunas, not only the ones that appear to change. Stasis is data."(pp.127-129)

The next article Gould and Eldredge discussed was a study of a particular asexual species by Ozawa. In this case they acknowledge that a gradualistic interpretation is indeed appropriate. However, this does not mean that they allowed this study to be read as a counter-instance to their theory. Instead it was reconstructed to be an 'exception that proves the rule' – an affirming case after all. They complimented Ozawa's study, declaring it "impressive" and professed to be "delighted with these results", asserting that his findings "reflect well upon our model." Ozawa, it seems, had used the correct methodology in his research. Gould and Eldredge "expect counter cases, especially among asexual forms" despite being "like all honest men, anxious to vindicate the substantive predictions of our model". More importantly though, they "hope that punctuated equilibria will serve as an organizing device for reorienting the central study of evolutionary tempo – away from a biased consideration of rare cases towards a fair assessment that can resolve some important issues in evolutionary theory. In this case Ozawa used our model to recognise that adequate tests must include an explicit study of geographic variability." (p.129)

With Gould and Eldredge's treatment, Ozawa's study became an affrimation of the importance of punctuated equilibria. The fact that there was phyletic gradualism in this case, they asserted, did not reflect badly upon their model because it was an asexual lineage, and special rules apply.[137] Also, they said, Ozawa's study demonstrates how the methodology of punctuated equilibria gives a "fair assessment" as opposed to the "biased" appraisals of gradualism. (Note that here the word 'bias' was used to mean a predisposition of data rather than human prejudice.) Later in the article the apparent gradualism of asexual lineages was reconstructed so that they, also, became tractable to a punctuational description.[138]

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[137] I like to call this strategy (excluding cases that refute one's theory on the basis that they require exceptional explanations) *Monster Barring*. The term comes from Imre Lakatos, who used it in the context of mathematical theories. See (Lakatos 1976).

[138] There were so many rhetorical devices present in Gould and Eldredge's articles that it is impossible to discuss them all. Note here, for instance, two that were discussed in the analysis of the 1972 article First

Gould and Eldredge reserved their most comprehensive analysis for Gingerich who had been their "most forceful and cogent critic." Their debasement and reconstruction of his claim to have found gradualism in the *Hyopsodus* lineage takes over five pages (pp.129-134, none of the other critiques ran to more than three pages). Apart from the length, though, their critique of Gingerich was not substantially different. Once again, they used the criteria of the methodology of punctuated equilibria to debase Gingerich's data which was, they wrote, "inadequate in principle to validate gradualism" since it presented "no study of geographic variation." They then proceeded to reconstruct his data in order to show that it actually supported punctuated equilibria (despite the fact that it was "inadequate"). Focus was given to a figure reproduced from Gingerich's article, which he believed demonstrated gradualism. Gould and Eldredge contended that the "dotted guidelines that Gingerich draws about his data are gradualistic interpretations, not literal renderings of the evidence." They stated that a "literal interpretation of …[the data]… would support our model of punctuated equilibria" and offer strong "comfirmation" for the "most important implication of punctuated equilibria", which is species selection.[139] (pp.130-131)

Gould and Eldredge's criticism of the gradualists made quite a contrast with the treatment they gave those that found in favour of punctuated equilibria. In a sub-section titled "*Cases that confirm punctuated equilibria.*" they claimed that punctuated equilibria had become the preferred programme – "most published commentary has been favorable."[140] They did not spend much time analysing the articles of those who found in favour of punctuated equilibria – there are 16 studies cited with minimal comment. in less than three pages. In the few cases where they did comment it was to point out the use of the methodology of punctuated equilibria. For instance: "Fortey has followed both our primary recommendations for a reformulation of method in the study of evolutionary tempos – study all taxa and consider stasis as data."; they cited two articles, one by Johnson and the other by Ager, that apparently stressed the importance of studying geographical variation. They summarised by asking the reader what would happen if everyone followed the methodology of their programme and then provided the answer – "What would happen if paleontologists carried out large-scale, unbiased studies that admitted stasis as data and considered all taxa in a fauna? We cannot avoid the prediction that punctuated equilibria would assume even greater importance." (pp.134-137)

What can one say about the conspicuous lack of comment passed by Gould and Eldredge in this sub-section? What we have is an age-old political strategy in action. The implied assertion is that one's opponents views are partisan but that in the case of one's

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there is the assertion that punctuated equilibria can resolve "important issues in evolutionary theory", with an innate implication that its predecessor cannot. Second there is an identification with the reader – Gould and Eldredge are "honest men" who are "anxious" that their work be well received, whilst at the same time they can grasp the bigger issues of paleontology. The reader is thus led to the conclusions that the authors were advocating without feeling inferior to them.

[139] The above examples of Gould and Eldredge's criticism of their opponents illustrates a generalisation about scientific criticism – that scientific criticism is based on a rejection of the *practice* of opponents.

[140] Continuing from this quote Gould and Eldredge wrote "We are especially pleased that several paleontologists now state with pride and biological confidence a conclusion that had previously been simply embarrassing ("all these years of work and I haven't found any evolution.")." This is a continuation one of the themes introduced in the 1972 article – that, if adopted, the practice of punctuated equilibria would raise the status of paleontology.

own, the facts speak for themselves. Gould and Eldredge's assertion that their opponents views are biased is totally explicit – they tell us so over and over again. They did not feel the need to stress the impartiality of their allies views to the same extent however – it is mostly implicit. Illustrative of this dichotomy was their comment on a paper by MacGillavry – he was "forced by his own observations to abandon a previous commitment to gradualism".(p.136) In this case we see both sides of the dichotomy – MacGillavry was biased toward gradualism, but the 'facts' forced him to change his mind.

4.1.3: The new orthodoxy.

One of the principle themes of Gould and Eldredge's 1972 article was that punctuated equilibria and phyletic gradualism were equally representative of the data of the fossil record, but that punctuated equilibria should be preferred because it was a logical consequence of modern biological theory (specifically Mayr's theory of allopatric speciation). By the time that the 1977 article was produced, however, there was a change in their argument as to why paleontologists should prefer punctuated equilibria; punctuated equilibria, they contended, gives better fit to the data of the fossil record after all.

In the abstract to the article they declared that phyletic gradualism had been an "a priori assertion from the start" and "was never 'seen' in the rocks" They declared that gradualism was an "empirical fallacy" and that paleontology has wasted a century looking for it in the fossil record, describing this as a "sorry situation". Punctuated equilibria was the remedy to this situation because it argued that "*stasis is data*". (pp.115-116) Gould and Eldredge's treatment of those who purported to find gradualism in the fossil record has already been discussed above; debasing the practice of the gradualists, they claimed that their methodology was faulty and their interpretations biased. They reconstructed the data to demonstrate that punctuated equilibria was a better interpretation of the data than gradualism.

Another principle theme of the 1972 article was a call to arms for paleontology. Punctuated equilibria was proclaimed to be the flagship of the revolution against the dictatorship of phyletic gradualism. By 1977, however, Gould and Eldredge had softened this aspect of their presentation of punctuated equilibria. No longer was it revolutionary; instead it was offered as the reasonable line, contrasting with the apparent dogmatism of gradualism. With this change of rhetoric, Gould and Eldredge attempt to construct a new order in paleontology – one where punctuated equilibria was the orthodox view while gradualism was biased and extreme .

In the introductory section of the article ("Gradualism and Stasis" (pp.115-118), for example, they wrote that despite "all the hubbub it engendered, the model of punctuated equilibria is scarcely a revolutionary proposal." They "merely urged" paleontologists to consider the implications of allopatric speciation for their interpretations of the fossil record. In the next section ("What Eldredge and Gould Did (And Did Not) Say" pp.118-120), where they respond to some general criticisms of their 1972 article, they expanded this construction. Some critics had, apparently, accused them of attempting to establish a new dogma. Their response was: "We have never understood

punctuated equilibria in this light. We see it as fundamentally expansive – as a more adequate picture that should extend the range of paleontological activity by valuing types of data previously neglected." Punctuated equilibria is thus presented as a programme of freedom that expands and extends the domain of paleontology. Continuing from the latter statement, they displayed their magnanimity: "We never claimed either that gradualism could not occur in theory, or did not occur in fact …" In the same section, by contrast, they present gradualism as a dictatorial doctrine that constrains paleontology: "Our unhappiness with gradualism arose from *its* status as restrictive dogma. For it has the unhappy property of excluding a priori the very data that might refute it."

Another ancient political strategy was used in their attempt to construct a new orthodoxy around punctuated equilibria– the cultivation of powerful allies. Punctuated equilibria (and thus themselves) was associated with several of the principal actors involved in the construction of the modern synthesis. They subpoenaed George Simpson, quoting him as a supporter: "As Simpson …, with his unfailing insight, recognized in three lines (where others have misunderstood in entire papers), our model tries to "clarify and emphasize ideas nascent in previous studies in the synthetic theory."" (p.117) Sewall Wright was assigned precedence to one of their ideas to and it was suggested that the idea should thus be called "Wrights rule"[141] (pp.139-140) – a lovely example of paying tribute to gain favour. They also garnered the support of Ernst Mayr and claimed him as one of their own (that is, a punctuationist): "… we wish to record our debt to Ernst Mayr who has so forcefully and consistently supported the idea that speciation is the stuff of evolutionary change. … We also note that Mayr, with his notion of the "genetic revolution" …, is the architect of a punctuational view of speciation within modern neo-Darwinism." (p.140)

4.1.4: Making more black boxes.

In 1975 paleontologist Steven Stanley proposed a theory to explain long term trends in evolution ((Stanley 1975b), see Section 2.3.7). Called 'species selection', it was presented as a logical consequence of punctuated equilibria.. Now, when a theory becomes the basis for other theories it strengthens the position of the former immensely. Dissenters cannot dispute the initial theory without also disputing the later ones. The number of people with investments in the initial theory increases, and dissenters are thus faced with increased opposition.[142] Another bonus for the initial theory is that it will be seen as a fruitful research programme. Paleontologists choosing areas to research will be attracted to it, having seen that others have found it to be fertile ground.

Gould and Eldredge were well aware of this and devoted an eight-page section to a discussion of species selection and its potential applications. The title of this section – "Punctuated Equilibria as the Basis for a Theory of Macroevolution: The Speciation

[141] Specifically this idea was that speciation is random re the direction of evolutionary trends within a clade, and was analogous to the microevolutionary tenet that variation is random re the direction of evolutionary trends in a population.

[142] For instance, let us imagine a young paleontologist who disliked Gould and Eldredge's theory. Let us also imagine that this paleontologist was a junior staff member in Stanley's faculty. This paleontologist would be much less likely to undertake a line of research that was in opposition to punctuated equilibria.

Theory" (p.139) – is most illuminating . Punctuated equilibria was gaining momentum and they felt it timely to expand its domain of authority. The fact that species selection was referred to as a "Theory of Macroevolution" was a claim for wider disciplinary control for paleontology in evolutionary biology. They wanted evolutionary biology to be split in half - there would be microevolution and macroevolution, with palaeontology having authority over the latter. A research programme was envisioned whose area of expertise was all the long term trends in evolution, with punctuated equilibria as the core (or "Basis") of the programme.[143]

Stanley, also, clearly saw the potential for punctuated equilibria and species selection to give paleontology a wider field of authority. The article cited by Gould and Eldredge, (Stanley 1975b), apart from being an exposition of species selection, is an argument for the decoupling of macroevolution and microevolution, the premise being that natural selection is not sufficient to render large scale evolutionary trends. Consider this statement, taken from the last paragraph in his article: "[Species selection] … is of great consequence for population biology. Contrary to the 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 turn not to population genetic studies of established species, but to studies of speciation and extinction in order to decipher the higher-level process that governs the general course of evolution." (p.650)

In the first paragraph of their section on species selection Gould and Eldredge's hopes were even more transparent. They related to the reader the excitement they had felt writing the 1972 article, an excitement generated by the potential their theory had to give paleontology a field of research that was both important and theirs alone: "When we were writing our initial paper, no conclusion excited us more than the insight offered by punctuated equilibria for a new interpretation of evolutionary trends." They went on to challenge the authority of population genetics over macroevolution: "… speciation is the raw material of macroevolution, and genetic substitution cannot simply be extrapolated to encompass all events in the history of life." They explicitly stated the format that the decoupling of microevolution and macroevolution would take. Species selection, they contended, follows from two premises – punctuated equilibria and "Wright's rule".[144] Basically, the argument was that species play a role in macroevolution analogous to mutations in microevolution, providing the raw material that is selected at this 'higher' level. For species selection to be truly analogous to natural selection, two conditions must

[143] Gould and Eldredge had proposed a form of species selection in 1972 without explicitly naming it. However, at that stage the concept was rather vague and its role in their quest for wider disciplinary authority was accordingly less significant. In 1972 they had been loathe to call the theory 'species selection' as they did not want to alienate readers by challenging the core Darwinian belief – that natural selection is the prime agent of evolution. In 1977, however, they agreed that the theory should be called 'species selection', but were once again very careful not to challenge the primacy of natural selection: "… we believe that "species selection" represents no more than the operation of natural selection at higher levels. … [we] hope that the relationship of species selection to Darwinian theory will not be misconstrued." In fact, they were so worried about this that later in the article they suggested it be called "speciation theory" despite having stated that they did not object to the name 'species selection'. (pp.139-140) I will refer to the theory by the name 'species selection' in my analysis.

[144] It was in this crucial section of the article that they courted Mayr, Simpson and Wright as allies.

be satisfied: one, that species originate relatively quickly and then remain as stable entities for a geologically relevant period of time (punctuated equilibria); two, that the direction of speciation is random re the direction of any trend ("Wright's rule"). Mutation and natural selection, they argued, "were [previously] regarded as sufficient to render macroevolution; one only had to extrapolate …. But if we [Gould, Eldredge and Stanley] … are right, then speciation interposes itself as an intermediate level between macroevolutionary trends and evolutionary events with populations. … All movement from microevolution to macroevolution must be translated through the level of the species …" And, one might add, all macroevolutionary trends are the property of paleontologists. (pp.139-140)

The remainder of the section was devoted to suggested applications of species selection. For a research programme to be successful, it must prove to be a fertile source of new research ideas for scientists and be able to reconstruct important interpretations from the old programme. It is also extremely advantageous if it can be seen to resolve questions that the previous programme had trouble with. If all these things are achieved it will be seen as encompassing the old programme and having more besides. Gould and Eldredge were well aware of these issues: "… it should perform as all good theories to resolve paradoxes, reinterpret old observations, and synthesize under a common rubric phenomena previously uncoordinated." They suggested that species selection would be a copious source of such applications: "To cite *just* four examples of its potential application: …" (p.140, my italics).

The first of these applications was Stanley's "elegant proposal to resolve, at least in part, the classical paradox of why so inefficient a system as sexual reproduction appears so commonly in nature." The details of this proposal are not important here, but what is important is that this is an example of a paleontologist taking authority over an issue that traditionally was not within the paleontological domain and providing an answer to a question that had remained at best vaguely answered. Gould and Eldredge knew this to be important and made sure the reader knew it too: "[Stanley's proposal is] … an eminently paleobiological input to a traditional neontological dilemma." (p.140)

The second application was to the question of why specialised species are more prone to extinction than ones that are adapted to a generalised way of life. Gould and Eldredge claimed that the traditional explanation for this phenomena, which was couched "in terms of morphological adaptation", was another example of "prior prejudice constraining paleontological thought", going on to show how the question can instead be addressed using species selection.[145] They thus implied that their methodology brushes away the cobwebs of old biases. The third application addressed the phenomenon of adaptive radiation. Once again, traditional interpretations had a "hidden assumption" of gradualism. Punctuated equilibria and species selection, they implied, can give an unbiased assessment. The second and third applications thus had a very similar format to their criticism of the gradualist literature, discussed above, with debasement of the gradualist practice on the basis that it is biased and reconstruction in terms of the new research programme (with the presentation implying objectivity). (pp.140-141)

The fourth application was a nice example of Gould and Eldredge's reconstruction of the gradualist programme in favour of their own. Previously gradualism

[145] The "prejudice" they referred to here is described elsewhere as 'universal adaptationism'. This apparent prejudice is one of the major themes of Gould's writings over the years.

had been admitted in asexual lineages, though not as a counter-example to punctuated equilibria on the basis that asexuality was an exceptional case. With species selection, however, they found they were able reconstruct asexual evolution in terms of their theory. A diagram was given displaying the reconstruction in simple pictorial terms, and a caption provided whose first line told the reader what was achieved: “The resolution of apparent gradualism in asexual lineages to punctuational events at the level of clones.” (Fig. 9, p.142)

At the end of the section Gould and Eldredge indulged in some speculations as to what other biological phenomena and their corresponding traditional interpretations might be reconstructed in terms of punctuated equilibria and species selection. In conclusion, they reaffirmed their main point - that paleontologists, whilst remaining within the Darwinian research programme, had the opportunity to obtain an area of expertise that would be all their own. “Secure in this status [as part of evolutionary biology], paleontologists now need to emphasize that the higher-level study of long times and large clades requires a separate apparatus of evolutionary theory not available in the study of living organisms. We believe that the need to translate micro to macroevolution through the level of speciation guarantees that paleontology shall not be a derivative field, but shall provide essential theory to any complete science of evolution.” (p.144)

4.1.5: Pluralism, Marxism and punctuated equilibria.

The fifth section of the 1977 article is unusual for a scientific article, though perhaps not so unusual for one involving Gould. Entitled “Towards a General Philosophy of Change” it places Gould and Eldredge’s new research programme within the context of a general social and philosophical movement. (pp.145-147) Gould, a most proficient, prolific and popular historian of science, often likes to point out that scientific movements are coupled to the cultural context in which they are produced. However, he still sees external influences as biasing science away from true objectivity. Good (objective) science, he believes, occurs *despite* the influence of culture. Assessing science, under this ideology, is a matter of sorting out the true scientific insights from those that are artefacts of preconceptions.

Specifically Gould and Eldredge wrote that “the punctuational view” was a trend in Western intellectual thinking and they associated this line of thought with Marxist dialectics. (p.146) They denied, however, that the formulation of their theory was influenced by Marxist ideology, though it must be said that it was a rather bold move to even discuss Marxist dialectics on the same page as punctuated equilibria.[146] It is well known that one of the principal agendas of Gould’s writing over the years has been to break down the barriers between science and other disciplines like history and philosophy and the fact that he was willing to apply this to his own work shows the extent to which he believes in the cause.

Gould and Eldredge began the section by contending that “gradualism is a metaphysical stance embedded in the modern history of Western cultures: it is not a high-order empirical observation, induced from the objective study of nature.” As an example,

[146] Indeed the authors of punctuated equilibria were accused at one point of being Marxist conspirators. See Section 2.1.1.

they discussed Darwin who, they wrote, had "cleaved so strongly to gradualism" not because he needed to in scientific terms but because he "translated Victorian society into biology where it need not reside". Gould and Eldredge did not consider this a discredit to Darwin. Rather they only wanted "to point out that even the greatest scientific achievements are rooted in their cultural contexts – and to argue that gradualism was part of the cultural context, not of nature."(p.145)

Punctuational ideologies, they confessed, had also prejudiced science. In some socialist countries Hegel's dialectical philosophy had become official policy. A Soviet pamphlet was quoted that related a punctuational version of Darwinism to the nature of social change, Eldredge and Gould commenting that "[i]t is easy to see the explicit ideology *lurking* behind this general statement about the nature of change. May we not also discern the implicit ideology in our Western preference for gradualism?"[147] (my italics) Considering this official Soviet philosophy, they wrote, it was not surprising that Russian paleontologists had long favored a "punctuational view of speciation". (pp.145-146)

Despite conceding that punctuational ideology had corrupted evolutionary science in some countries and admitting that "one of us learned his Marxism … at his daddy's knee" Gould and Eldredge emphatically denied that their version of punctuationism was ideologically influenced. They debased the work of the Russian paleontologists, stating that their ideas were "devoid … of reference to synthetic evolutionary theory and the allopatric model …", implying that Soviet punctuational biology was a product of prior prejudice. This dogmatism was contrasted with the authors open-mindedness: "[we] emphatically do not assert the "truth" of this alternate metaphysic of punctuational change." Soviet punctuationism was thus discussed only to provide a contrast with Gould and Eldredge's own theory, the implication being that the latter was based on good scientific principles where the former was not.

Ostensibly they pleaded for an open-minded approach to evolutionary science, espousing "pluralism in guiding philosophies." This munificence was contradicted, however, by their claim that gradualism is always underwritten by punctuationism and that punctuationism is therefore the superior philosophy: "We believe that gradual change characterizes some hierarchical levels, even though we may attribute it to punctuation at a lower level … we do believe that the punctuational metaphysic may prove to map tempos of change in our world better and more often than any of its competitors …". On one hand Gould and Eldredge constructed an image of themselves as objective philosophers and undogmatic pluralists. On the other they asserted that gradualism had corrupted evolutionary biology and that it could always be reduced to punctuationism at a different level. This kind of dichotomous argument is typical of scientific discourse, and they simply carried the practice into a philosophical discussion. (p.146)

Gould and Eldredge's characterisation of themselves as pluralists in this article was undermined by the dogmatism they displayed when assessing their human and conceptual rivals. They placed punctuated equilibria within a trend of thought in Western intellectual disciplines, but rather than recognising their own biases and admitting that perhaps their theory has been influenced by that cultural context they instead claimed that their theory was a natural consequence of objective scientific practice and that it was part

[147] The word 'lurking' in this statement is illuminating, insinuating that there is something wrong with ideology influencing views of nature, that it corrupts rather than guides science.

of a trend of thought (punctuationism) that promised to "map tempos of change" in the world "better" than the gradualistic one. Their plea for pluralism is thus seen as a rhetorical device without substance. They attempted to convince the reader of their magnanimity yet they were as unrelenting and opinionated as the gradualists they debased for being biased.[148]

Gould and Eldredge missed the point of pluralistic philosophies - that they are based on respecting the perspectives of others and acknowledging the possibility that there may be more than one 'right answer'. They also missed the point regarding the nature of intellectual movements. As they saw it the relationship between their research programme and the larger movement of punctuational thinking ends with membership. That is, they can see their programme as being part of a whole, but do not believe that the whole informs their programme.

There is a dialectical relationship between a trend and the constituents of that trend (whether those constituents be scientists, musicians, wearers of fashion, etc.) The constituents certainly make up the trend – in fact they do so by definition. However, as the trend evolves it also influences the constituents. A person may join a movement thinking it gives an improved worldview. But, in joining that movement they alter it – they bring new experiences and ideas. These new experiences and ideas will in turn influence those who are already part of the movement, whose modified ideas thus change the nature of the movement, etc. etc. In short, a movement is an evolving dialectical relationship between a worldview that has been formed and informed by a body of ideas and experiences and the people who bring those ideas and experiences and are informed by that worldview. Gould and Eldredge thus overlooked one half of the relationship between the larger movement of punctuationism and their own programme.

4.1.6: Three main themes.

The last section of Gould and Eldredge's 1977 article ("Suggestions For a Program of Research") was a reiteration of the article's major themes. (pp.147-149) Here they espoused a new methodology for paleontology (one that gave a wider and "unbiased

[148] Mary Rosner and Georgia Rhodes ('Science, gender and "The Spandrels of San Marco and the Panglossian paradigm", in (Selzer 1993), pp.82-105) discuss the 'pluralism' of Gould (and co-author Richard Lewontin) in the context of the article 'The Spandrels of San Marco and the Panglossian Paradigm: a critique of the adaptationist programme' (Gould and Lewontin 1979). In writing my analysis of Gould and Eldredge's articles (particularly their professions of pluralism) I was influenced strongly by Rosner and Rhodes discussion. They find that whilst Gould and Lewontin argued for a "plurality of interpretative explanations … in many ways an implicit argument for a feminist approach to science … [the] … method that forwards this argument is by and large patriarchal and thereby mirrors the behaviour Gould and Lewontin explicitly … condemn.". They, say Rosner and Rhodes, "acknowledge the rival [theory], but circumscribe its domain of action so narrowly [by finding it largely unacceptable] that it cannot have importance in the affairs of nature … Gould and Lewontin repeatedly point out the right from the wrong, the "we" from the "they" …" Rosner and Rhodes discussion is framed in the analytical techniques of feminist theory: "Instead of looking for connections between their perspective and that of the … scientists they examine, as some feminists might do in order to reduce antagonisms, Gould and Lewontin set up oppositions between themselves and these "rivals," whom they attack for being unscientific and ridiculous." With a few changes of names and titles, their article could quite easily be read as a discussion of Gould and Eldredge instead of Gould and Lewontin.

assessment" of the tempo of evolution), claimed that species are not merely arbitrary divisions in continuous lineages but are "true, basic and stable evolutionary unit[s]" and asked paleontologists to test species selection (instructing them how to go about doing so). All this was a prelude to the principal objective of the article which was, in a continuation from 1972, a call to arms for paleontologists. Gradualism was a regressive research programme that "yielded much in the way of discouragement and rather little in concrete suggestions for research." and had failed paleontologists because it had "not asserted the theoretical independence of paleobiology". Their research programme, by contrast, offered paleontologists new methodologies and systems of interpretation that would provide "for a fruitful study of evolutionary tempos and modes" and would improve their disciplinary status and independence.

Overall Gould and Eldredge's 1977 article was very much a direct sequel to their 1972 article, addressing the same major themes – the inherent bias in the practice of gradualism, the improved status that comes with the practice of their research programme – with some slight shifts in the form of their rhetoric. Three themes introduced in 1977 were particularly important:

1. The rhetorical shift from criticism of gradualism as a reified object to criticism of scientists who espoused gradualism ('gradualists'). This changed the nature of the dichotomy they had created in 1972. Paleontologists versus phyletic gradualism became punctuationists versus gradualists. These gradualists were marginalised in the text, being characterised as biased, narrow-minded and old-fashioned.
2. Gould and Eldredge moved very quickly to make sure species selection was seen as an integral part of their research programme. They recognised its potential to give paleontologists disciplinary authority over macroevolution and attempted to make it known as a logical consequence of punctuated equilibria.
3. In an unusual strategy for scientists, Gould and Eldredge placed punctuated equilibria within a general intellectual trend, claiming that this trend (punctuational thinking) was a better metaphysic than gradualism when it came to plotting temporal change in both the human and the natural world. In creating this association they ran the risk of hindering acceptance of their research programme.

4.2: 1986 –making history.

In 1986 Eldredge and Gould produced their third joint article on punctuated equilibria: 'Punctuated Equilibrium at the Third Stage' (Gould and Eldredge 1986). It was published in the 'Points of View' section of the journal *Systematic Zoology* and was not a 'scientific' article as such, but rather a discussion of the history of their theory. However it was not what one would call 'straight history' – it did not simply document the trajectory of punctuated equilibria. Rather Eldredge and Gould narrated a story which was offered as evidence for the veracity of punctuated equilibria.

The history they constructed was framed by an apparently "perceptive statement" attributed to the nineteenth century biologist Agassiz: "… when a new doctrine is presented, it must go through three stages. First people say that it isn't true, then that it is against religion, and, in the third stage, that it has long been known." (p.143) The title of the article made it clear that Eldredge and Gould believed punctuated equilibria to have

passed through all three of these stages. However Agassiz's statement was not presented as a framework that they had intended to use to interpret the history of their theory. Rather they tried to convince the reader that the correspondence between Agassiz's statement and the history of punctuated equilibria was foisted upon them: "The latest round of commentary on punctuated equilibrium, … has completed the cycle and demonstrated, in a most *uncanny* way, the wisdom of Agassiz's remark. Punctuated equilibrium – first dismissed as false, then rejected as apostasy against Darwinism, and now depicted as the necessary and logical outcome of what the Modern Synthesis always knew – has evidently come of age." (my italics)

The key word in the quote is 'uncanny', implying that the authors had not intentionally created the accord between Agassiz's statement and their theory but that they had come across it by accident and it had taken them by surprise. They did admit some bias in their presentation: "A documentation of, and partisan perspective on, this sequence, with a discussion of reasons for the transition, may be in order." However this is only a partial admission. The 'fact' that punctuated equilibria followed the sequence was taken for granted - it was only their perspective within that sequence that was acknowledged to be partisan. The choice of the active voice as register completed the rhetorical effect of the article. The active voice facilitates identification with the reader who, in this case, is supposed to read the article, have a laugh with Eldredge and Gould and say 'By golly, Agassiz was spot on! Isn't it funny, the way that people react to new ideas. Anyway, this punctuated equilibrium idea must have a fair bit of merit then.'

Next came their discussion of the 'three stages' of the history of punctuated equilibria. In the first stage punctuated equilibria's opponents "argued, on empirical grounds, that punctuated equilibrium was false". They examined the work of Gingerich, describing his opposition to punctuated equilibria as " most influential." The arguments, apparently, "went back and forth", but in the end, they wrote, "we established two empirical phenomena … the reality of stasis as pervasive and important; and the prevalence of a punctuational pattern underlying many large-scale evolutionary trends …" with the consequence that punctuated equilibria "could no longer simply be dismissed as false" and hence proceeded to the second stage."

This second stage coincided with punctuated equilibria's rise to prominence. For a number of reasons, such as the famous macroevolution conference in Chicago 1980 and the infamous use of punctuated equilibria by creationists, punctuated equilibria came to the notice of 'neontologists'.[149] The neontologists had, they claimed, reacted to punctuated equilibria "as a threat to traditional views labelled either as Darwinism, neo-Darwinism or the Modern Synthesis – Agassiz's second stage." There were, apparently, two main reasons for this rejection of punctuated equilibria – the "good reason" that punctuated equilibria, and particularly stasis, "did not accord with the usual view of how natural selection operated through geological time …" and the "bad reason" that punctuated equilibria was mis identified with saltationism.

It should be noted that I do not agree with Eldredge and Gould's interpretation of this period (punctuated equilibria in the early to mid 1980s). Firstly it was not as if the 'neontologists' simply saw punctuated equilibria as contrary to neo-Darwinism of their own accord. Rather, with articles like 'Is a New and General Theory of Evolution

[149] A 'neontologist' being an evolutionary scientist engaged in the study of extant populations.

Emerging?" (Gould 1980b) Gould constructed the oppositional nature of punctuated equilibria. It should also be remembered that the two principal punctuated equilibria articles of 1972 and 1977 were couched in revolutionary terms. The neontologists could also be excused for mistakenly identifying punctuated equilibria with saltationism, given Gould's attack on natural selection and proposals to reconsider saltationism (Gould 1980b) Also I do not think that most neontologists really believed that punctuated equilibria was necessarily anti-Darwinian. Rather they attempted to interpret it in terms that they could understand – in terms of the tenets of neo-Darwinism. It was not so much punctuated equilibria itself that they saw as against neo-Darwinism but rather some of the conclusions drawn from it, such as the claim that, due to punctuated equilibria, natural selection at the population level now had little importance.

For reasons that the authors "do not fully fathom", around the mid 1980s punctuated equilibria moved into stage three. Identifying two major reasons for this shift – the acceptance of stasis as an important phenomenon and "the potential importance of higher-level selection …". They continued on to provide evidence in the form of quotes from neontologists that punctuated equilibria had indeed passed to the third stage.

Up to this point it was unclear what motivated Eldredge and Gould to write this article beyond, perhaps, wishing to 'set the record straight'. Only in the last few paragraphs did their intentions become apparent. Basically they were constructing acceptance of punctuated equilibria into evolutionary biology – acceptance on their own terms. They asked where the "confusion" of punctuated equilibria with anti-neo-Darwinism had come from when all along punctuated equilibria had been only presented as a simple extension of neo-Darwinism? Answering this rhetorical question themselves they wrote that "confusion, we think, lies in a general failure of microevolutionists to grasp the hierarchical model that does embody the radical content of punctuated equilibrium. Higher-level selection is an addition to, not a refutation of, the conventional Darwinian view of selection upon organisms."[150] With this history Eldredge and Gould constructed the composition of the contemporary field of evolutionary science. It was taken as a given that hierarchy is important and that those who didn't think so simply didn't understand it.

Looking at this article in the context of Bourdieu's struggle for authority it can be seen that Eldredge and Gould were attempting to construct a situation in which punctuated equilibria would become indispensable. Consider the following passage from the second last paragraph, where they lobbied for recognition of the importance of paleontological data: "… Dawkins (1985) maintained that species selection cannot be of much value because it will not explain the complex adaptations of organisms. Of course it cannot but, as Hamlet said, 'there are more things in heaven and earth, Horatio, than are dreamt of in your philosophy.' … patterns in the history of diversity … are as surely attributes of species and their success as complex adaptations are properties of organisms and their triumphs." They hoped that punctuated equilibria would become as essential to macroevolutionary studies as natural selection was to microevolutionary studies.

[150] Note that according to Eldredge and Gould's narrative the "confusion" came from the failure of the microevolutionists to understand rather then the punctuationists to communicate. Perhaps it did not occur to them that their presentation of punctuated equilibria had at times been most confusing, especially for neontologists.

To reiterate, no new 'scientific' data or theory was presented in the article; rather it was an historical construction presented as evidence in a scientific debate. In this story punctuated equilibria was the misunderstood prophet. Rejected initially then exiled for being anti-establishment, punctuated equilibria emerged to be the basis of a renaissance in evolutionary thought, all the stronger for the ordeals it underwent,[151] with the only extant detractors being those that still couldn't understand the message. By analogy, Eldredge and Gould created their own 'religion' in which punctuated equilibria was up there with natural selection and genetics as a key prophet.

4.3: 1993 - declaring victory.

In their fourth joint punctuated equilibria article, 'Punctuated Equilibrium Comes of Age', Gould and Eldredge effectively declared victory in the debate over the importance of punctuated equilibria to evolutionary theory. (Gould and Eldredge 1993) This declaration was made in the first paragraph of the article in very strong terms: "We … believe that primary controversy has ceded to general comprehension, and that punctuated equilibrium has been accepted by most of our colleagues … as a valuable addition to evolutionary theory." The reader was not informed as to exactly who these colleagues actually were, although later in the article it is hinted that the reference was to evolutionary biologists as well as paleontologists ("Many evolutionary theorists … have been persuaded by punctuated equilibrium that maintenance of stability within species must be considered as a major evolutionary problem.") The alleged 'general acceptance' was explicated as comprehension – dissenters, apparently, needed only to understand punctuated equilibria in order to accept it.[152] As is customary for essays in which Gould has had a hand, rhetorically the reader was left with little choice; one could either accept punctuated equilibria and thus be part of the informed, intelligent majority or dissent and be part of an unenlightened minority.

The evidence for punctuated equilibria's 'victory' was based on a reconstruction of the history of the concept and the empirical basis of paleontology. "We claimed no new discovery, but only a novel interpretation for the oldest and most robust of paleontological observations: the geologically instantaneous origination and subsequent stability … of morphospecies", they wrote, thus presenting what was one of the principal inferences of punctuated equilibria as an empirical given. In 1972 they had said that both phyletic gradualism and punctuated equilibria were in accord with the data of paleontology, but that punctuated equilibria should be preferred because it was more in line with contemporary biology. They had reconstructed the history of their theory to make it read as if all they had done was to take fossil data literally from the very start. Initially they asked colleagues to look at the data through their new lens of punctuated equilibria and to see punctuation and stasis. Now they were asking them to look objectively at the data, admit that it consists of punctuation and stasis and to perceive punctuated equilibria as a theory that describes this pattern.

Once accepted, the main consequence of punctuated equilibria was the validation of paleontological data. This was the principal intention of the theory – it was hoped that

[151] A classic example of Latourian 'staging' – see Section 1.2.

[152] This was consistent with Gould and Eldredge's previous punctuated equilibria article of 1986, where they claimed that the main barrier to acceptance of punctuated equilibria was incomprehension.

with punctuated equilibria paleontologists could interpret their data without having to pay tribute to the tenets of microevolution. Gould and Eldredge stressed this point in detail, firstly by pointing out that historically paleontologists were compelled to consider their data unreliable (the imperfection of the fossil record), then by reminding the reader that stasis was not considered worthy of study until punctuated equilibria came along and lastly by reinforcing the link between punctuated equilibria and macroevolutionary interpretations of evolutionary trends: "If punctuated equilibrium has provoked a shift in paradigms for macroevolutionary theory …, the main insight for revision holds that all substantial evolutionary change must be reconceived as higher-level sorting based on differential success of certain kinds of stable species, rather than as progressive transformation within lineages …".

The primary mission of the article was thus to emphasise the importance of this new way of looking at macroevolution for paleontologists: "The main point may be summarized as follows. Most macroevolution must be rendered by asking what kinds of species within a clade did better than others … or what biases in direction of speciation prevailed among species within a clade. Such questions enjoin a very different programme from the traditional 'how did natural selection within a lineage build substantial adaptation during long stretches of time?' The new questions require a direct study of species and their differential success; older queries focused downward upon processes within populations and their extrapolation through time." As evidence that this new way of perceiving paleontological data had taken hold, they present the case of "[highly esteemed biologist George] Williams, who so stoutly defended classical Darwinism against older, invalid and very different forms of group selection, now acknowledges the importance of such clade selection in macroevolution."[153]

The rest of the article had a similar theme to the previous punctuated equilibria articles. Examples of "exciting direct extensions of punctuated equilibrium" were given and evidence of the validity of punctuated equilibria as a macroevolutionary model was presented from other scientists research, such as Stanley, Yang, Cheetham and Fortey. A new demonstration of the scope of punctuated equilibria was also presented in the form of "Tests from living organisms" – that is, from neontological data. This lead into the final section of the article where Gould and Eldredge examined "Difficulties and prospects" facing punctuated equilibria, most of the difficulties, of course, arising from neontological appraisals of punctuated equilibria. This final section addressed objections made by evolutionary biologists to elements of punctuated equilibria. The authors adopted a very even-handed approach to these objections, and the section must be read as a sincere attempt to communicate across the disciplinary divide. This attempt, however, fell short because they failed to relate to the experience of the evolutionary biologists.

Initial "semantic and terminological muddles" had been cleared up, with the result that punctuated equilibria was no longer misidentified with saltationism and stasis was no longer considered to be "rock-hard immobility". The "potential lack of correspondence between biospecies and paleontological morphospecies" had been worrisome, but "available studies", they wrote, had affirmed "the identity of paleontological taxa and true biospecies (Jackson and Cheetham were cited in this respect – see Section 6.1.4.)

[153] Williams was one of the founders of the idea of 'inclusive fitness' which, in concert with the notion that genes are the target of natural selection, banished genetic selection from evolutionary science. See Section 2.3.1.

With these difficulties out of the way Gould and Eldredge felt they could move on to a more "justified" objection raised by evolutionary biologists. One of the major claims of the punctuationists was that most evolutionary (morphological) change occurs at speciation events. Evolutionary biologists had rightly pointed out, they wrote, that "no [biological] validation of such a position has emerged".

Up to this point the authors' attempts at communication were sound. They had recognised that there was a difference between their experience and that of the evolutionary biologists and were thus in a good position to facilitate constructive dialogue. Unfortunately, however, they faltered at the next step, failing to recognise the position of the evolutionary biologists to be as valid as their own. Instead they simply assumed that punctuated equilibria was correct, that morphological change does coincide with speciation and that the evolutionary biologists must be missing something: "The pattern of punctuated equilibrium exists … and is robust. *Eppur non si muove*; but why then? For the association of morphological change with speciation remains as a major pattern in the fossil record." So, whilst it seems that their attempt to communicate with the evolutionary biologists was sincere, by not recognising their opponents experience as fully valid they had set themselves at odds with them.[154]

Gould and Eldredge pointed out what the evolutionary biologists had missed – "a brilliant but neglected suggestion of Futuyama", who had suggested that although "morphological change may accumulate anywhere along the geological trajectory of a species. But unless that change be "locked up" by acquisition of reproductive isolation (that is speciation), it cannot persist or accumulate and must b washed out during the complexity of interdigitation through time among varying populations of a species." The authors believed that "Futuyama's simple yet profound insight may help to heal the remaining rifts and integrate punctuated equilibrium into an evolutionary theory hierarchically enriched in its light."

They may indeed have sincerely wished to "heal the remaining rifts" but once again they had set themselves in opposition to those that they were attempting to communicate with. After telling the evolutionary biologists that their experience of speciation was not valid they continued on to tell them where they were going wrong. This type of response to a difference of opinion (advising the other party where they went wrong or what they can do to rectify the situation) is what human relations expert Robert Bolton calls a "communication spoiler" ((Bolton 1986),pp.15-16) for the basic reason that it does not establish true empathy with the other person/s but rather places oneself in a position of superiority to them.[155]

Gould and Eldredge's assumption that there is consensus amongst evolutionary biologists that morphological change is concentrated at speciation events was ill founded. Indeed when asked about this most of my biological correspondents were sceptical. Professor John Endler of the University of California gave a typical reply:

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[154] This difference in attitudes was subtle but most important. It is the difference between saying 'In my experience I have found X. You say you have found Y. What do you think is causing this discrepancy between our experiences?' to 'I find X, you find Y. Where do you think you have gone wrong?'

[155] Bolton lists twelve "barriers to communication": criticising; name-calling; diagnosing; praising evaluatively; ordering; threatening; moralising; excessive/inappropriate questioning; advising; diverting; logical argument; reassuring. He comments that these responses are "more likely to block conversation, thwart the other person's problem-solving efficiency, and increase the emotional distance between people than other ways of communicating." (p.17)

> "In order to prove that there really is an association one would have to collect some real data (rather than lawyer-style verbal arguments) and ask whether the frequency of morphological change occurs more frequently at the time of speciation more often than chance. This has not been done to my knowledge, just has I have yet to see a plot of rate frequencies. An absurd situation scientifically to argue in the absence of hard data analyzed quantitatively. There is an additional serious problem in that virtually all species are identified morphologically. This ensures that cladogenesis will appear to be associated with morphological change in cladograms because the detection of species is dependent on morphological change. This guarantees that there will be an association between speciation and morphological change! So the whole thing becomes tautological and based upon the human tendency to make categories even when there are gradients. I don't see how we can escape this artifact in the fossil record, unless one were to use some complex multivariate means to describe morphology and use some other criterion to detect speciation. Very difficult if not impossible. One way to calibrate this would be to work with crops and dog breeds which have known speciation times and rates and see if such a thing happens." (Endler 1999a)

A few of the biologists did, however, believed in the possibility of a relationship between speciation and morphological change. Professor Alan Templeton of Washington University, for example, was quite positive about the idea:

> "I think there is no problem in population genetics with the idea that many adaptive changes are concentrated into speciation events and indeed that adaptive changes are active contributors to the process of speciation. … Population genetics in general has been less concerned with stasis, particularly because stasis at the morphological level (the domain of PE as applied to paleontology) does not imply stasis at the gene pool level. … However, speaking for myself and population geneticists such as [Professor X], I certainly feel that most morphological and adaptive changes are indeed concentrated into speciation events." (Templeton 1999)

Gould and Eldredge completed the article with a philosophical flourish, placing punctuated equilibria within an across the board scientific movement: "contemporary

science has massively substituted notions of indeterminacy, historical contingency, chaos and punctuation for previous convictions about gradual, progressive, predictable determinism.". They recognised of themselves that they could equally well be "panderers to fashion" but hoped that they "had a spark of insight about nature's constitution" This conclusion to their article is not intended to give the reader serious reason to doubt Gould and Eldredge's theses. Rather it is identification with the reader via humility – it says 'we (Gould, Eldredge and the reader) are all in the same boat, small and insignificant in the face of history, uncertain where the tides of change will take us.'

4.4: A summary and a question.

The principal motivation for the rhetorical deconstructions presented in this chapter and the previous one was to illuminate the history of punctuated equilibria by precisely identifying the range of strategies employed by Eldredge and Gould in their 'punctuationist' struggle. The articles were all written in a similar style, with the active voice predominant, differing in subtle but important ways. The differences represented the changing strategies employed by the authors as they reacted to evolving circumstances in their professional lives. A quick summary of the objective of each article will provide a good overview of these changes:

- In 1972 they attempted to create a revolution in paleontology. To this end they created a dichotomy with paleontologists on one side and phyletic gradualism on the other. They also sought to establish punctuated equilibria as a logical consequence of allopatric speciation.
- In 1977 they declared that punctuated equilibria was now orthodox rather than revolutionary. There was a concomitant change in the dichotomy they had created in 1972 – paleontologists versus phyletic gradualism became reasonable (punctuationist) paleontologists versus reactionary (gradualist) paleontologists. They also attempted to establish punctuated equilibria as the necessary condition for species selection.
- In 1986 they attempted to maintain the momentum of the punctuationist campaign by providing a history of punctuated equilibria in which the theory triumphed over the prejudices of evolutionary biologists.
- In 1993 they declared that the objectives of the punctuationist campaign had been met.

The question now becomes: how did the rest of the evolutionary science community, from both within and without paleontology, react to Eldredge and Gould's constructions? This question was partially answered by the citation analysis of the 1972 article (see Section 3.4), where it was found that punctuated equilibria had met most of its authors' objectives within paleontology itself but that in other sub-fields of evolutionary science its influence was rather limited. The question will be further addressed in Chapters 5 and 6, which provide a history of punctuated equilibria in the 1980s and 1990s and appraise its contemporary status in evolutionary science via analysis of correspondence with practising scientists and analysis of textbooks from paleontology and evolutionary biology.

Chapter 5

Early 1980s – the peak of the controversy.

5.1: Overview.

In the early 1980s the credibility of neo-Darwinism was under attack from a number of internal and external sources. In no particular temporal or consequential order, these included: a mounting creationist push in the United States that was beginning to have a debilitating effect on the authority of evolutionary science in general society[156]; the impact of the Alvarez mass extinction hypothesis, which challenged adaptationist assumptions about causes of differential success amongst species; the continuing debate over sociobiology, with the added spice of the (extremely right-wing) National Front's (mis)use of quotes from sociobiologists such as Richard Dawkins and Edward Wilson; the *Nature* controversy over museum exhibits; and, last but not least, there was the continuing anti-syntheticist claims of the punctuationists.

These challenges combined to produce an atmosphere of uncertainty in evolutionary science. Many of the fundamental principles of the Modern Synthesis that had been generally accepted since the 1940s became the subject of open scepticism. This was reflected in the social structure of the field, where the centrality of population biology (and population genetics in particular) was widely questioned.[157] Many of the dissenting authors were punctuationists and Gould, in particular, was extremely active in this respect. The book *Dimensions of Darwinism* is a good example. Editor Michael Grene brought together a collection of essays from a wide range of evolutionary scientists, asking them to address contemporary evolutionary issues. Many subjects were discussed in the book but it was punctuationism that was most prominent, with four of the chapters dealing solely with the debate over punctuated equilibria. (Eldredge and Gould 1972)

The early 1980s saw the peak of the controversy over punctuated equilibria. The number of publications citing Eldredge and Gould's 1972 paper was greater at this time than any other, the increase coming not from paleontologists, amongst whom there was no significant rise in interest, but from evolutionary biologists (population geneticists,

[156] Witness the famous Ronald Reagan quote that 'Evolution is, after all, just a theory'.

[157] This movement, questioning the veracity of Darwinism and/or neo-Darwinism, was perhaps most clearly evidenced by the appearance of large number of books purporting to discuss general issues of Darwinism. Through the 1950s, 1960s and most of the 1970s lay guides to Darwinism were essentially intended to introduce readers to the basic principles as accepted by the community of evolutionary scientists. (For example, Maynard Smith's *The Theory of Evolution* (Maynard Smith 1958).) In the early 1980s, however, books accessible to lay readers including essays questioning the basic tenets of neo-Darwinism began to appear.[157] (See for example (Cherfas 1982), (Milkman 1982)and (Grene 1983))

zoologists and ecologists) amongst whom there was a marked rise in interest.[158] On both sides of the disciplinary divide the tone of the articles also became more antagonistic. Punctuationists presented some very challenging statements, via both written publications and oral presentations at conferences, and the syntheticists were moved to respond in numbers, feeling that punctuationism had become a threat to their authority.[159] Most of these syntheticists were evolutionary biologists and particularly population geneticists (who had even more reason to be faithful to the Modern Synthesis, given that it placed the tenets of their discipline as the foundation of all evolutionary explanation).

What follows in this chapter is a description of the trajectory of punctuationism from the early to mid-1980s. However the intention is not to provide an all-encompassing narrative but rather to examine the struggle over punctuated equilibria and to see how it affected evolutionary science. Hence a few of the key events and publications will be examined in detail, in order to more precisely understand the nature of the struggle, whilst other events and publications that were perhaps of equal importance are mentioned only in brief. Essentially the idea of the chapter is to come to terms with the character of the struggle and not to simply recapitulate the trajectory of punctuated equilibria throughout the period.

If it is recalled that a field (in this case evolutionary science) is defined by the actions of the participants, by the criss-crossing individual strategies of the members of the field, then it becomes apparent that the actions of the punctuationists, who were members of the field of evolutionary science, of necessity had an effect on the structure of the field. However even a cursory examination of these interests, of the trajectory of the actors' actions, reveals nothing more than an anarchic struggle. It seems that each actor was simply pursuing their personal agendas, that there was no uniting theme to the struggle. A good case in point is the *Nature* exchange discussed in Section 5.5, where scientists from several disciplines were invited to present their views about another scientist's research into punctuated equilibria. Each scientist held a unique perspective and there was no agreement about what questions were at issue let alone what form answers might take.

This thesis, however, argues that there were two particular interests shared by almost every scientist. The first of these was an interest in establishing one's own research programme as central. The typical scientist hopes that his or her methods of research become universally accepted as valid and important, and are employed by others. In the context of the debate over punctuated equilibria, this interest mostly took the form of a disciplinary dispute (with some exceptions). From this frame of reference the entire punctuationist research programme is seen as a petition for increased authority within the field of evolutionary science. Specifically the authority the punctuationists

[158] See Section 3.4.

[159] There is a need at this point to recall the distinction between the theory of punctuated equilibria and the research programme that is punctuationism. Punctuated equilibria the theory is a set of statements that addresses the practice of paleontology. In this sense it does not concern evolutionary biologists. However it has also been an attractor for a wide range of critiques of neo-Darwinism in general. It is this set of critiques that forms punctuationism. Viewing this along the lines of Imre Lakatos, the theory of punctuated equilibria is the 'hard core' of the research programme and punctuationism, the various criticisms of the Modern Synthesis that are based on punctuated equilibria, is the 'heuristic periphery'. It was punctuationism rather than punctuated equilibria that really came to the forefront of evolutionary science during this time.

aimed for was a general acceptance that the only way to understand macroevolution is via their research programme. The evolutionary biologists, in general, reacted by defending their discipline.

The second interest that almost all scientists hold might be described as 'the pursuit of universal facts'. To be a scientist one has to believe that the phenomena that one studies are amenable to explication by available means. Also, from the 'selfish', career minded point of view, if a scientist comes to be seen to have 'discovered' a 'fact' and if that 'fact' is seen to be of consequence then he or she gains much social capital. (The notion of a 'fact' having much in common with Latour's 'machine', which is defined as an object (either physical or cognitive) that can withstand trials of strength (against sets of data produced by other scientists) and are useable by and useful to other scientists. (Latour 1987))

For many scientists involved in the punctuationist-syntheticist dispute the pursuit of this interest took the form of an attempt to communicate with the opposing discipline. This was because the number one issue was the apparent disarticulation of microevolution and macroevolution (which was of course mirrored by the declaration of independence by the punctuationist paleontologists). The task was thus to forge a new relationship between microevolution and macroevolution, how the data and theory or, in social terms, to show that evolutionary biology and paleontology could be reconciled

In this particular case study the combination of these two interests was the principle factor determining the shape of each participants strategy. On the punctuationist side it has to be said that their 'revolution' was created specifically to cater to these interests. They constructed the anomaly (the disarticulation between macroevolution and microevolution) and attempted to establish their research programme as the only path to reconciliation (between paleontology and biology). The examples discussed below provide cases in point: Gould's challenges; Eldredge's hierarchical scheme (perhaps the most complete thesis in this respect); Vrba's work on species selection or sorting; the empirical studies of Williamson and others.

For the evolutionary biologists it was perhaps more difficult to integrate the two interests as in their case they represented opposing forces. On one had they wanted to defend their territory and on the other they wanted to receive kudos for solving the anomaly. Maynard Smith's contributions are perhaps the best example of this. On one hand he welcomed paleontologists to the 'high table' of evolutionary theorising. On the other he attacked the validity of the punctuationists' assertions. (Maynard Smith 1993)[160] The articles of Stebbins and Ayala are also good examples of biologists facing this dilemma. ((Stebbins and Ayala 1981), (Stebbins 1982) and (Ayala 1982))

[160] This book contains a collection of Maynard Smith's essays, most of which were written in the 1980s.

5.2: Important issues of the time.

5.2.1: The general climate.

In the early 1980s the factors listed above combined to produce an atmosphere of uncertainty about neo-Darwinism. This general climate affected the reception of punctuated equilibria by evolutionary scientists. The tone of the literature suggests that many scientists thought it a bad time to challenge synthetic theory. More pertinent, however, was the relationship each of these challenges had to punctuationism and the roles that particular punctuationists played in the dramas that unfolded around them: the Alvarez hypothesis seemed to support the punctuationist claims for less ubiquitous adaptation and was welcomed by most punctuationists; Gould was a prominent anti-creationism campaigner, as was Eldredge; Steven Rose (a border-line punctuationist) was vocal in the 'fight' against sociobiology and racist biology. A brief summary of each of these challenges and their relationship to punctuationism is provided below.

5.2.2: Creationism

When the authority of a scientific field is subjected to an internal challenge, (i.e. from a disparate scientific discipline) it is possible for the incumbents to redraw the boundaries of their field around the upstart discipline and hence retain much of their original prestige. Such tactics have been used by scientists time and again throughout history. The debate over punctuated equilibria is a classic example. Many syntheticists responded to the punctuationist challenge by attempting to absorb punctuated equilibria into neo-Darwinism, asserting that punctuated evolution was always part of neo-Darwinism with roots to be found in the work of Mayr or Wright or even Darwin himself.

A more dangerous type of challenge to the authority of any scientific field, however, is one that comes from an external source. It is then impossible for the incumbents to redraw the boundaries of their field around the upstarts. The creationist movement of the 1980s was a classic example of just such a challenge, in this case to the authority of evolutionary science. This was no internal jockeying for power within science. Rather the creationists sought to impose a new 'science' upon the American people, to create a new field based on the Bible rather than *The Origin of Species*. In the internal struggle over punctuated equilibria each side attempted to impose the definition of evolution that suited their interests. In the debate over punctuated equilibria, as in all the internal debates in evolutionary science, there was a tacit assumption amongst the scientists that evolution (the phenomenon) exists. The creationists, by contrast, questioned the existence of evolution altogether, their movement thus threatening the very heart of evolutionary science.

The first line of attack for the creationists was the teaching of the evolution story in schools.[161] Over the course of the twentieth century evolutionary scientists had come to have total authority over human origins - it was their story that was taught in the schools. The creationists demanded that school teachers present creationism as an equal to evolution. To achieve this aim they created 'creation science', a story of human origins based on *Genesis*[162] but without any direct reference to the bible. They argued that 'creation science' was not a religious doctrine but rather was equally as scientific as evolutionary science and hence ought to be taught alongside evolution as a competing theory in school science classes.

In the early 1980s the creationists were successful in convincing the legislatures of two states in the USA, Arkansas and Louisiana, to pass 'balanced treatment' laws. These laws decreed that if evolution was to be taught in a school 'balanced treatment' had to be given to 'creation science'. In accordance with the Fourteenth Amendment of the US constitution, which prohibits the teaching of religion in schools, the laws specifically prohibited teachers from making any reference to religious literature. The laws were challenged in the state courts by the American Civil Liberties Union (ACLU) and were ruled to be unconstitutional. The ACLU argued that 'creation science' was not a science at all and that the 'balanced treatment' law was a thinly veiled attempt to introduce religion into school curriculums. The creationists tried to have the decisions overturned by successively higher courts, taking their case all the way to the US Supreme Court in 1987, but were frustrated at each stage.[163]

Now, the focus of an external struggle (such as that between the creationists and the evolutionary scientists) is essentially the same as that of an internal struggle (such as that between the punctuationists and the syntheticists), recalling that in the words of Bourdieu the focus is "the monopoly of scientific *authority*" where authority refers to an "agent's socially recognised capacity to speak and act legitimately … in scientific matters." (Bourdieu 1975). In particular the creationists were attempting to introduce a new definition of valid science. However an external struggle does not have the 'specificity' of an internal struggle. In this case, for instance, the creationists were more interested in selling their 'science' to the American public than to the scientists.

For scientists, and particularly evolutionary scientists, the fact that the creationists managed to convince state legislatures to pass their educational reforms was an issue of serious concern. It undermined their standing in general society by debasing their capacity to speak authoritatively about the history of life. Hence it was not surprising that

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[161] The details that follow were principally procured from three sources, (Gorman 1982), (Larson 1985) and (Numbers 1992).

[162] Specifically 'creation science' was based around four key tenets: that a creator created the world from nothing; that in this creation the creator created distinct kinds of animals and plants that cannot give rise to new kinds; that a world-wide flood caused fossils and other geological phenomena; that the universe was created within the last 10,000 years. The identity of the creator is left undetermined.

[163] The creationists have never given up their campaign to debase scientists' authority over the history of life. In 1994 school teacher John E. Peloza, with the backing of the creationists, brought the Capistrano Unified School District of California to court. In an interesting change of tack he claimed that in requiring him to teach evolution the authority's actions were compelling him to present a religious belief in his classes. The creationists argued that 'evolutionism' was a state supported religion in that it represented a belief in 'secular humanism'. The court ruled against the creationists, citing the 1987 Supreme Court ruling that belief in a divine creator of the universe is a religious belief but that the scientific theory that higher forms of life evolved from lower forms is not.

scientists from all sides of the punctuationist-syntheticist debate were galvanised in defence of evolution. Internal antagonisms were put aside in the attempt to present a united front against the creationists. Indeed at the first ACLU challenge to the validity of the 'balanced treatment' decrees, in Little Rock, Arkansas, amongst the key witnesses were Stephen Gould, philosopher Michael Ruse and evolutionary geneticist Francisco Ayala. (The latter two were (and are) strong critics of punctuated equilibria.)

The ACLU case in Little Rock was based on a deconstruction of the creationist claims that their origin story is scientific rather than religious. That is they debased 'creation science', asserting that the practice of the creationists was not scientific. To do this they had to thwart the creationist attempt to introduce a new definition of valid science and reimpose the definition that suited the status quo. To this end the ACLU presented ten witnesses, five religious leaders from a range of faiths and five scientists. Stephen Gould, representing paleontology, was asked to describe the fossil evidence for evolution generally and also what the fossils had to say about the creationist claim of a world-wide flood. Ayala was asked to provide an account of the genetic evidence for evolution. In both testimonies the intimation was that the evolution story was based on deduction from hard physical evidence where the creation story was based on an attempt to foist *Genesis* upon the evidence, and hence that the evolution is scientific where the 'creation science' is not. Probably the most important witness for the ACLU, however, turned out to be philosopher Michael Ruse. He informed the judge about the Popperian definition of science, the principle criteria of which is that scientific theories must be testable and falsifiable. Armed with this 'authority' Judge William Overton duly ruled that creation science failed to fulfil these criteria and hence was not a science.

The ACLU's argument at the creationist appeals to higher courts did not change in form. In volume however, their case grew substantially. When the case came to the US Supreme Court they presented an 'Amicus Curiae Brief of 72 Nobel Laureates, 17 State Academies of Science, and 7 Other Scientific Organizations, in Support of Appellees.'[164] (Klayman, Slocombe et al. 1986) The gist of the argument presented in the document was that 'Creation Science' is actually religious dogma (the "prohibition [on endorsing particular religious beliefs in schools] cannot be evaded by re-labelling the religious ideas as science."), the bulk of the text thus being devoted to a demonstration of how it was based on *Genesis* and not 'hard' physical facts.

The scientists, via the ACLU, may have been successful in thwarting the creationists in the courts but, as has been shown by many surveys over the years, they have had less success in convincing the general public of the veracity of their evolution story. A recent publication reviewed fifty studies that have surveyed opinions about human origins and the teaching of evolution in public schools. (Bergman 1999) The majority of these surveys found that about 90 % of the public desired that both creation and evolution or creation only be taught in the public schools, that about 90 % of Americans consider themselves creationists of some form, and that about half believe that God created humans in their present form within the past 10,000 years. Bergman, for instance, cited a Gallup poll from 1972 in which 44% of the American public agreed with the statement 'God created man pretty much in his present form … within the past 10,000

[164] An 'Amicus Curiae Brief' is basically a statement to which authorities in a particular field put their name or the name of their institution.

years.' Agreement was inversely related to education and age but still 33% of college graduates agreed with the statement.

Almost every prominent evolutionary scientist has, at one time or another, published an essay debasing creationism. Gould in particular, principally via his monthly column in *Natural History* magazine, has been the strongest campaigner, anti-creationist polemics regularly flowing from his typewriter (see, for instance, (Gould 1983b), (Gould 1987a), (Gould 1987b) and (Gould 1988)). His arguments against creation science have been similar to those used by the ACLU in the courts – he has sought to debase their claims, asserting that their practice does not fulfil the criteria of a valid science. 'Evolution as Fact and Theory' (Gould 1983b) is probably the best exemplar of the deconstruction used by Gould against the creationists' rhetoric. In part, this essay was a reply to the use of quotations from punctuationists (particularly Eldredge and Gould) in creationist literature. The creationists had seized on the apparent disagreement within evolutionary science abut the accuracy of neo-Darwinism as evidence that the phenomenon of evolution was in doubt, misrepresenting the anti-syntheticist sentiments of the punctuationists as anti-evolutionist.[165]

Gould began the essay with a discussion of the difference between the phenomenon of evolution and the theory of evolution. The former, he wrote, is a fact that is beyond dispute while the latter is the set of ideas that attempt to explain and interpret the former and is thus open to debate. He then went on to interpret the significance of the apparent discord about Darwinism within evolutionary science. First he described "debates on fundamental issues of theory as a sign of intellectual health and a source of excitement." He then claimed that the controversy over neo-Darwinism was not a sign of growing doubts about evolution itself but rather was a demonstration that evolutionary theory was "enjoying uncommon vigor." He added a direct reference to the creationist misuse of punctuationist statements: "Creationists pervert and caricature this debate by conveniently neglecting the common conviction that underlies it, and by falsely suggesting that we now doubt the very phenomenon that we are struggling to understand." (pp.254-256)

It is after this clarification, this deconstruction of the creationist's reconstruction of the punctuationists, that we see the crux of Gould's debasement of creation science. Following Michael Ruse he used the Popperian definition of science, asserting that the difference between science and non-science is that scientific theories are falsifiable. The claims of creation science, he declared, are based on religious dogma. They are thus unfalsifiable and hence not scientific. This Popperian criteria has been used by Gould continually over the years to exclude creationism from the domain of authentic science.

Gould recognised that the creationist assault on evolutionary science was symptomatic of a more general discontent within society about science, scientists and their apparent dogmatism. He thus attempted to make an identification with readers who might harbour such discontent and asked them to redirect their negative feelings: "it is

[165] Basically they took anti-neo-Darwinism quotes and presented them as anti-evolution quotes. For example *Life – How Did It Get Here? By Evolution or Creation?* (Anonymous 1985), a publication from the Jehovah's Witnesses, quotes Niles Eldredge from one of his *Natural History* articles: "Niles Eldredge also admitted: 'The pattern we were told to find for the last 120 years does not exist'." (p.21) The author/s alleged that Eldredge was claiming that evolution is not evident in the fossil record. The original context of this quote, as I'm sure the reader has already gathered, was a discussion of punctuation versus gradualism, the claim being that gradualism (not evolution) does not exist in the fossil record.

true that scientists have often been dogmatic and elitist. It is true that we have often allowed the white-coated, advertising image to represent us … We have not fought it adequately because we derive benefits from appearing as a new priesthood. It is also true that faceless and bureaucratic state power intrudes more and more into our lives and removes choices that should belong to individuals and communities. I can understand that school curricula, imposed from above and without local input, might be seen as one more insult on all these grounds. But the culprit is not, and cannot be, evolution or any other facts of the natural world. Identify and fight your legitimate enemies by all means, but we are not among them." (p.261)

In 1982 Eldredge wrote an entire book addressing the creationist problem. (Eldredge 1982) John Maynard Smith, Richard Dawkins and the philosophers Daniel Dennett and Michael Ruse have all campaigned against the threat at different times. However Gould has been the most consistent and articulate anti-creationist activist. Via his monthly *Natural History* essays and best-selling books he has had the greatest access to the public ear of any evolutionary scientist (excepting perhaps Richard Dawkins) and he has repeatedly used that position to reiterate the attestation that creation science is unscientific. One might think that Gould's colleagues would be grateful to him for waging such a campaign, for protecting their interests. And indeed one does get a sense that over the years he has obtained much admiration in this respect. However some of Gould's most radical anti-Darwinian statements were also published in the early 1980s when the creationist controversy was at its peak and as we have seen some of these statements were used by the creationists as ammunition against evolution science. There was thus a degree of resentment amongst evolutionary scientists towards the punctuationists for providing the creationists with such opportunity and a feeling that it was time to close ranks against the creationists rather than challenge the basis of their field.

5.2.3: Mass Extinction

In 1980 the physicist Luis Alvarez, in concert with his geologist son Walter Alvarez, Helen Michel and Frank Asaro, published an article proposing that the mass extinction at the temporal Cretaceous-Tertiary (K/T) boundary was caused by the impact of an extraterrestrial body, such as an asteroid or comet. (Alvarez, Alvarez et al. 1980) Their thesis was based on geological evidence:

1. An extraordinary level of iridium is found at the K/T boundary.
2. Iridium is not a common element on earth but is common on some extraterrestrial bodies, so an increase in the level of iridium at a particular geological strata implies that the earth was struck by an extraterrestrial body at the time the strata was laid.
3. It is extremely improbable that two such major events – a mass extinction and a large asteroid strike – would occur simultaneously by sheer fluke.
4. Hence the two events must be related.

The Alvarez hypothesis received widespread coverage in the popular press, making the front cover of *Time* magazine. It also caused a storm amongst evolutionists,

scientists becoming passionate either in support or denial of the theory. The principal reason for the controversy within evolutionary science, and the reason that it related to punctuated equilibria, was that it questioned the efficacy of Darwinian processes in evolutionary trends. That is, if a large assortment of species were wiped out by a meteor then the causal process at work appears to be luck as much as survival of the fittest. Most paleontologists in fact rejected the theory when it first came out but many of the punctuationists welcomed it, seeing another opportunity to displace natural selection from the center of evolutionary explanation. They also saw in mass extinction an opportunity to question the frequency and importance of gradualism in evolution. (Detailed summaries of the controversy can be found in (Glen 1994) and (Raup 1986))

Gould, for instance, later commented that he supported the Alvarez hypothesis when it first came out "not for the reason of better insight into the evidence" but because mass extinction "simply matched my idiosyncratic preference for rapidity, born of the debate over punctuated equilibrium …" ((Gould 1996), p.152) This 'idiosyncratic' support for the theory did not have a negligible impact. Indeed William Glen observed that Gould provided "welcome and vital encouragement through sustained communication with the Alvarez group early on when only the iridium evidence was at hand and paleontologic backlash against the theory was strong."((Glen 1994), p.49)

The punctuationist links with the mass extinction hypothesis were, epistemologically speaking, rather tenuous. As theories they shared a broad philosophical perspective –both being catastrophic rather then uniformitarian – but technically speaking they had no relationship at all. Socially however the punctuationists outspoken welcoming of the theory assisted in radicalising punctuationism. The punctuationists came to be seen as a group who would support almost any theory that challenged the basic tenets of neo-Darwinism.

5.2.4: Sociobiology in the 1980s.

In the early 1980s the controversy over sociobiology was still raging. Fuel was added to the fire by the (mis-)use of quotes from sociobiologists in the literature of the National Front, an extreme right-wing group from Britain. Almost all the famous names were used- Dawkins, Wilson, Maynard Smith, Trivers, Jensen and Eysenck. For example they used this quote from Dawkins' *The Selfish Gene* in support of their thesis that racism is a natural human trait and should not be suppressed: "Universal love and the welfare of the species as a whole are concepts that simply do not make evolutionary sense." (Brons 1983) During this period the correspondence pages of the journal *Nature* were taken up with letters regarding the issue. The sociobiologists, it seems, were at first reticent to publish disavowals as they felt that to do so would simply gratify the racists, eventually acceding under the pressure of public calls to do so (especially from Steven Rose). However the controversy continued on as Rose and others continued to question the ethics of sociobiology and the underlying reasons as to why it could be used by racist elements to justify their agendas.

It was well known that Gould, Lewontin and other punctuationists were generally antipathetic to sociobiology, that they saw it as providing a scientific underpinning for the domination of the upper strata's of Western society. (see Sections 2.3.1 and 2.3.3.) This

contributed to the perception that punctuationism was somehow a left-wing research programme, that its aims were social rather than scientific. The association of punctuationism with left-wing politics led to the infamous ‘museum debate’ (discussed in Section 2.1.1).

5.2.5: Summary.

The peak of controversy over punctuated equilibria thus coincided with a time of uncertainty in evolutionary science. Because of this many evolutionary scientists were in a defensive frame of mind. And, as we have seen, many of the punctuationists were personally involved in other movements that were undermining the authority of neo-Darwinism. The association of punctuated equilibria with the Alvarez hypothesis and the anti-sociobiology movement lead scientists to associate punctuationism with radicalism and left wing politics. The fact that some punctuationists, particularly Gould, were also strong anti-creationism campaigners did not greatly affect this perception – they were merely pro evolution, not necessarily pro neo-Darwinism. As one might expect, the general air of uncertainty about neo-Darwinism and the association of punctuationism with left-wing radicalism affected the reception of punctuated equilibria. Moving on to the details of the debates over punctuated equilibria in the early to mid 1980s the fact that many of the critics of punctuated equilibria brought a hostile attitude to their evaluation needs to be borne in mind.

5.3: The punctuationists throw down the gauntlet.

5.3.1: Interests.

In the early 1980s the punctuationist ‘revolution’ reached its zenith. Interest in the theory spread amongst paleontologists as more of them began to see it as a source of fruitful research. Many of these scientists found that their empirical studies supported punctuated equilibria. Punctuationists gained confidence from this, increasing the zeal and frequency of their challenges to the tenets of synthetic theory. Their voices, also, began to be heard by a wider audience as more non-paleontologists took notice of their claims. Punctuationist arguments against synthetic theory became considerably more refined. Gould clarified his ideas about the relationship between punctuated equilibria, development constraints and ideas about adaptation. Eldredge extended his discussion of evolutionary hierarchy, culminating in the publication of an entire book on the subject. Elizabeth Vrba, a new entrant into the debate, streamlined the idea of species selection, taking it from a vague notion to a testable theory whilst others, such as Alan Cheetham and P. G. Williamson began long research programmes to test the predictions of the theory.

The punctuationists pursued a diverse range of interests during this time. However, as noted above, there were two interests that bound them, that made them a coherent lobby group rather than a loose collection of people. First was an interest in challenging the centrality of natural selection in evolutionary explanation which, in social

terms, translated into an interest in challenging the authority of population geneticists in evolutionary science. (For the paleontologist punctuationists this also meant promoting paleontology but not all the punctuationists were paleontologists.) The second interest was in establishing some kind of hierarchical schema in evolutionary science. This interest was based on two motivations – first a sincere belief that such an approach to evolution is the only feasible path to a coherent description of evolution and second to gain kudos by re-articulating microevolution and macroevolution.

5.3.2: The 1980 'Macroevolution' conference.

Perhaps the best indicator of the spreading interest in the punctuationist claims came in 1980 when the Chicago Field Museum of Natural History hosted a 'Macroevolution' conference that was attended by almost all the outstanding evolutionary scientists from both biology and paleontology. (The following account was provided by David Raup ((Raup 1999a)) It was an informal conference, organised principally by Raup and Joel Cracraft and was not associated with any particular professional society. Some 60 people were invited, almost all of whom came even though they had to pay their own expenses. Raup put this response down to the fact that the list of invitees was sent with the invitations and faced with such a list no scientist wanted to be the one that was left out.[166] Several science journalists were also invited and were encouraged to publish accounts of the conference since there were no plans to publish formal proceedings.

The aim of the conference was to bring paleontologists and evolutionary biologists together so they could discuss the "simmering differences between macro- and micro-evolutionary thinking." It turned out to be an "exciting" meeting, with the attendees generally displaying strong feelings about their differing views. Indeed Raup described the nature of the debates as "fairly nasty" (ibid) while John Maynard Smith reported "much misunderstanding, confusion and even indignation." However the latter also declared that he found the conference "immensely stimulating" and believed it could "only be good for evolutionary biology that people from different disciplines should meet, talk and, occasionally, listen." (Maynard Smith 1981)

Shortly after the conference science journalist Roger Lewin published his summary of the meeting in the journal *Science.* (Lewin 1980) This article, according to Raup, was a "bombshell" because Lewin "appeared to side with Gould et al against the mainstream population people." Lewin's article coincided with the publication of two rather inflammatory articles by Gould (see Section 5.3.3) and the evolutionary biologists felt compelled to reply – the dissenters could no longer be ignored. Indeed, according to Raup, "the mainstream evolutionary biologists were so mad at Gould (and company) that they hit stasis and [punctuated equilibria] especially hard." (Raup 1999a)

An examination of Lewin's article reveals that he did indeed favour the punctuationist position. He described the meeting as "one of the most important conferences on evolutionary biology for more than thirty years" and identified the main topics of discussion as "the tempo of evolution, the mode of evolutionary change, and the constraints on the physical form of new organisms." (p.883) It is, of course, impossible to

[166] George Simpson was one notable scientists who declined to attend, apparently because he thought the invitation list was too elitist.

judge the accuracy of Lewin's account but it can be said that his characterisation of the most important issues for discussion coincides precisely with the agendas set by the punctuationists, Lewin's characterisation of the Modern Synthesis, for example, was identical with that of the punctuationists. He labelled it as gradualist and pan-adaptationist:

> [The Modern Synthesis] "says the following two things. First, that point mutation within structural genes is the source of variability in organisms and that evolutionary change is the result of a shift in the frequency of genes within a population. The origin of species and the development of trends in groups of species are explained as a consequence of the gradual accumulation of these small genetic differences. The pace of evolutionary change, according to the Modern Synthesis, is slow. Second, the direction of evolutionary change is determined by natural selection working on small variations: the variants that survive are those that are best fitted to their environments. The shape of organisms – their morphology – is therefore viewed in the utilitarian light of adaptationism." (p.883)

In the paragraph following this Lewin discussed what he believed to be the "central question of the Chicago conference", which was "whether the mechanisms underlying microevolution can be extrapolated to explain the phenomena of macroevolution?" Lewin then acted as a medium to supply the answer that the conference came up with (although he qualified his statement): "At the risk of doing violence to the positions of some of the people at the meeting, the answer can be given as a clear, No." Lewin then spent the next page or so explaining why this "No" answer was given – in short because stasis is the general rule for species in the fossil record, not the gradual change postulated by the Modern Synthesis He described an "emerging picture of evolutionary change" coming from the conference – that of punctuated equilibria (pp.883-884).

Next Lewin gave accounts of discussions over species selection and adaptation, once again clearly leaning towards the views of the punctuationists. Consider, for example, his reporting of a comment biologist Ledyard Stebbins made about species selection shortly after the conference:

> " 'You don't have to invoke anything except the natural selection of small differences', Stebbins told *Science* shortly after the Chicago meeting. 'Pretty well everyone agreed on that,' he said, *giving what surely must be a polarised view of what actually transpired*." (my italics)

Lewin, apparently, did not consider the idea that there may have been others at the conference who had a different experience to himself, that some of the evolutionary biologists may have come away thinking that all the fuss about macroevolution was not

an issue for them. He simply assumed that his experience was the only valid one and that the recollections of Stebbins were biased. Probably the best exemplar of Lewin's punctuationist leanings is given by a caption he put to a photograph of Darwin (which, it must be said, seems rather superfluous to the article): "*The emphasis of gradual change of species began with the great man. A shift in emphasis is now due.*" (his italics) With these two short statements Lewin demonstrated his full absorption of the history of evolutionary science as constructed by Eldredge and Gould: 'Darwin was a gradualist' and 'Gradualism is no longer relevant'. (pp.884-886)

Despite Lewin's punctuationist leanings it can be garnered from his account that the debates at the conference were a microcosm of the extensive debates occurring in the literature at the time. The punctuationists argued that developmental constraints restrict the possibilities for adaptive evolution, the syntheticists countering with 'so what, we already knew that', the punctuationists returning "you may know it in principal but you don't use it in practice' and so forth. Whether any progress was made towards a re-articulation of microevolution and macroevolution is questionable. In social terms that the paleontologists and biologists were attempting to communicate with each other, however, as will become more apparent in the following sections, it seems they did not have the means to do so.

5.3.3: The early 1980s: Gould at his most extreme.

In the early 1980s Stephen Gould he produced over ten articles explicitly challenging the Modern Synthesis. All his usual subjects were discussed in one or more of these articles – the history of paleontological thought and paleontology's new found independence, the decoupling of macroevolution from microevolution, the (non)centrality of natural selection and adaptation in evolutionary explanation and developmental constraints. Gould felt the time was ripe to turn up the heat on the syntheticists. He did not expect that all the statements he made at this time would become accepted - he was not in the business of building Latourian 'black boxes'. Rather he sought to create controversy, kicking up a fuss to see what would turn up when the dust settled.

In 1980 Gould published two articles, sequential in an issue of *Paleobiology*, in which he made very strong statements about punctuated equilibria, macroevolution and the status of neo-Darwinism ((Gould 1980c) and (Gould 1980b)). Indeed the period in which he wrote these articles has been characterised by some commentators as 'punctuated equilibria's radical phase'. (see (Ruse 1989), pp.121-124 and (Hoffman 1992) for instance) Gould's two articles, combined with Lewin's account of the macroevolution conference, elicited strong responses from some evolutionary biologists.

The first of the two articles, 'The Promise of Paleobiology as a Nomothetic Evolutionary Discipline' (Gould 1980c), analysed the history of paleontology, looking specifically at explanations for a perceived deficiency of theoretical approaches to evolution, and gave a summary of new practices that were revitalising the discipline. Gould was asked to write such an essay by one of *Paleobiology*'s editors, Thomas Schopf, who felt that despite the changes that had taken place in paleontology over the course of the 1970s most paleontologists were still reticent to theorise about evolution. (p.116)

Gould responded to Schopf's charge by constructing, in an admittedly "partisan statement", a history that polarised paleontological practice into passive and active. The 'passive' practice, of course, was the old methods, based on "an approach to biology that condemns us to imitation and exemplification, rather than encouraging novelty." (pp.96-97) The new 'active' practice was epitomised by paleobiology, with an approach that sought to "fish intelligently in its [biology's] pool of concepts, never fail to ponder how its principles might work differently (or not at all) in geological time, recognize that macroevolution has a theory of bounded independence based upon paleontological data, and, above all, feed the fishes [of biology] with our own special food." (p.108)

The rhetorical structure of the article is typical Gould. His tactic was to inform paleontologists that their practice was deficient whilst avoiding a position of superiority over them, identifying with the reader by disclosing his own fallibility: "I confess that, as a graduate student, I was so taken by the simplicity and unifying power of 'the Modern Synthesis' that I could imagine no higher task for paleontology than the faithful nurturing of its hegemony." (p.103) Rather than blowing his own trumpet he extolled the virtues of a third party, in this case someone that paleontologists could not fail to appreciate, George Simpson: "Simpson's style of science has finally taken root in paleobiology. *Models in Paleobiology* … was purposely constructed as an exemplification of it. This journal is its conscious embodiment." (p.99)[167]

'The Promise of Paleobiology as a Nomothetic Evolutionary Discipline' was aimed specifically at paleontologists. The second article in the sequence ('Is a New and General Theory of Evolution Emerging' (Gould 1980b)) was aimed at scientists across the whole of evolutionary science. It was here that Gould made his most radical claims about the contemporary status of neo-Darwinism and the Modern Synthesis – the proclamations of this article were more ambitious than any that he had made before or has made since.[168] Specifically Gould argued that the Modern Synthesis had "broken down on both of its fundamental claims: extrapolationism … and nearly exclusive reliance on selection leading to adaptation." (p.119) He attempted a comprehensive debasement of the Modern Synthesis, a total destruction of the basis for its explanation of evolution. The evidence for his claims was based on translation and reconstruction. That is, he took statements and findings from other scientists, moved them into a new context and reinterpreted them so as to support his overall argument.[169] His rhetorical stance was that of a third party, a journalist simply reporting the facts. Anticipating the counterpunches that his article would incite he attempted to place himself as a reluctant destroyer, as the messenger who brings ill tidings (and we all know that there's no point blaming the messenger). The article also provided a nice example of Latourian 'stacking' – gathering references and presenting them in a persuasive manner.

The first step in Gould's attempted debasement of the Modern Synthesis was delineation – the target must first be identified before it can be destroyed. He used a statement from the widely respected evolutionary biologist Ernst Mayr for this purpose – the basic gist of which is that syntheticists believe that microevolution is caused by the

[167] The journal was *Paleobiology* whilst *Models in Paleobiology* was the book in which Eldredge and Gould's 1972 article was published.
[168] Indeed, in later years he backed away from some of the statements he made in this article.
[169] Not, of course, that this is an unusual thing for a scientist to do - rather it is quite usual. However Gould provided no new evidence from his own research. The article thus has the format of a scientific review.

gradual accumulation of genetic change in populations under the guidance of natural selection and that macroevolution is the simple extrapolation of this process into geological time. He recounted how, as a student, synthetic theory had "beguiled [him] with its unifying power" but that since then he had "been watching it slowly unravel". He was "reluctant to admit it" but "if Mayr's characterization of the synthetic theory is accurate then that theory, as a general proposition, is effectively dead, despite its persistence as textbook orthodoxy." Gould thus attained the definition of synthetic theory that he wanted without taking personal responsibility for it, avowing that he wasn't happy to see its disintegration. (p.120)

Gould's debasement of synthetic theory was based on a characterisation of it as part of a reductionist tradition. He opposed this with "a concept of hierarchy." Synthetic theory, he stated, "drew most of its direct conclusions from studies of local populations and their immediate adaptations" and then extrapolated "to larger-scale events". He argued for the existence of "two major higher levels: speciation and patterns of macroevolution." that are independent of the processes at the population level. Regarding the level of speciation, it is intriguing that Gould actually rejected allopatric speciation, the very same process that had been the foundation of punctuated equilibria.[170] After providing a short summary of it, he stated that he had "no doubt that many species do originate in this way" but that "it now appears that many, perhaps most, do not."

Allopatric speciation is not crucial to the logical construction of punctuated equilibria. Rather all punctuated equilibria needs is a process of speciation that is fast in geological time and in Gould's eyes, it seems, the faster, and hence the more punctuated, the better. Gould focussed attention on some new "punctuational models of speciation" coming from "several quarters" within evolutionary science (principally citing a group of molecular biologists). These models all had the common attribute of predicting speciation in ecological time and Gould saw in them a chance to sever the last tie of paleontological dependence upon population genetics. Previously he and Eldredge had argued that speciation was a population genetic process that became invisible in geological time. Now he was airing the possibility that even speciation might be independent of population genetics (or at least, the kind of population genetics practiced by syntheticists). He dubbed this division between population genetic processes and speciation the 'Goldschmidt Break', allying himself with the general direction of Goldschmidt's ideas (that speciation is a process that is distinct from ordinary ecological processes) but not the specifics. (pp.121-124)

Gould's argument for the independence of patterns of macroevolution from population genetic processes was essentially a restatement of the punctuationist claims of himself, Eldredge and Stanley. Again he distanced himself from full accountability for the claim of independence by citing Sewall Wright as a precursor, dubbing the partition the 'Wright Break'. He debased the traditional emphasis on gradual transformation as a prejudice caused by a "cultural tie to the controlling Western themes of progress and ranking by intrinsic merit" and re-emphasised the non-adaptive nature of punctuationist claims. (pp.125-128) In this article, then, Gould asserted that the processes of speciation, as well as macroevolution, are independent of synthetic theory. The claim about macroevolution had always been a part of the punctuationist agenda and indeed was the

[170] Later he recanted this claim, and once again asserted that allopatric speciation is the most common form of speciation.

heuristic basis for their attempt to achieve independence of practice. The claim about the processes of speciation, however, was new.

It is difficult to believe that Gould thought his peers would actually accept the new claim. It was based on a small amount of evidence - the fact that some molecular biologists had found some chromosomal rearrangements was not strong evidence for the presence of an overall trend, especially when one is up against a theory as widely accepted as allopatric speciation. So if Gould did not really believe that his peers would accept his claims about speciation the question arises as to what his real motivations were. It seems he had two purposes in mind. First, he wanted to incite reaction, to get the population geneticists and the traditional syntheticists to reply and to get people discussing the independence of macroevolution. Second he wanted to make an ambit claim. This is a well known strategy to both political and military tacticians. One claims more than one really wants, and the opposition is then relieved to give up what was one's actual objective in the first place. Unions, for instance, strike for $50 a week when they want twenty. An army takes over 100 square miles then, in negotiation, agrees to give back eighty. Gould claimed independence from population genetics for speciation and macroevolution, when really he only wanted macroevolution.

The two articles discussed above were not the only ones that Gould published on this subject in the early 1980s – indeed he produced a large number in a short space of time. The time, apparently, was right to hammer the (punctuationist) point home. Each of these publications have similar content and rhetorical structure to the two discussed above so a brief summary of their main points will suffice:

- In 1980 Gould published 'The Evolutionary Biology of Constraint', an attack on the perceived over-emphasis of natural selection and adaptation in neo-Darwinism. (Gould 1980a). The essential argument here was that the design possibilities for evolution are so constrained by limitations in the (genetic) developmental programming of organisms that natural selection is restricted to choosing between a finite number of pathways. This was contrasted with the apparent belief of neo-Darwinists that natural selection can choose any direction in 'design space'. His critique was thus based on a characterisation of neo-Darwinism as a 'Panglossian Programme' (see Section 2.3.3.) He presented empirical evidence from his own work on snails to back up his assertions as well as using the evolution of the human brain as an example.
- In 1981 Gould teamed up with Elizabeth Vrba to publish 'Exaptation – A Missing Term in The Science of Form'. (Gould and Vrba 1982) This was also an attack on the perceived belief of neo-Darwinists in ubiquitous adaptation. The authors argued that a strong division should be made between "features built by natural selection for their current role" and "features that now enhance fitness but were not built for their current role". They proposed that the former still be called adaptations but that the latter should be called exaptations. They alleged that there is a tendency for evolutionists to automatically assume that current utility implies historical genesis[171] and that this is a bias left over from pre-Darwinian creationist days when everyone believed in intelligent design by God. They presented several examples to back up

[171] That is, that a feature of an organism serving a set of functions was built by natural selection for those functions.

their assertions –feathers, for instance, initially evolved for insulation and were later coopted for use in flight.

- In 1982 Gould wrote the introduction for a reprint of Goldschmidt's *The Material Basis of Evolution* (Goldschmidt 1982(1940)). In it he defended Goldschmidt's general attitude to the study of evolution without endorsing the specific details of Goldschmidt's research programme. Gould characterised this general attitude as a belief that "change in hereditary type can only occur within the possibilities and limitations set by the normal process of development" and that "animals must be viewed as organic wholes and that our organic world of divergent *Baupläne* cannot be rendered by models of strict continuity in transformation" Here, then, Gould garnered a most unusual ally, given that Goldschmidt and his 'hopeful monsters' had long been a laughing stock of evolutionary science. He characterised the affinity between his views and Goldschmidt's as "the idea that evolution works through a hierarchy of distinct levels with important independent properties".[172]
- In 1982 Gould wrote a chapter for the book *Darwin Up To Date* ('Punctuated Equilibrium – A Different Way of Seeing', (Cherfas 1982), pp.26-30). The book was aimed at a general audience, although a degree of scientific literacy was required to read it. He used the opportunity to provide a general, lay account of the punctuationist position, particularly emphasising the emergence of a hierarchical perspective on evolution.
- In the same year Gould produced a chapter for the book *Perspectives on Evolution* ('The Meaning of Evolution and Its Role in Validating a Hierarchical Approach to Macroevolution'(Milkman 1982), pp.83-104). This essay was more technical than the paper published in *Darwin Up To Date* but was otherwise very similar. Once again the importance of hierarchy was emphasised as he argued, for instance, that "the key issue of the independence of macroevolution is not whether species selection operates in all trends (it does not), but whether the necessity, under punctuated equilibrium, of regarding trends as a higher-level sorting of species implies a new level in a hierarchy of evolutionary explanation."
- Again in 1982, Gould provided a chapter for the book *Evolution and Development* ('Change in Developmental Timing as a Mechanism of Macroevolution') (Bonner 1982), pp.333-346), reiterating his views about the importance of developmental constraints for evolutionary science.
- A paper Gould published in the journal *Science* contained another statement of the generalised punctuationist perspective on evolution – that natural selection and adaptation are not the be all and end all of evolution and that a hierarchical perspective is needed. ('Darwinism and the Expansion of Evolutionary Theory', (Gould 1982a)). He claimed that Darwin himself was more pluralistic than the current syntheticists, and that a hierarchical evolutionary theory would capture his

[172] The introduction to *The Material Basis for Evolution* was not the first time he had allied himself with Goldschmidt although it is the most well known. Five years earlier in one of his regular *Natural History* essays he had done the same. (Gould 1977c) This time, however his proposals were even more radical – he did not reject the 'hopeful monsters'! He discussed some experiments of Goldschmidt that had "demonstrated that large final differences reflected the action of one or a few "rate genes" acting early in growth." and stated that "if we do not invoke discontinuous change by small alterations in rates of development, I do not see how most evolutionary transitions can be accomplished at all." (p.30)

vision better than neo-Darwinism. Darwin was thus pronounced an ally of punctuationism.

- With the exception of 'Is a New and More General Theory of Evolution Emerging' the most influential piece Gould wrote during this time was 'The Hardening of the Modern Synthesis', a twenty page article published in the book *Dimensions of Darwinism* ((Grene 1983), pp.71-92). This contained a complete version of Gould's version of the history of the Modern Synthesis. He argued that the Modern Synthesis of the 1930s was tolerant to a wide range of ideas about the processes that cause evolution but that come the 1940s the synthesis 'hardened' to an exclusive focus on natural selection leading to adaptation, a focus that apparently dominated the field for ensuing thirty years or so (presumably until he and his fellow punctuationists came along). Gould justified his assertion by referring to the works of Dobzhansky, Wright and Simpson, following their literature over the relevant period with particular focus upon the differences between earlier and later editions of their major texts, attempting to demonstrate that over time they had an increasing commitment to strict adaptationism.

Over the years Gould has covered a wide range of subject matter in his evolutionary writings. However there is one theme that runs through all - an interest in breaking the hegemony of natural selection and adaptation in evolutionary science. For Gould, breaking adaptation's hegemony would achieve twin objectives. First, via punctuated equilibria, it would increase the authority of his own discipline, paleontology. Second, and probably closer to Gould's heart, it would break down what Gould sees as evolutionary dogma.[173] Gould appears to feel a moral responsibility to challenge dogma wherever he sees it. Witness, for instance, his incessant campaigning against the creationists, which has been beyond the call of (evolutionary) duty. In one of his undergraduate courses he identifies the 'four horsemen of evolution', gradualism, progressivism, adaptationism and determinism He believes that these four ideologies have sailed right through the Darwinian revolution of the nineteenth century and have continued up to the present day. Through his writings, university courses and public appearances he has consistently challenged all of these 'dogmas', with varying success. He has also regularly been an advocate for marginalised figures in the history of science, like Lamarck and Goldschmidt. ((Gould 1979b) and (Gould 1982c))

For Gould punctuated equilibria has been more than a simple theory about the nature of the fossil record. It has also been a means to challenge the authority of population genetics in evolutionary science, to break the reduction of macroevolution to microevolution. Further than this, however, he has used it as the basis of a research programme that he has in turn used for wide ranging attacks on perceived evolutionary dogmas. This research programme, which I have termed punctuationism, owes its existence more to the constant campaigning of Gould than to the actions of any other individual.

[173] Dogma, in this sense, being beliefs that are uncritically accepted.

5.3.4: Other punctuationists in the early 1980s.

Gould was by far the most prominent punctuationist of the early 1980s, his often radical statements doing more to attract attention to punctuated equilibria than any other event or publication. However he was not the only active punctuationist of the time. Eldredge continued his research into evolutionary hierarchy, expanding and elaborating his ideas about evolutionary hierarchy. Stanley Salthe, an evolutionary biologist, also campaigned strongly for the notion of evolutionary hierarchy, while Rose and Lewontin continued to pursue their individual anti-adaptationist agendas.[174] South African paleontologist Elizabeth Vrba, a new entrant into the debate, became influential. Others such as P. G. Williamson and Alan Cheetham began long empirical research programmes based on punctuated equilibria.

Each of these scientists had different reasons for holding an interest in punctuated equilibria. For Eldredge, of course, punctuated equilibria was his theory and his reputation was inextricably linked with it. Salthe saw evolutionary hierarchy as the way forward for his discipline (evolutionary ecology) and punctuated equilibria was a major part of that. Rose and Lewontin, who were only borderline punctuationists, shared Gould's interest in debunking adaptation. Vrba, Cheetham and Williamson saw punctuated equilibria as a source of fruitful research.

5.3.5: Eldredge

As the theory of punctuated equilibria was Eldredge's idea he had strong motivation to build a large research programme around that theory – evolutionary hierarchy was the manifestation of this interest. He, along with most of the other punctuationists, also held an interest in increasing the authority of paleontology at the expense of population genetics. His notion of evolutionary hierarchy, with its emphasis on the importance of independent levels of evolutionary explanation, was a natural (punctuationist) critique of the Modern Synthesis and lent itself easily to the independence campaign. Eldredge published several articles relating to this theme in the early 1980s ((Eldredge 1983) and (Eldredge and Vrba 1984) for instance). As an example of his work during this time, however, a short examination of two books that he published in the mid 1980s will suffice.

In 1985 Eldredge's book *Unfinished Synthesis: Biological Hierarchies and Modern Evolutionary Thought* was published the objective being to provide the framework for a (punctuationist) hierarchical evolutionary research programme. (Eldredge 1985) As the title of the book suggests, Eldredge argued that the neo-Darwinian synthesis was incomplete but was careful not to argue that any of the syntheticist's theories were actually erroneous, preferring, in the usual punctuationist fashion, to simply challenge the primacy of their 'gene's eye view'. His new, hierarchical approach was intended to hasten the completion of the Darwinian (punctuationist)

[174] Neither Rose nor Lewontin should strictly be labelled 'punctuationists'. However if forced to make a choice between labelling them 'punctuationist' or 'syntheticist' one would choose the former. Their activities in the early 1980s have already been documented to a certain extent (see Sections 2.3.1 and 2.3.2).

revolution and provide direction for future research. His strategy was thus reappropriational rather than oppositional, in that he did not set himself up in opposition to neo-Darwinism but instead attempted to redraw its boundaries so that it included his own position.

Eldredge's new approach to evolutionary science was codeveloped with Stanley Salthe (Eldredge and Salthe 1984) and involved two interconnected hierarchies – a genealogical one (codon, gene, organism, deme, species, monophyletic taxa) and an ecological one (enzyme, cell, organism, population, local ecosystem, biotic regions, entire biosphere). He argued that "the interaction of the nested individuals within each hierarchy … has given us the history of life on earth – evolution" and the organism, which is the only individual represented in both hierarchies, is the nexus of interaction between them He suggested that insight into a wide range of persistent problems in evolutionary science would be provided by focussing attention upon these hierarchies and the interactions between them. (Eldredge 1985)

As with much of the punctuationist literature, there is a symmetry in *Unfinished Synthesis* between the epistemological and the social. That is Eldredge's challenge to the primacy of natural selection and the gene in evolutionary explanation directly corresponded to his challenge to the authority structure of evolutionary science. Summing up his book Eldredge wrote that the main benefit of a hierarchical approach to evolution was that a "broader set of phenomena can be acknowledged as directly relevant to evolutionary biology than has customarily been the case." (p.214) Reinterpreted within the social context of the debate this quote was an attempt to assert the authority of formerly minor disciplines with evolutionary science, such as Eldredge's own paleontology. (To see this one simply has to replace the word 'phenomena' with the word 'disciplines' in the latter quote: 'a broader set of DISCIPLINES can be acknowledged as directly relevant to evolutionary biology than has customarily been the case.')

Unfinished Synthesis was Eldredge's technical account of punctuationism. the book that he published soon after this, *Time Frames: The Rethinking of Darwinian Evolution and the Theory of Punctuated Equilibrium* makes a nice companion in that it provides Eldredge's personal account of the punctuationist revolution and a lay guide to the significance of punctuated equilibria (Eldredge 1986). The same perspective was presented in both books – that neo-Darwinism was incomplete because it ignored the existence of evolutionary hierarchies. The first part of *Time Frames* was devoted to a chronicle of Eldredge's time as a young research student, describing the frustration he felt trying to find Darwin's 'insensibly graded series' when the trilobites he was studying seemed not to change at all. Over time he came to believe that the "lack of change" was not just an absence of data, but was rather a bona fide evolutionary phenomenon. This lead, he recounted, to he and Gould giving the phenomenon a name – stasis – and later to punctuated equilibria (p.67-70).

Most of the book, however, was devoted to explicating punctuationism in all its aspects, from its consequences for notions of adaptation to a discussion of species selection and macroevolutionary trends. In each case the underlying sentiment was the same – that under punctuated equilibria paleontologists can gain increased authority. Consider for instance this quote (the context was a discussion of species selection): "And paleontologists, for a welcome change, are the very ones who have the data needed to investigate such notions: at last, the very coarseness of our data is just what is needed for

us to see the forest for all the trees. Species stick out like sore thumbs in the fossil record." (p.153) Here Eldredge used irony to make his point. In the past, it was implied, biologists had contended that paleontological data were not fine enough to make assertions about evolution but now, with the new focus on species in macroevolutionary time, the situation was reversed.

5.3.6: Salthe

Evolutionary biologist Stanley Salthe was not a new entrant into the punctuated equilibria debate in the 1980s (see (Salthe 1975) for instance), however it was then that he became a prominent actor, teaming up with Eldredge to campaign for the notion of evolutionary hierarchy and co-writing 'Hierarchy and Evolution' (Eldredge and Salthe 1984). In 1985 he published his hierarchical manifesto, *Evolving Hierarchical Systems: Their Structure and Representation* ((Salthe 1985). This book will be the focus of analysis here.) Salthe was an example of a biologist attempting to come to terms with the macroevolutionary challenge. It is already noted that he espoused a hierarchical structure for evolutionary theory. His system in fact involved two interacting hierarchies, one genealogical and one ecological (in the same fashion as Eldredge). He did not, however, banish the philosophical attitude of reductionism. Rather he saw it as essential to research at each individual level, his hierarchy allowing reductionist research to make sense in the wider scheme of things. He believed that most biologists actually recognised the importance of hierarchy but did not apply it to their work the reason being that no "framework exists that would allow such an application" (p.ix). The intention of *Evolving Hierarchical Systems* was to supply such a framework.

Technically Salthe was not a punctuationist as he did not actually use punctuated equilibria. However he credited the punctuationists with having brought the deficiencies of the Modern Synthesis to the attention of evolutionary scientists: "The need for this fuller characterization of biology was dramatically brought to the attention of the scientific community in the reaction that followed the publication of the idea of punctuated equilibrium …" He asserted that punctuated equilibria had shown that "Synthetic Theory suffers from a lack of articulation of its parts" and identified these parts as "population-based selection-drift theory with its reductionist focus on gene frequencies…", theories about speciation and "a loose conglomeration of patterns and interpretations relating to macroevolution" that have "no pattern of relationships amongst themselves and relate only in an *ad hoc* manner to the speciation theories." Salthe proposed that a hierarchical system would allow these parts to become articulated as well as allowing the incorporation of "ecological theory" and "the theory of developmental constraints in evolution" (pp.187-189). He identified Wright's shifting balance theory as a precursor to evolutionary hierarchy, in that it represented organic evolution as a complex phenomenon of interacting processes, and, in a reconstruction of history, characterised it as outside of the synthesis: "… and indeed some might say that theory is not really a part of the Synthetic Theory at all, but something different." (p.255)

It is worthwhile comparing Salthe's treatment of punctuationism with that of Maynard Smith, Stebbins, Ayala and Templeton (as explicated in Section 5.4), for whom there was the problem of attempting to juggle opposing interests – the need to defend

one's discipline and the wish to resolve the apparent anomaly (the decoupling of microevolution and macroevolution). Salthe, however, was not a population geneticist - he was an evolutionary ecologist, so punctuationism was not a threat to his discipline as such. Hence he could simply concentrate on the attempt to re-articulate macroevolution and microevolution or, socially speaking, on the attempt to resolve the rift that had arisen between population geneticists and paleontologists. To contribute to a major breakthrough such as this would, of course, have earned him much social capital (apart from personal satisfaction) and would also have raised the status of his own discipline.

5.3.7: Vrba.

The most important new entrant into the debate during this time was the South African paleontologist Elizabeth Vrba. She was precisely the kind of paleontologist that the punctuationists of the 1970s hoped would arrive on the scene. A specialist on fossil antelopes, she was well versed in contemporary biology and genetics, had absorbed the punctuationist version of the history of evolutionary science and believed that paleontology was central to evolutionary science. Indeed she was almost the archetype of a punctuationist paleontologist.

Her first influential publication was the article 'Evolution, Species and Fossils: How Does Life Evolve?' (Vrba 1980). In it she displayed almost complete absorption of the punctuationist rhetoric, characterising the nature of the debate as one between punctuated equilibria and the "conservative and widely accepted [belief] in phyletic gradualism (slow uniform evolutionary rate, which commonly produces species by phyletic speciation in sympatry)" She attributed a "revitalization of evolutionary thinking among palaeontologists" to Eldredge's 1971 and Eldredge and Gould's 1972 articles, crediting them with having inspired paleontologists to "have a fresh look at what their data could really mean." Her account of the history of gradualism in evolutionary science was identical to the portrayal given by Gould and the other punctuationists. For instance she located the roots of gradualism with Darwin, describing how he held on to his beliefs despite the advice of Huxley, and described Simpson as a "confirmed gradualist". (pp.61-64)

It was in this article that Vrba first formally proposed her theory of macroevolutionary trends, the 'effect hypothesis'. The basic gist of the theory is this:

1. Punctuated equilibria is assumed to be the prevalent form of evolution.
2. Under punctuated equilibria the probability of phenotypic evolution is approximately equal to the probability of allopatric speciation, which in turn is approximately equal to the probability of a small population becoming isolated in a new environment.
3. Stenotypic species (those with specialised survival strategies) are more likely to satisfy the latter two conditions than eurotypic ones (with generalised survival strategies) and are thus more likely to speciate.
4. Thus, because of this differential rate of speciation, "in time the net result must be an evolutionary trend of increased specialization." (p.80)

The theory thus links a series of effects: Evolutionary trends are an effect of differential speciation; Differential speciation is an effect of the differing degrees of environmental specialisation between species; Environmental specialisation is an effect of adaptation to environment in microevolutionary time. The 'effects hypothesis' was thus almost identical to species selection. It used the same assumptions (punctuated equilibria, allopatric speciation, the randomness of speciation with respect to the direction of evolutionary trends) and came to the same conclusion regarding the cause of macroevolutionary trends – the differential success of species. However Vrba came to a different conclusion over the significance of evolutionary trends. When discussing species selection Gould, Eldredge and Stanley had, at different times, proposed that it could cause adaptation over time. Vrba instead proposed that the trends were simply for increasing specialisation. She thus offered an interpretation of long term trends with no adaptive speculation, producing a theory that was thus more punctuationist than that of the original punctuationists. She did not however, assert her theory to the exclusion of all others, merely wishing to point out that "trends may be *effects* of any factors which result incidentally in differential speciation rates." (p.80)

Vrba continued to pursue her agenda of modifying and expanding punctuationist ideas throughout the 1980s and into the 1990s. She teamed up with Gould to discuss the apparently misconceived attitude of most evolutionary scientists to adaptation (Gould and Vrba 1982). With Eldredge she co-authored an article discussing evolutionary hierarchy (Eldredge and Vrba 1984), whilst also regularly producing publications that expanded on her ideas about the cause and significance of macroevolutionary trends (for instance (Vrba 1983) and (Vrba 1985))

In 1984 she made her ideas about the nature of species selection less ambiguous (Vrba 1984). "*Species selection per se*" she wrote "*is a pattern of differential species survival within and among clades and not a process or cause of that pattern.*" (p.318) She argued that it should be called 'species sorting' so as not to give the impression that any causal process was implied. This was in contrast to her earlier attitude, as displayed in the 1980 article discussed above, in which she declined to negate the claims of her punctuationist colleagues. Her proposal was accepted by most punctuationists. Two years later she again teamed up with Gould to write a further explication of the difference between selection and sorting and to discuss the significance of this for hierarchical evolutionary perspectives (Vrba and Gould 1986).

Vrba was (and is) respected as a scientist on both sides of the divide. Punctuationists welcomed her correction and subsequent extension of species selection. Eldredge, for instance, described her effects hypothesis as "the most interesting and valuable contribution to the paleontological side of modern evolutionary theory to have been proposed – since punctuated equilibria." ((Eldredge 1986), p.172) In 1985 Maynard Smith gave a scathing review of the book *Beyond neo-Darwinism* (a largely punctuationist collection of essays). However he excepted Vrba from his criticism: "I except Vrba; in this respect, as in others, she is a good woman fallen among thieves." ((Maynard Smith 1993), p.161)

5.3.8: Empirical Studies in the 1980s.

During the 1980s paleontological research programmes aimed at testing punctuated equilibria against the fossil record became more frequent.[175] The ten year gap between Eldredge and Gould's original proposal and the publication of studies about punctuated equilibria was to be expected for a number of reasons. Firstly many of these studies were actually begun in the mid to late 1970s, so publication in the early 1980s was quite natural. Secondly punctuated equilibria presented a new approach to analysing fossil data and it took several years of exposure to convince paleontologists that it was a fertile area for research. Added to this, scientists involved in testing punctuated equilibria had to fulfil a whole new set of criteria that was more exacting than previously required for assertions about macroevolutionary patterns. Eldredge and Gould had effectively raised the bar by asserting that to differentiate between phyletic gradualism and punctuated equilibria in the fossil record one needed to study fossil species that were both relatively abundant and taken from a stratigraphic section that was unbroken through a relatively long time frame.

In 1985 paleontologist Richard Fortey provided what is still the most complete summary of the problem of fulfilling such criteria (Fortey 1985). He pointed out that it is almost impossible to produce a positive test for the punctuations in punctuated equilibria because of the difficulty in differentiating between a break in a sequence and a punctuated speciation event and that stasis must therefore be the focus. Fortey's article was an articulation of what most researchers in the area already knew – most studies were indeed focussing not on speciation events but on stasis. The other main empirical problem for a punctuated equilibria versus phyletic gradualism test, wrote Fortey, is the question of species identification. How does one decide when a species is sufficiently different to make it a new species and which character or set of characters should be measured? Many fossil species are incompletely preserved so that often there are only one or two morphological characters available for measurement. It is debateable whether such data are sufficient to test for punctuated equilibria. Alan Cheetham, for instance, later demonstrated that at least occasionally the most variable characters in a species are not the ones that change when speciation occurs, and that studies based on a small number of characters can thus be deceptive. (Cheetham 1987)

One of the larger studies of the 1980s that purported to demonstrate punctuated equilibria was completed by P. G. Williamson, a colleague of Gould at Harvard University. Williamson studied mollusc fossils from the Turkana basin in Africa, and claimed that he had sufficient resolution to document speciation events as well as stasis. He continued on to assert that his study, and punctuated equilibria in general, implied that the neo-Darwinian explanation of evolution was incomplete as it did not encompass stasis, identifying developmental constraints as the likely cause. (Williamson 1981) Williamson's study and his subsequent assertions about neo-Darwinism prompted replies from a number of evolutionary biologists: Charlesworth and Lande claimed that natural selection could explain the reported pattern (Charlesworth and Lande 1982); Fryer, Greenwood and Peake claimed that the pattern was simply the result of the species reaction to environmental fluctuations and that no speciation had actually occurred at

[175] I owe my understanding of the rather technical studies discussed in this section to two advanced paleontological textbooks, (Kemp 1999) and (Smith 1994).

all.[176] (Fryer, Greenwood et al. 1983); Cohen and Schwartz claimed there was some doubt there had even been any change in morphology and that the reported changes could be due to migration from other species (Cohen and Schwartz 1983).

Other important studies purporting to demonstrate punctuated equilibria at this time were:

- Coope's analysis of fossil beetles from the most recent geological era, the Quartenary. He found no morphological change over almost 2 million years and that the species he studied were identical to extant species. (Coope 1979)
- Cheetham's analysis of marine bryozoans. He examined the form of 46 characters for over 4.5 million years and found very little change in most of them. He did find some directional change in some characters, but found that these were not the ones that changed during speciation events. He then claimed that his study demonstrated a decoupling of macroevolution from microevolution. (Cheetham 1986)
- Stanley and Yang's comparison of fossil marine bivalves from a recent geological period (the Pliocene) with their extant relatives. They found that evolution had zigzagged over time yielding only trivial net change. (Stanley and Yang 1987)

There were of course other paleontological studies that purported to find gradualism in their data.[177] The common thread in such studies was the claim that when the fossil record is sufficiently dense gradualism is exhibited. Interestingly one researcher, studying radiolarians from deep sea core samples, found that gradualism, stasis and punctuations were exhibited at different times (Lazarus 1986) This study was an interesting portent for the future, when the dichotomous relationship between gradualism and punctuationism that Eldredge and Gould had constructed began to unravel, both being accepted as valid possible interpretations (see Section 6.1.3).

The point to be made about all these studies is that, come the 1980s, punctuated equilibria provided a focal point for many paleontological research programmes and had raised the standard of criteria necessary to make assertions about the nature of macroevolutionary patterns. Thus whilst it had not fully succeeded in the sense of becoming accepted dogma (as is the usual criteria for judgement of the success of scientific theories amongst some philosophers of science) it had made a major contribution to the revitalisation of paleontology (which the author of the present thesis would contend had been Eldredge and Gould's primary objective).

5.3.9: Summary of punctuationist activity in the early 1980s.

In the period from the late 1970s to the mid 1980s punctuated equilibria was the focus of considerable scientific activity. Two connected movements constituted this activity. Within paleontology the theory of punctuated equilibria proper became the focus of research for scientists such as Cheetham, Vrba and Williamson. It thus matured into a

[176] They claimed that the observed patterns were the result of an 'ecophenotypic' effect - some species have the capacity to alter their morphology in response to changing environments without altering their genetic make-up.

[177] See ((Kemp 1999), pp.144-5) and ((Smith 1994), p.184) for discussions of such studies.

valid research programme. In a broader sense, (i.e. across evolutionary science in general) punctuationism matured from a rather haphazard collection of criticisms of the Modern Synthesis to an elegant critique, as the notion of evolutionary hierarchy became more refined.

Indeed evolutionary hierarchy became an umbrella under which criticisms of the Modern Synthesis were gathered. The argument for independence of levels was mirrored in the social challenge taking place, as paleontologists and scientists from other subdisciplines of evolutionary science argued for heuristic independence. In the words of Gayon, "the 'hierarchical pleading of many paleobiologists resembles an efficient argument in favor of heuristic autonomy. Therefore, one may think that it does not concern so much the structure of evolutionary *theory* as the control of research programs." ((Gayon 1990), p.39)

The challenge was thus put to the syntheticists. They could not continue to ignore the punctuationists and hope they would go away. In Bourdieu's terms, the punctuationists had, over the period since Eldredge and Gould's 1972 article, accrued considerable amounts of social capital in their fight. Many scientists had been brought into the punctuationist fold. Punctuationism had infiltrated all the major journals, explicit challenges to synthetic theory were out in the open and paleontologists began publishing the results of large empirical studies. Punctuationism could no longer simply be ignored – its incursions had to be dealt with and the syntheticists were compelled to answer punctuationists' criticisms.

5.4: The biologists' reactions.

5.4.1: Interests.

In the early 1980s the number of biological publications concerning macroevolution in general and punctuated equilibria in particular was at its greatest. The punctuationist challenge to the authority of biology (and especially population genetics) over macroevolution had, over the decade from Eldredge and Gould's 1972 article, steadily gained momentum. With neo-Darwinism simultaneously under attack from several other sources the syntheticists felt they could no longer ignore the punctuationist challenge. Their whole discipline was under siege and articles in defence of their theories and practice began to appear in numbers (see Section 3.4).

The strongest opposition came from population geneticists. Given that punctuationism presented an explicit challenge to their authority this was only to be expected and they attempted to debase the claims of the punctuationists in this respect. However they also displayed an interest in attempting to resolve some of the problems constructed by the punctuationists (such as: What is the source of stasis?; If macroevolution and microevolution are decoupled, what causes long term evolutionary trends?), recognising that punctuated equilibria was a potential source of fruitful research It was thus necessary for them to reconcile two opposing interests: on one hand they wanted to refute punctuationism altogether; on the other they wanted to be the scientist that solved the anomalies stemming from punctuationism. The attempt to juggle these

opposing interests thus had a large influence on the rhetorical structure of their responses to the punctuationist challenge.

5.4.2: Maynard Smith – authority number 1.

Population geneticist John Maynard Smith is considered by many to be the pre-eminent evolutionary biologist of modern times. From the early 1960s his name has carried a large amount of social capital. He was, and is, considered to be *the authority* on evolutionary biology. In the early 1980s Maynard Smith published a series of articles responding to the punctuationist challenge, the form of these replies becoming an archetype for his syntheticist colleagues. He reconciled the opposing interests related above by accepting punctuated equilibria as a valid theory whilst debasing punctuationism as a research programme. That is he accepted that the core statements of punctuated equilibria could well be correct but strongly rejected the notion that punctuated equilibria in any way cast doubt on the core tenets of neo-Darwinism.

The target of Maynard Smith's debasement was thus the logic of implication that led from punctuated equilibria to punctuationism rather than punctuated equilibria itself. In essence he rejected the imposition of the punctuationists into his field. He was quite happy for them to rewrite the books within paleontology (the minimum claim) but was adamant that they should stay out of evolutionary biology. His reaction was thus a rather predictable one – 'Do what you like in your own country but don't stray across the border' – and, as we shall see, this was typical of the syntheticists at that time.

In 1981 Maynard Smith responded to Gould's anti-neo-Darwinist claims with the paper 'Did Darwin Get It Right?', published in the *London Review of Books*. ((Maynard Smith 1993), pp.148-156)[178] From his choice of journal it is clear that Maynard Smith was aiming at a wide readership and not a specialised biological, or even evolutionist, audience. It is apparent that he thought the public in general needed to be told that the radical views of Gould were not characteristic of the rest of the field. He began by reconstructing the punctuationist position, in order to debase the hostile claims about neo-Darwinism, splitting the doctrine into two parts, a 'minimum' and 'maximum' claim. The minimum claim was that the fossil record displays a punctuated patten. The veracity of this claim was something that paleontologists had to decide for themselves and while aspects of it (such as stasis) were of some interest for biologists, he did not believe it was a challenge to neo-Darwinism. The maximum claim, which he strongly rejected, was that "evolutionary change, when it does occur, is not caused by natural selection operating on genetic differences between members of populations, as Darwin argued and as most contemporary evolutionists would agree, but by some other process." (p.149)

In 1983 Maynard Smith provided a chapter for the book *Dimensions of Darwinism.* ('Current Controversies in Evolutionary Biology', (Grene 1983), pp.273-286) Similar in structure to the article discussed above ('Did Darwin Get It Right?'), Maynard Smith divided the punctuationist's claims into two parts (this time calling them "minor" and "major"). However here he was aiming at a biologically literate audience and was more critical of punctuated equilibria.

[178] The book of the same name (*Did Darwin Get It Right?*) cited here is a collection of Maynard Smith's articles.

He debased aspects of the minor claim, contending that it was impossible to detect punctuated speciation events as any rapid transition in the fossil record cannot be distinguished from migration and that paleontologists thus cannot declare a punctuation in the fossil record to be a speciation event. In *Macroevolution: Pattern and Process* Stanley had attempted to establish that stasis was prevalent in the fossil record by listing the duration of species identified by other paleontologists in paleontological literature. Maynard Smith also sought to debase this enterprise: "My second comment is that it will be little use to analyze the durations in the fossil record of particular named forms, as Stanley… attempts, because this is to study the habits of taxonomists rather than the evolution of organisms. There is no alternative to a statistical study of populations." He did however concede that stasis occurred in the fossil record at least occasionally and that this was an unsolved problem for population geneticists, proposing two possible explanations: constrained development, as per Gould, and stabilising selection. (p.274)

Maynard Smith was intensely critical of species selection. He reconstructed it, identifying four possible 'readings' then debased each one in turn. The first 'reading' was that species selection acted via emergent properties, such as "the "capacity to evolve rapidly" and "the likelihood of speciation". He recognised that these properties probably exist but contended that they could not have important effects: "most evolutionary trends … could not be explained in this way." Second was the coincidence of reproductive isolation with new traits that affect individual survival (i.e. the punctuationist claims that speciation and morphological change are coincidental). He admitted that if this was common then a process that could be called species selection would be implied but placed doubt upon its frequency: "… I do not think species arise in this way … I do not think the number of speciation and extinction events would be large enough to account for the extent of adaptation observed." Third was the replacement of one species by another. He stated that to call this species selection would be "misleading" as it is clearly reducible to individual selection. Fourth, taxic radiation into new adaptive zones. Once again he claimed that this is reducible to individual selection. (pp.278-281) Maynard Smith's debasement of species selection must be seen as an attempt to retain natural selection as the sole evolutionary process, the motivation for this coming, at least in part, from a desire to protect the centrality of his own discipline (population genetics) within evolutionary science.

Maynard Smith also debased the possibility of developmental constraint as an explanation for stasis. He recognised that constraints limit the amount of variation, but asserted that only stabilising selection could account for stasis: "…developmental constraints alone could not account for stasis, unless it were true that *no* variation is possible, which is manifestly not so." He also denied the punctuationists originality in their ideas: "It is worth adding that the concept of developmental constraints is not new." (p.282)

A year later Maynard Smith published 'Paleontology at the High Table' ((Maynard Smith 1993), pp.125-130, first published in *Nature*, May 1984) Here he gave a qualified welcome to paleontologists as they joined the community of evolutionary scientists. Ostensibly he wanted to discuss some of the issues brought up during a series of lectures given by Gould[179] and at a subsequent seminar, and he attempted to give the reader the impression that he or she was being presented with an unbiased view of the

[179] The 'Tanner Lectures', held annually at Cambridge.

debates that occurred at the time. However, a close reading of the text shows that Maynard Smith did not agree with the arguments of the punctuationists and that his account was duly biased against their ideas.

He recognised that historically paleontologists have not been respected as contributors to evolutionary theory: "Since [Simpson showed that the data of fossil record was consistent with the synthetic theory in the 1940s] the attitude of population geneticists to any palaeontologist rash enough to offer a contribution to evolutionary theory has been to tell him to go away and find another fossil, and not to bother the grownups." He then mentioned that through the work of a "group of paleontologists" (i.e.Eldredge, Gould, Stanley et al) the situation had changed somewhat. In the lectures Gould had stressed the importance of two "theoretical modifications to the Darwinian scheme", these being punctuated equilibria and a hierarchical view of evolution. Maynard Smith deconstructed the rhetoric of Gould's presentation in order to debase his claims. For instance Gould had apparently presented punctuated equilibria "as a fact the whole world knows". Maynard Smith questioned the empirical basis of this: "I am persuaded that morphological evolution proceeds at very different rates at different times, but can see little evidence that rapid change is necessarily associated with the splitting of lineages …". The reconstruction took the by now usual form of stating that the punctuations are merely a different interpretation of the same data: "one man's punctuation is another man's gradualism." (pp.125-126)

Regarding the stasis part of the theory Maynard Smith was more positive. He accepted that stasis as a phenomenon occurs often enough to call for explanation. Geneticists maintain that it can be explained by stabilising selection, whereas the paleontologists believed that selection cannot remain stable for such long periods of time and that stasis is more likely to be caused by developmental constraints. He provided a mild debasement of the paleontologists point of view; they had cited C. H. Waddington in support of their view, but Maynard Smith claimed that they misrepresented him: "… for Waddington, the uniformity of the wild type was itself the product of normalising selection, and not a manifestation of an intrinsically stable state." Maynard Smith included a discussion of the idea of evolutionary hierarchies and species selection, the basic gist of his argument here was that whilst species selection may occur it cannot account for what he saw as the most important aspect of evolution – the adaptation of individuals.

5.4.3: Other population geneticists.

The responses of other population geneticists at this time followed similar patterns to that of Maynard Smith. They were happy to allow the punctuationists to form theories about macroevolution and were interested in some of the ideas thrown up but were adamant that microevolution should remain their exclusive property, denying that punctuated equilibria cast doubt on the basic tenets of the Modern Synthesis. Their attitude came down to: 'Ok, you can have macroevolution but don't go any further. Microevolution is ours and we'll defend it in the strongest possible fashion.'

One early reply to Gould's claims that illustrates this attitude came from population geneticists Ledyard Stebbins and Francisco Ayala, both highly respected

within evolutionary science. Their rather technical response, given in the article 'Is a New Evolutionary Synthesis Necessary?'. (Stebbins and Ayala 1981), was published in the journal *Science*. They agreed that macroevolutionary patterns cannot be derived from microevolution and recognised the validity of paleontological theorising about macroevolution but did not believe that this debased the Modern Synthesis; rather they charged Gould with mis-characterising neo-Darwinism, of erecting a "straw man", and asserted that all the new punctuationist claims could be easily incorporated into synthetic theory. In particular they argued that both gradualism and punctuated equilibria are compatible with the theory of population genetics. Hence whilst population genetics could not decide between the two, neither could punctuationism challenge the veracity of population genetics at the microevolutionary level. They urged that "the study of microevolution *is* important to macroevolution because any theory of macroevolution that is correct must be compatible with well-established microevolutionary principals and theories." Essentially Stebbins and Ayala appeared to be saying to the punctuationists 'Yes, you can have your macroevolutionary theories, we won't challenge your authority in that respect, but your theories do not impinge on our authority and you still have to make them consistent with population genetics.' (pp.967-970)

Stebbins later wrote a separate article discussing the punctuationist claims – 'Modal Themes: A New Framework for Evolutionary Syntheses' (Stebbins 1982). On this occasion Stebbins took the role of mediator, accepting the claims of the punctuationists at face value and discussing the possibility of united research between evolutionary biologists and paleontologists to address the apparent inconsistencies. In particular he suggested comparative studies of extant species with their recent fossil record (choosing, of course, species that are well represented in the recent fossil record), an approach that was to prove fruitful in the 1990s (see Section 6.1.4).

Another population geneticist to respond to the punctuationist claims was Alan Templeton. His article 'Adaptation and the Integration of Evolutionary Forces' was ostensibly a reply to Roger Lewin's account of the Chicago macroevolution conference. ((Templeton 1982), this article is examined in detail in Section 5.4.4.) Templeton strongly defended the reduction of macroevolution to population genetics and the primacy of natural selection and adaptation as the cause of evolutionary trends. The empirical evidence he offered for his counter-claims, however, came from population and developmental genetics. There is no real attempt to tackle the punctuationist claims on their own turf – that is, he did not attempt to refute the punctuationists according to their own criteria but rather attempted to reinstate the traditional criteria. In effect, he side-stepped their attack and attempted to counter-punch.

An important reply to the punctuationist challenge was 'A Neo-Darwinian Commentary on Macroevolution', written by evolutionary biologists Brian Charlesworth, Russell Lande and Montgomery Slatkin. (Charlesworth, Lande et al. 1982) The authors rejected the punctuationist attempt to impinge on their discipline in the strongest fashion, citing large numbers of empirical studies alongside their refutations of the punctuationist claims. Indeed, in the very first sentence they cited an entire generation of scientists: "The neo-Darwinian synthesis that resulted from the integration of Mendelian genetics into evolutionary theory has dominated evolutionary biology for the last 30 to 40 years, due largely to its agreement with a huge body of experimental and observational data."

(p.474) They thus immediately constructed a dichotomous relationship, with themselves and 40 years of empirical evidence on one side and the punctuationists on the other.

The rhetoric of the entire article was constructed in similar fashion. They first defined the opposition, reconstructing the punctuationist claims into four separate notions: "We shall discuss four patterns in the fossil record that form the main components of the punctuational theory: stasis, the association of morphological change with speciation, evolutionary novelties, and phylogenetic trends." Over almost twenty pages they sought to refute all punctuationist claims associated with each of these notions, citing large numbers of references spanning the entire history of their discipline – from Darwin in the 1860s to Haldane in the 1930s to their own contemporary studies. In essence they were seeking to demonstrate that punctuated evolution had always been part of Darwinism, and later neo-Darwinism, and that the claims that punctuated evolution were a problem for neo-Darwinism were thus baseless. The tactics of reconstruction and debasement were also a major part of the rhetorical structure of their paper, as evidenced by the following statement: "the genetic mechanisms advocated by some punctuationists are either already a part of the neo-Darwinian theory [reconstruction] or are seriously lacking in empirical support [debasement]." (p.475)

5.4.4: A typical example.

Debate between the punctuationists and the syntheticists in the early 1980s was characterised by a *lack of communication.*. The quality of their discussions suffered from a *lack of genuine empathy*, participants on both sides failing to develop any real understanding of the concerns of those from the other side.[180] This was particularly true of scientists from the two disciplines with most at stake – population geneticists and paleontologists. Publications attempting to reconcile the punctuational and synthetic views of evolution invariably failed to consider the concerns of their opponents. With both sides failing to address the issues of concern to the other there was thus little chance of resolution.

Population geneticist Alan Templeton's article 'Adaptation and the Integration of Evolutionary Forces' has been chosen for analysis as a typical example of this lack of communication for several reasons. Firstly, and despite the fact that he failed to develop any real empathy for the punctuationist position, Templeton was making a sincere attempt to reconcile the micro and macro views of evolution. Secondly he was not a high profile scientist and is thus a better example of a typical in-the-trenches scientist than, say, Maynard Smith or Stebbins. Thirdly he was (and is) not particularly anti-punctuationist – in personal communication he has expressed quite positive views about the theory (one of his remarks about punctuated equilibria is quoted in Section 4.3).

Specifically Templeton's paper was an answer to Roger Lewin's account of the Chicago Macroevolution Conference (see Section 5.3.2)., and he argued that evolution is primarily a process of adaptive anagenesis where "a *population* acquires traits that tend to enhance survivorship, mating success, and/or fertility with respect to a particular environment" (my italics – to stress the fact that for Templeton evolution is a phenomenon of populations). Cladogenesis (speciation) is, in this perspective, merely a

[180] Empathy is, of course, the basis of communication.

side-effect of anagenesis, occurring when two populations are isolated and undergo adaptive change independently. He then characterised the punctuationist perspective, citing Lewin's article and Stanley's *Macroevolution*: "This idea has recently been challenged, with many evolutionists now claiming that both speciation and the origin of major features in macroevolution have little, if anything, to do with adaptation. (Lewin, 1980) … the major trends of evolution under this view are attributed instead to the process of speciation (which is regarded as involving mechanisms that are qualitatively different from those occurring during evolution within a species) and higher level processes such as 'species selection' (Stanley, 1979) " (pp.15-16).

Templeton then asserted that "the internment of adaptation is premature" and that "adaptation is still alive and well and playing a critical role in the origin of species in both the anagenetic and cladogenetic senses." (p.16) The bulk of the article that followed consisted of evidence confirming these assertions. In order, there was:

- A six page discussion of population genetics – specifically he discussed sickle cells.
- A three page discussion of developmental genetics - specifically the consequences of regulatory genes for ideas in population genetics.
- A three page discussion of Wright's shifting balance theory.
- A three page conclusion in which he returned to discuss the claims of the punctuationists and basically declared that their arguments re adaptation are unfounded because there is "no incompatibility" with population genetics.

A closer look at the text reveals that his argument, as a whole, was saturated with incomprehension of the punctuationist's ideas. For instance during his discussion of sickle cells he states: "We must never forget that *adaptive processes are manifest only at the level of a population reproducing through time* …" (p.20, his italics). He thus implied that the punctuationists had in some way challenged the idea that the processes which produce adaptations occur at the level of populations. This does not seem to be the case at all – rather their contention was that whilst adaptations may be produced by processes best explained at the population level, there are processes at other levels that influence which adaptations persist in macroevolutionary time. They may have claimed that the adaptation wasn't as important to evolution as claimed by syntheticists but no punctuationist ever claimed that macroevolutionary processes produce adaptations.

Templeton used Wright's shifting balance theory as a medium to reconstruct punctuated equilibria so that it is absorbed into the former's explanatory domain (and thus into standard neo-Darwinism) – "the shifting balance theory", he wrote, "predicts that periods of evolutionary transition will be intense but brief and lead directly to a very static adaptive situation." Now, the idea of 'demes' was central to Wright's theory – a deme being any coherent group of interbreeding individuals. It is possible to consider species as demes and one can then validly say that Wright's theory is indeed very closely related to punctuated equilibria – that punctuated equilibria is a special case of Wright's theory. However Wright's theory, as applied, was primarily a theory of populations. He did not attempt to apply it to the fossil record. So whilst Templeton's identification of a relationship between Wright's theory and punctuated equilibria was valid he was

incorrect in asserting that the former was a precursor to the latter; rather punctuated equilibria was a new application Wright's theory. (pp.24-27)

In his conclusion Templeton asked whether the pattern of punctuated equilibria was "incompatible with the implications of the adaptive process?" He answered this question in the negative, stating that it was "critical to realize that punctuated equilibria is merely a description, not a mechanism or a process" and that "Darwin himself predicted just such a pattern of macroevolution …" Now, he was correct asserting that Darwin predicted a punctuated pattern for the fossil record but did not understand what the issues of concern for the punctuationists were in this respect. Whilst Darwin did indeed state that such a pattern would be expected for macroevolution it was not the focus of his thesis – he was more concerned with individual selection and how it affects the structure of populations. He may have seen that species could be stable entities but he did not consider that as a consequence of this there may be important processes at levels higher than that of the individual. And that was the crux of the punctuationist argument – that whilst punctuated equilibria might be descriptive (explanation of its existence being reducible to population processes) it implies the existence of higher level processes. These processes were not about adaptation as such – rather they were about what happens to adaptations after they arise. So when the punctuationist replied in the positive to the question that Templeton asks above (about punctuated equilibria having implications for adaptive processes) they were not necessarily circumscribing the importance of the population processes that he studied. Rather they are looking at what happens after such processes have taken place. (pp.27-28)

Later Templeton stated that "punctuated equilibria is compatible with Darwin's view of adaptive evolution … [and] … with the view of adaptive evolution outlined in this chapter.". As this statement stands one would have to agree with Templeton – punctuated equilibria was indeed 'compatible' in that it did not refute Darwin's and Templeton's views. However this is not what he meant by the above statement. When he stated that punctuated equilibria is 'compatible' he actually meant 'reducible' to his notion of adaptive evolution - that it could be explained by the standard notions of his own discipline and was therefore unnecessary. The following statement, which was the crux of his argument for the 'compatibility' of punctuated equilibria with standard neo-Darwinism, demonstrates this

> "To illustrate this point [that punctuated equilibria is compatible with his notion of adaptive evolution], consider the classic model of speciation in which an ancestral population is subdivided into two or more isolated subpopulations by some extrinsic barrier to gene flow. Under this model, intrinsic isolating barriers then arise as a pleiotropic consequence of the adaptive processes occurring separately within the subpopulations. However, most extrinsic geographical or ecological barriers to gene flow are temporary in nature, so the chances for speciation under this model are often a function of how rapidly adaptive divergence occurs. Unless intrinsic isolation arises

> rapidly enough, the extrinsically isolated populations will simply fuse together upon secondary contact." (p.28)

To the punctuationists the validity of this statement was beside the point as for them the issue was not the microevolutionary cause of punctuated equilibria but what happens at scales of time in which adaptive processes are no longer visible. Templeton clearly had not developed any empathy with the punctuationist perspective. He bypassed their major issue of concern and thus failed to realise genuine communication.

The rest of the conclusion was similar in nature. Consider this statement for example: "the inference that the pattern of punctuated equilibria indicates that adaptive processes are unimportant in speciation or macroevolution is not valid." He was correct that the punctuationists believe adaptive processes to be essentially instantaneous, and thus perhaps 'unimportant', events in macroevolutionary time but they have never claimed that adaptation is unimportant to speciation. Templeton, it seems, had the two issued confused. The essay concluded with a debasing statement: "When adaptive processes are treated in a more rigorous and detailed fashion, no incompatibility is apparent." The uncommunicative nature of this last statement is symbolic of the whole article; it may well be correct that there is compatibility between adaptive processes and punctuated equilibria, especially when analysis is rigorous, but the fact remains that the adaptive processes that he discussed in this article are not the target of criticism from the punctuationists. It was not the nature of the processes themselves that the punctuationists disputed, nor their existence. Rather they were concerned with how those processes related to the time scales of their own discipline and their bone of contention was the assumption, mainly propagated by population genetics like Templeton, that those adaptive processes can be extrapolated to explain macroevolution. (pp.27-31)

In essence Templeton took the arguments of a group of people who are mostly paleontologists and refuted them with population genetics, clearly misunderstanding the nature of their assertions. At no stage in the article was there any real attempt by him to try and comprehend the reasoning behind the claims of his opposition - he was unable to establish any *empathy* with the punctuationists. This lack of understanding for their perspective caused him to attempt communication solely from the level of his own perspective – population genetics. Other population geneticists would have read his article and nodded their head in approval. Paleontologists would have read it and thought it irrelevant. The chances that any constructive communication between the punctuationists and the syntheticists could occur in this fashion was nil.

The form of this article was not at all unusual for the time; rather it was the most usual form. In the 1980s the literature of the debate over punctuated equilibria and macroevolution is dense with similar articles. Syntheticists wrote articles claiming that punctuated equilibria can be reduced to population genetics and is therefore unnecessary. Punctuationists wrote articles saying that adaptive change in populations is not important to macroevolution. Neither side seemed capable of couching their arguments in terms that the other would understand nor were they making any great attempt to understand the issues of concern for the other side. They were concerned with furthering the cause of their own disciplines (population genetics and paleontology) and could not see the other side as anything but a threat.

5.5: An exchange from *Nature.*

A good example of the kind of debate extant across the broader field of evolutionary science in the early 1980s can be found in an exchange in a 1982 edition of *Nature* - a five page discussion of Williamson's Lake Turkana studies. (Mayr, Boucot et al. 1982)[181] The discussion began with an editor's introduction in which stasis was identified as the 'real problem' for neo-Darwinism. The first section proper was written by Ernst Mayr ('Questions Concerning Speciation'), who was supportive of Williamson's findings, agreeing with the contention that it was not stabilizing selection that was responsible for the observed stasis but developmental constraints, which he equated with his own notion of "cohesion of the genotype". Mayr, however, did find some weaknesses in the study: the evolution in the "12 lines of sexually reproducing organisms" was "exactly paralleled by events" in a related asexual lineage implying, apparently, that the changes were "not genetic at all, but merely modifications of the phenotype"; the "lineages never truly seem to have passed through a narrow population bottleneck as is demanded by the theory of peripatric [allopatric] speciation." Following Mayr's section came one by paleontologist Arthur Boucot of Oregon State University ('Ecophenotypic or Genetic'). He reiterated Mayr's misgivings about the possibility that the observed changes in the molluscs were ecophenotypic rather than genetic and suggested that a comparison with related extant species could help resolve the issue.

Charlesworth and Lande ('Morphological Stasis and Developmental Constraint: No Problem for Neo-Darwinism'), addressed the general topic of stasis, an issue the editor had identified as the most important to have arisen from Williamson's study. They sought to refute the assertion that stasis must be explained by developmental constraint via a rhetorical process of reconstruction and debasement: "The view he holds, that stasis is due to developmental constraints, is equivalent to saying that the characters concerned lack genetic variability, so that selection is ineffective. [reconstruction] But there is evidence for substantial levels of heritable variability in most morphological characters that have been studied, including snail shell traits. [debasement]" Charlesworth and Lande thus contended that either the characters in question were "selectively neutral" or natural selection was acting "towards an intermediate optimum phenotype."

Ecologists Lev Ginzburg and Jay Rost of the State University of New York ('Are Punctuations Artefacts of Time-Scales?') focussed on the "punctuated pattern" that Williamson had found, suggesting that it "may well be an artefact of sampling time scales." As a demonstration of how this might occur they discussed an "imaginary example" of a population of *E. coli* being cultivated in a laboratory. In this example, if the scientist looks at the sample irregularly (say once every two weeks) changes appear punctuational but if the sample is examined hourly (every hour) changes appear gradual. How this discussion is supposed to have related to punctuated equilibria in the fossil record is unclear - the punctuationists were not claiming that punctuations would not look gradual in finer-grained time-scales. Rather their thesis was based on the notion that the coarse-grained time-scale of geology, in which punctuations (and stasis) do appear, is an equally valid vantage point from which to view evolution. In their eagerness to reassert

[181] Williamson's study is discussed in Section 5.3.8.

the importance of the ecological time-scale Ginzburg and Rost missed the whole point of punctuated equilibria.

Paleontologist D. W. Lindsay ('Punctuated Equilibria and Punctuated Environments' - only one paragraph) noted that the "observations of stasis interspersed with rapid change may simply reflect changes in the direction and intensity of the selective pressures" and that "we [paleontologists, it is presumed] ought to consider a punctuated environment in thoughts on punctuated evolution." As with Ginzburg and Rost, it appears that Lindsay had not grasped the main thrust of the punctuationists' arguments – that ecological changes are not measurable in the geological time-scale. It would be fair enough for Lindsay to demur regarding this notion but the fact that he did not even mention it shows he lacked understanding. In Williamson's study the proclaimed periods of stasis are very long and it was implied that to identify a stable environment as the cause was unreasonable. Lindsay did not discuss this.

Williamson was given the opportunity to reply in the final section ('Williamson Replies'). Regarding Mayr's criticism of his use of peripatric speciation, Williamson conceded that this was an issue but believed that it was "possible to resolve the conflict" and hinted that he had a solution: "I hope to address this topic in a forthcoming paper." He then turned his attention to Mayr and Boucot's contention that it was not possible to distinguish between genetic and ecophenotypic effects in the mollusc lineages, providing three refutations: that the new forms often coexisted with their ancestral forms; that many of the lineages "are still extant and widely distributed in Africa" and that such ecophenotypic responses are not evident; that the "morphological transformations are invariably unidirectional in character space, and required some $10^3 – 10^4$ generations to accomplish … hardly the nature or time-scale of a conventional ecophenotypic response."

Turning his attention to the criticisms of Charlesworth and Lande, Williamon strongly disputed their reconstruction of the notion of developmental constraint, claiming that the "question is not so much whether variation exists for selection to work on, but rather what, if anything, selection can actually *make* of this variation in nature" and that developmental constraints can stop morphological trends even where sufficient variation and selection exists. More interesting is his reply to Charlesworth and Lande's contention that stabilising selection is an adequate explanation for stasis, for in this instance Williamson cast himself as having the orthodox Darwinian view. He compared the punctuationist invocation of constraint for temporal stasis with the (apparently) neo-Darwinist view that "stabilizing selection is an inadequate explanation for … range-wide phenotypic coherence in modern species" and that "developmental constraints of one form or another" must be invoked. Indeed, he asserted, punctuationists were not outrageous in this respect but were rather "following the lead of conventional neo-Darwinian students of *geographic* variation."

Williamson replied to Ginzburg and Rost's criticisms by arguing that it was the extrapolation from one time-scale to another that was the issue and not whether the punctuations themselves were considered to be gradual or punctuated.[182] Resorting to irony, he noted that Lindsay, in suggesting that "selection pressure is a *sine qua non* of evolutionary change" has ignored "such staples of conventional neo-Darwinism as

[182] Basically if one assumes gradualism then one can extrapolate from one time-scale to another as the rate of change will be constant. However if one assumes a punctuated pattern then one cannot extrapolate because the rate of change is not constant.

founder effect, genetic drift, mutation pressure and the appearance of ‘super-fecund’ mutants”. Then, reinterpreting, he extrapolated Lindsay’s logic, asserting that to follow it through would mean that selection pressures were extant for less than 1 per cent of the time and the remaining 99 percent of the time “selection pressures were ‘so low or minimal’ – for 5Myr – that no significant changes occurred in any lineage.” Regarding this (reconstructed) assertion Williamson wrote: “Lindsay finds this unsurprising. I find it incredible!”.

The major theme to emerge from the above exchange was the large variation in interests displayed by the scientists. The biologist Mayr was concerned that Williamson’ fossil data could not differentiate between genetic and ecophenotypic effects. This concern was shared by paleontologist Boucot. Mayr was also concerned about the validity of Williamson’s invocation of peripatric speciation but, in contrast with his fellow biologists Charlesworth and Lande, seemed quite happy with Williamson’s explanation for stasis . Charlesworth and Lande, for their part, wanted to reassert traditional neo-Darwinian explanations for stasis. The ecologists Ginzburg and Rost were worried about time-scales. They did not really discuss punctuated equilibria at all, simply reasserting the importance of the time-scale of their own discipline. Paleontologist Lindsay wanted to reassert the importance of fluctuations in the environment for evolutionary trends. Williamson’s replies were a simple reassertion of points made in his initial study – in only one case (Mayr and peripatric speciation) did he concede there to be a problem and in that case he promised to find a solution.

This exchange is symbolic of events across the broad field of evolutionary science, in that a diverse range of interests were brought to analyses of punctuated equilibria. There was no agreement as to what set of problems needed to be resolved. This is not unusual for a scientific controversy and is in fact quite usual. Questions of what issues are at stake invariably form the focus of scientific controversies, with each scientist attempting to set an agenda to suit their own interests. And, looking at the response of each of the scientists in the above exchange, we can see that in each case the particular scientist attempted to reformulate the issues in such a way that their own sub-discipline would have become the central point of inquiry.

5.6: Summary.

Before the 1980s interest in punctuated equilibria was mostly limited to paleontologists. However during the period from the early to mid 1980s interest in the theory and its associated research programme, punctuationism, increased markedly across the whole of evolutionary science. This can readily be seen in the citation history of Eldredge and Gould’s 1972 article. The number of citations by paleontologists remained steady throughout the period but the number of citations by biologists increased markedly.

Closer examination of the literature reveals that the reason biologists became more interested in punctuated equilibria during this time was that they felt they had to answer the punctuationist challenge to synthetic theory. That is, they were not so much interested in the theory of punctuated equilibria itself - they did not actually intend to try and use the theory as the basis for research. Rather they were more interested in showing

that it did not have the impact on synthetic theory that the punctuationists were claiming. This was especially true of population geneticists who, given that their discipline was the basis of synthetic theory, had the most to lose.

Scientists involved in the debate over punctuated equilibria have always displayed a diverse range of interests. This was particularly true in the period from the early to mid 1980s, simply because the number of scientists interested in punctuated equilibria and the range of disciplines represented was greater than during any other period. There were two principal interests that were shared by almost all of the protagonists – an interest in promoting the authority of their own discipline and an interest in the pursuit of universal 'facts'.[183]

The pursuit of these two interests, however, resulted in very different strategies depending on which discipline the particular protagonist came from. For the punctuationists, who were mainly paleontologists, it was easy to combine the two interests. Indeed the entire punctuationist research programme was constructed to cater for the simultaneous pursuit of these two interests. However for the syntheticists, who were mostly population geneticists, the simultaneous pursuit of these two interests posed more of a dilemma. Maynard Smith was the first to devise a rhetorical strategy to deal with the situation. He split punctuated equilibria into two parts. The first part could be safely accepted as an interesting idea without endangering the authority of population genetics. The second had to be rejected outright. Many syntheticists followed his (rhetorical) lead.

The ambit claims of the punctuationists (particularly Gould – see Section 5.3.3) had the hoped for effect, in that the population geneticists during this period seemed to accede to paleontology's demands for theoretical independence in exchange for allowing natural selection to remain unchallenged as the central microevolutionary process. After Gould made his radical claims about the consequences of punctuationism for neo-Darwinism the syntheticists were so preoccupied with defending their authority over microevolution that they hardly seemed to notice that the paleontologists had taken macroevolution away from them. Alan Templeton's response is a good example of this (Section 5.4.4). Ostensibly his article was an attempt to discuss punctuated equilibria but in reality all he did was re-emphasise the strengths of his own discipline, population genetics.

In social terms, then, it seems that by the mid-1980s the punctuationists had achieved their number one objective – they had gained a measure of independence for paleontology from the sovereignty of population genetics. To be sure, the processes of population genetics (natural selection and adaptation) were still considered to be the foundation of almost all evolutionary change at the microevolutionary level, and in absolute terms were thus still the foundation of macroevolutionary trends as well. However the punctuationists had managed to create theoretical independence for macroevolution – they had convinced most of their evolutionary colleagues that the processes of microevolution could not be used to predict the patterns macroevolution. Paleontologists naturally became the masters of the new, independent, macroevolution, the punctuationists having carved out a niche of authority for them.

[183] 'Facts' in this sense being ideas that the scientist truly believes are a good description of the data that they have procured, are useful to other scientists and will gain peer respect for the particular protagonist.

This new social order can also be exemplified by comparing the widespread admiration for Vrba with the disdain for Gould. After his radicalism of the early 1980s Gould became something of a pariah in many circles of evolutionary science. His ambit claims may have had the effect he had hoped for; however they also had the side-effect of leaving him, in the eyes of many evolutionary scientists, permanently associated with such radicalism. Vrba, on the other hand, symbolised the new order. In her reformulation of species selection she steered well clear of any challenge to the omnipotence of natural selection in microevolution, indeed was overt in her recognition of it, and made sure her theorising was limited to her own area of authority, macroevolution.

After the controversy of the early to mid 1980s the debate over punctuated equilibria cooled down. The punctuationists had achieved their initial objective – they had broken the authority of population genetics over macroevolution and claimed the territory for themselves. The syntheticists were comfortable with the new order – microevolution, which is a much larger field than macroevolution in research terms, was still theirs and macroevolution had never really been that important to them anyway – it was not the basis of substantial research for them. However debate over punctuated equilibria has never disappeared entirely. It has continued on a low simmer right up the present, being fuelled mainly by the egos of the most famous actors from both sides of the drama – Gould and Eldredge on one side, Maynard Smith and Dawkins on the other. The occasional outburst of hostility has kept the debate fresh in people's minds.

The rest of the evolutionary science community have, since then, pretty much got on with their jobs. For most evolutionary biologists this has meant simply continuing on their merry way – in the end punctuated equilibria had no effect on their practice. However within paleontology punctuated equilibria has become an indispensable theory, essential for any paleontologist studying macroevolutionary trends and for many paleontologists and a few evolutionary biologists, punctuated equilibria has become the basis of large research programmes.

Chapter 6

The late 1980s and the 1990s.

6.1: The history.

6.1.1:Summary.

From the mid-1980s on the intensity and scale of the controversy over punctuated equilibria decreased although the theory remains controversial.[184] Indeed the theory is still the locus of heated debate and has maintained a reputation as an unsettled issue in evolutionary science. This is largely due to the fact that many of those that have continued to argue about punctuated equilibria are high-profile scientists and scientific commentators (such as Gould, Maynard Smith, Eldredge, Ruse and Maynard Smith). There has been no substantial change in the rhetorical structure of the discussion between these scientists, except perhaps that at different times each side has declared victory (see, for instance, (Gould and Eldredge 1993) and (Maynard Smith 1993)) This high profile dispute has hidden the fact that for most biologists and paleontologists punctuated equilibria is no longer controversial and has carved out a comfortable niche for itself within which it has continued to grow.

Within paleontology punctuated equilibria has had two significant impacts. Firstly the punctuationist history of paleontology, in which paleontology was the ugly duckling of the evolutionary sciences that became a swan under the auspices of punctuationism in the 1970s, has become generally accepted. Paleontologists no longer doubt their own authority to make theoretical assertions about macroevolutionary patterns and they see punctuated equilibria as the precursor that led to this way of thinking. Secondly punctuated equilibria has become recognised as one of several important models of macroevolutionary change[185] and as a valid foundation for large-scale research programmes.

In general biologists have come to respect the independence of paleontology and its authority over macroevolution. Punctuated equilibria played an important role in the formation of this belief in the early 1980s, stimulating discussion on the topic. After the mid-1980s, however, many biologists came to view the theory as irrelevant to their discipline. They continued to respect it for the historical role it played and recognised that it probably had important applications within paleontology but in the end found that it was not a fruitful source of research agendas. There have been a few important exceptions to this trend, with biologists such as Stanley Salthe continuing to investigate

[184] The citation analysis of Eldredge and Gould's 1972 article (Section 3.4) and the section in this chapter detailing scientists' responses to a questionnaire about punctuated equilibria (Section 6.2) sections contain evidence for the assertions made in the following paragraphs.

[185] Paleontologists now recognise a full spectrum of macroevolutionary models as possible descriptors of macroevolutionary change (see Section 6.1.3).

the relationship between microevolution and macroevolution (or, socially speaking, between paleontology and biology) sometimes in concert with paleontologists.

Looking back over the period since the mid 1980s and over the whole field of evolutionary science we can thus discern three separate movements in which punctuated equilibria was central – continued debate by high-profile scientists about the significance of punctuated equilibria, paleontological research about the significance of punctuated equilibria for macroevolution and (some) biological research about the impact of punctuated equilibria on microevolutionary theory. These three movements were all linked by an interest in examining the relationship between macroevolution and microevolution. However there is one major difference between the former and the latter two. In the first movement punctuated equilibria was (and is) still an object of dispute, one side claiming that it is crucial to all evolutionary theory the other that it is insignificant. In the second and third movements punctuated equilibria was no longer an object of dispute, having become recognised as an at least common macroevolutionary pattern whose frequency and consequences needed to be investigated.

6.1.2: Two books and a controversy.

The year 1989 was a red letter one for both Eldredge and Gould. Eldredge published his book *Macroevolutionary Dynamics: Species, Niches and Adaptive Peaks*, in which he attempted to address the issue of adaptation from a punctuationist perspective (Eldredge 1989). Gould's *Wonderful Life: The Burgess Shale and the Nature of History* was also published that year and went on to become a best-seller. (Gould 1989) This book, in which Gould described new interpretations of fossils from the Burgess Shale and then used them to illustrate his philosophy of evolution, sparked a small controversy focussed on issues similar in nature to the larger controversy over punctuated equilibria. In the 1990s both Eldredge and Gould sought to expand the punctuationist research programme. The examination of the aforementioned publications that follows illustrates the directions they took.

In the preface to *Macroevolutionary Dynamics* Eldredge asserted that it was time to refocus attention on adaptation. Over the previous 20 years attention had been diverted "from the traditional Darwinian focus on adaptive transformation of the phenotypic properties of organisms through natural selection." He claimed that additional causal elements, from the level of the gene up to species selection, had been added to scientists' understanding of evolution but that the processes that cause adaptation had correctly remained "the central theme of theoretical evolutionary biology." And yet, he declared, the processes of adaptation had continued to be poorly understood. In particular he asserted that "we still do not know very much more about the nature of the processes underlying the stasis and change of phenotypic features than Darwin himself was able to specify" and went on to list the kinds of questions he believed should be asked about these processes: "When does adaptive change occur in evolution? What determines the stasis so commonly observed throughout the histories of most species? What factors govern the degree of adaptive change when it does occur?" ((Eldredge 1989) pp.vii-viii)

Macroevolution was thus an attempt to resolve the macroevolution-microevolution divide or, in social terms, an attempt to communicate with biologists.[186] In this attempt to communicate, however, he did not venture outside the punctuationist stronghold. He assumed punctuated equilibria to be accepted as predominant and framed all queries in punctuationist terms. His book must thus be seen as an attempt to move the topic of adaptation within punctuationist territory and claim it as his own rather than to meet biologists halfway. Eldredge, it seems, had come to believe that without an account of adaptation no explication of evolution could be complete and thus moved to complete the punctuationist world-view by directly addressing the issue.

In the first half of *Wonderful Life* Gould provided an historical account of the collection and interpretation of Cambrian fossils from the Burgess shale.[187] The first paleontologist to analyse these fossils was Charles D. Walcott early in the twentieth century, who interpreted the myriad organisms as ancestors of modern phyletic groups. The science community accepted his interpretations and Walcott's collection sat neglected in dusty museum drawers until the 1970s when a team of paleontologists (Harry Whittington and his students Derek Briggs and Simon Conway Morris) re-examined the fossils with modern techniques. They found that Walcott's phyletic interpretations were, in many cases, extremely inaccurate and re-classified them. In many cases they could not place the organisms within modern phyletic groups.

Gould regarded Whittington and company's caution in classifying the new organisms as evidence that they represented new phyla and claimed that in Cambrian times there was thus many more phyla than now or at any other time in evolutionary history (the phylum is one of the major groupings in taxonomy – it describes the basic body-plan). The mass extinction that followed the Cambrian explosion, in Gould's account, thus had the effect of decreasing diversity for all time to come. He contended that, in phyletic terms, the tree-of-life looked more like a Xmas tree than a conventional one – wide at the base and thin at the top. Gould also claimed that the Burgess Shale fossils proved that if one 'replayed life's tape' things would turn out differently, that the phyla that survived the Cambrian extinction had done so only by chance and that if history were replayed a totally different set of phyla (and therefore body-plans) would survive. Gould thus used Whittington and company's reinterpretations of the Burgess Shale fossils as evidence for one of his favourite theses – that history is a 'contingent process' and that evolution is, in the long-term, an essentially non-deterministic process. If we accept this as being the case then, by consequence, we must also accept that evolution is not adaptive in the long term. In this sense then his book *Wonderful Life* must be placed on the 'heuristic periphery' of the punctuationist research programme.

Gould's reading of the Burgess Shale provoked a great deal of discussion, most authors disagreeing with his interpretation. Partly this was because many of the species that he had declared to represent new phyla were later found to be members of existing ones. He had, it seems, jumped the gun, interpreting Whittington and company's initial caution about classifying the new species as evidence that they were unclassifiable. Indeed, the principal researchers later disputed Gould's interpretation of their work (see

[186] As I have reiterated throughout this thesis these two interests are mirror images of one another.

[187] The Burgess Shale fossils are particularly important for two reasons. Firstly soft body parts have been fossilised, a rare process that provides the paleontologist with extra insight into the physiology of the organisms. Secondly the fossils are from the period just after multi-cellular life first appeared on the planet.

(Briggs, Erwin et al. 1994) and (Conway Morris 1998) for instance). Conway Morris gave a particularly harsh assessment in his own book about the Burgess Shale - in fact it seems that one of the principal motivations he had for writing it was to debase Gould's assertions. In the introduction he described the latter's world-view as "arid" and "deeply flawed" (p.9) Throughout the book he repeatedly declared Gould's assertions about the Burgess Shale to be either erroneous or trivial, summarising his thoughts about *Wonderful Life* with the following statement: "I hope by now that I have persuaded you that whatever importance is attached to the Burgess Shale, it is not in the operation of either historical contingency or in the fable of re-running the film of the history of life." (p.205) The crux of Conway-Morris's argument against Gould was that evolutionary convergence makes historical contingence unimportant - that whilst it may be true that the destiny of particular lineages is decided by essentially random processes particular biological features will become manifest regardless. Most of *Wonderful Life*'s critics made the same point. Maynard Smith, for instance, pointed out that both eyes and flight have evolved independently many times (Maynard Smith 1992). Their criticism can thus be seen as an attempt to debase Gould's claims about evolution being essentially non-adaptive in the long term.

A comparison of Eldredge's *Macroevolution* and Gould's *Wonderful Life* reveals the diverging approaches they took to further development of the punctuationist research programme. Both had a strong commitment to strengthening paleontological authority over macroevolution but they differed in their perspectives on adaptation. Eldredge thought that the time had come to recognise adaptation as central to any understanding of evolution and sought to provide a macroevolutionary, punctuationist account of it. Gould, on the other hand, held that adaptation was insignificant at macroevolutionary levels. He contended that the widespread belief in long-term adaptive progress in evolution was a product of anthropocentric bias. Over the 1990s Gould was particularly vocal on this topic and was eventually inspired to formulate his ideas in a large monograph, the book *Full House*, in which he argued that evolution's apparent progress towards increasing complexity is actually an artefact of random variation constrained by a lower limit.[188] (Gould 1997b)

6.1.3: The overall influence of punctuated equilibria on paleontology.

In July 1992 paleontologists, Doug Erwin and Richard Anstey organised a symposium, held at the National Meeting of the Geological Society of America in Chicago, to celebrate the twentieth anniversary of the publication of Eldredge and Gould's 1972 punctuated equilibria article. A similar symposium was also held in Cincinnati in October of the same year. This was a rare event in science – a celebration of

[188] Gould's argument proceeded thus: the complexity of life has a lower limit in single celled animals but no upper limit; long-term evolution is random with respect to complexity (that is, a decrease in complexity is equally as likely as an increase); systems consisting of random walks limited on one side but not the other will spread away from the limit; humans have misconstrued the elongation of the tail of this spread as a march towards higher progress. Gould used the analogy of the drunk on the sidewalk to illustrate his argument. A drunk stumbling randomly back and forth on a pavement with a wall on one side and a gutter on the other will eventually end up in the gutter for the simple reason that he bounces of the wall but falls into the gutter.

the milestone of a discourse. In evolutionary science celebrations are usually reserved for the anniversaries of Darwin and his work (his 150th birthday, 100 years since publication of *The Origin of Species*, etc.).

The fact that paleontologists chose to acknowledge twenty years of punctuated equilibria was an implicit recognition that it remained an important theory for them. Erwin and Anstey later cited the symposium presentations as the inspiration for their (edited) book *New Approaches to Speciation in the Fossil Record* (discussed at length below). However neither Erwin nor Anstey were strong supporters of punctuated equilibria - neither has found strong evidence for it in their own research. Rather they simply recognised that punctuated equilibria had played an important historical role in establishing macroevolutionary patterns as a focus for research.

In the 1980s many of the critics of punctuated equilibria characterised it as a flash-in-the-pan, an idea that only became well known because of the writing skills of Gould. They alleged that it has no substance and that its influence would thus gradually dwindle away to nothing. It must be said that, as far as paleontology is concerned, this does not seem to be a good representation of the status of the theory. Rather, in a number of ways, it has indeed been very influential in paleontology. The question is "In what way is it important?" Is it simply the case that Eldredge and Gould challenged the hegemony of population genetics in evolutionary science? Clearly punctuated equilibria contributed to the rise of paleontology as a major speaker in evolutionary discussions. But has its influence spread beyond the purely rhetorical? Has it spawned any research programmes?

New Approaches to Speciation in the Fossil Record is a collection of ten articles about species, speciation and what the fossil record has to tell us about them and is a good exemplar of the influence of punctuated equilibria in paleontology. (Erwin and Anstey 1995) In their introductory chapter editors Erwin and Anstey professed two motivations for gathering the collection: "First, paleontology was largely ignored by Daniel Otte and John A. Endler in their 1989 edited volume, *Speciation and Its Consequences.* Yet in our view paleontology must play a pivotal role in understanding speciation. Second, we were spurred to action by the fine papers presented at the symposium the two of us organized to commemorate the twentieth anniversary of the 1972 paper by Niles Eldredge and Stephen Jay Gould, …" (p.1). These two motivations are illuminating, especially the first which illustrates the lack of disciplinary cross-fertilisation between paleontology and evolutionary biology. Basically Erwin and Anstey were saying 'they published their book on speciation, so we'll publish ours'. I think it is safe to assume that not many evolutionary biologists read Erwin and Anstey's book and that not many paleontologists read Otte and Endler's.

The fact that *New Approaches to Speciation in the Fossil Record* was partly inspired by a symposium to celebrate punctuated equilibria's 20th year might suggest that it is not a good candidate for an objective appraisal of the influence of the theory. However the editors stressed that the articles should be about *new* ideas and not cover old debates:

> "Eldredge and Gould's paper sparked a wide-ranging (and often divisive) debate on patterns in the fossil record as well as some fundamental conceptual advances. It also encouraged paleontologists to examine evolutionary

> patterns with new ideas in mind and to develop new approaches to testing hypotheses with the data of our profession. In organizing the symposium, and this volume, we decided to emphasize newer approaches to analyzing speciation patterns in the fossil record, particularly the contributions of younger paleontologists. We sought to avoid reopening many of the (often fruitless) debates which so exercised evolutionary biologists, sociologists, paleontologists, and others during the first decade following the proposal of punctuated equilibria. So as not to simply revisit the arguments and unresolved debates of the 1970s, we decided to exclude discussions of species selection and many other aspects of the controversy over punctuated equilibria versus phyletic gradualism." (p.2)

So, balancing the fact that the book was inspired by a symposium where punctuated equilibria was the main focus, was the conscious effort of the authors (or at least the editors) to avoid previous and debates about the theory. However punctuated equilibria still has a very prominent position in the book - of the ten research articles, five of them were about punctuated equilibria and four where strongly informed by it.

I asked one of the editors, Robert Anstey about the influence of punctuated equilibria in the book:

GRIMSHAW: "I've had a good look at '*New Approaches* …' I understand that the book was inspired by a celebration of punctuated equilibria's birthday. Hence it is not surprising, I guess that all the articles are either about or are strongly informed by punctuated equilibria. However you did say in the introduction that you wanted to focus on new topics rather than old debates. Hence I found the emphasis on punctuated equilibria a little surprising."

ANSTEY: "The question about the influence of PE [punctuated equilibria] in *New Approaches* is well taken As a stereotype alongside its partner stereotype, PG [phyletic gradualism], both dominate the discussion of evolutionary tempos. Other tempos have emerged since 1972. These include punctuated gradualism, simultaneous gradualism and punctuation, versions of semi-gradualism, semi-punctuation, and mosaic evolution. …

Prior to PE [punctuated equilibria], most paleontologists working with evolutionary goals focused on transitions among species, or among genera, or even families. This tradition of studying evolution within higher taxa rather than within species extends well back into the 19th century, and has produced such venerable icons as the evolution of the horse. Evolution within species was considered both less interesting and less tractable because of the difficulties of detailed sampling within

> species in the fossil record. Taxonomic practices in paleontology were dominantly typological up into the 1960s, and variation within species was, apart from a few studies like that of Gryphea, either unknown, unresolved stratigraphically, or in some lineages so large as to frustrate the efforts of taxonomists trying to identify things. Books like "Quantitative Zoology" by Simpson et al. were beginning to direct the study of variation in fossils, and new multivariate statistical techniques were beginning to influence taxonomic studies through the end of the 1960s. Numerical taxonomy was still relatively novel in paleontology in 1972. The PE "paradigm" then coincided in time with the arrival of new analytical tools that suddenly made the analysis of intraspecific variation not only possible, but potentially interesting as well. I do credit E&G [Eldredge and Gould] with creating interest in levels of variation that had hitherto been ignored." (personal communication, 6/10/99)

In the introduction to *New Approaches* Erwin and Anstey presented a table summarising the previous 22 years of paleontological studies of evolutionary tempo. They found that "[no] single pattern appears dominant, and their variety suggests that new research agendas are needed to investigate the conditions under which any one of them might be predicted", and that the "greatest departure [from Eldredge and Gould's predictions] may be the preponderance of studies illustrating *both* stasis and gradualism in the history of a single lineage." Hence it seems clear that as of 1995 punctuated equilibria, whilst remaining an important macroevolutionary model, had not become the covering theory that Eldredge and Gould had hoped it would become. However it is also clear that punctuated equilibria had achieved its authors number one objective – it had given paleontologists the confidence to make authoritative statements about macroevolution.

6.1.4: Can biology and paleontology be reconciled?

One of the major proclamations of the punctuationist revolution was that the relationship between microevolution to macroevolution as constructed by the proponents of the Modern Synthesis was no longer valid. In disciplinary terms, the punctuationists rejected the extrapolation of theory from population genetics into the realm of paleontology. Over the course of the debate scientists from both sides have attempted to forge a new relationship between macroevolution and microevolution. Generally, however, such attempts have suffered from two major problems.

First, the imposed criteria for a valid punctuated equilibria/phyletic gradualism test have proved difficult to satisfy. In essence the punctuationists asserted that to test for punctuated equilibria in the fossil record one needs to look at species that are geographically widely dispersed and are well represented in long stretches of geological strata known to have been deposited at a uniform rate. To make a comparison with extant

descendant species it is also required that the fossil record of the species involved remain unbroken up to the present. These criteria cannot readily be met. Relatively large amounts of money and time would be required and a potential researcher would need a substantial measure of social capital to have the opportunity to undertake such a programme and even then they would want to be sure that such research would be fruitful – the success of a scientist's career being dependant on producing results. In essence *any attempt to meet the criteria for a valid test of punctuated equilibria required a large commitment.*

The second major problem was the poor quality of communication between biologists and paleontologists. Scientists from both sides of the debate failed to understand the concerns of those from across the divide. Some authors did attempt to address issues from the perspective of the other discipline but, lacking a deep appreciation of the opposing discipline, their efforts invariably fell short. The difference between the time-scales used by the disciplines was the most common stumbling block, often causing the most basic terms of discussion, such as the word 'species', to become the topic of dispute.[189] In short, *biologists and paleontologists came to evolutionary studies with such disparate perspectives that it was very difficult for them to communicate*.

There are two ways one can attempt to bridge this disciplinary divide. One is to become an expert in both fields. This is of course an extremely difficult thing to do in this age of increasing specialisation. One needs a large amount of social capital (degrees, publications, etc.) to claim that one is an authority in a particular field. It would be extremely difficult for one person to obtain enough capital to be considered an expert in two fields. The paleontologist Elizabeth Vrba, for instance, has the reputation of being well versed in contemporary biology, but she would not profess to be an expert in the area (her work is discussed in Section 5.3.7).

The other approach is for scientists from both fields to work together on the same project. Unfortunately there are very few examples of such teamwork taking place. It has already been noted that a large commitment is required for a paleontological attempt at meeting the criteria for a valid test of punctuated equilibria. Biologists have been even more reticent to participate in such research programmes centred on punctuated equilibria, which is not surprising when the fact that punctuated equilibria is generally not considered an important theory in biology is taken into account. Indeed there is only one example of a sustained joint research programme between a paleontologist and biologist attempting to address the macroevolution-microevolution divide - the joint projects of paleontologist Alan Cheetham of the Smithsonian Institution and biologist Jeremy Jackson of the Scripps Institution of Oceanography in California. They undertaking research together since 1986, comparing data from living and fossil cheilostome bryozoans (microscopic animals that form aggregates in a similar fashion to coral).

Alan Cheetham completed his Phd in 1959 at Columbia University. In 1966 he gained a position at the Smithsonian Institution, where he has been employed ever since. He first heard about punctuated equilibria in 1971 when Eldredge and Gould presented the theory at the Annual Meeting of the Geological Society of America. In his own

[189] For biologists species are simply interbreeding populations and are thus a day-to-day proposition whilst for paleontologists species are sets of morphologically identical fossil organisms often spanning millions of years.

words, his initial reaction "was much like that expressed by many of my paleontologist colleagues", that "PE was unnecessary … [because] … everyone knows that evolutionary rates vary". In 1977 Cheetham heard Gould speak at the North American Paleontological Convention. Gould emphasised that whilst punctuated equilibria may seem obvious there were two queries that remained unanswered– the "question of whether one evolutionary pattern is prevalent" and whether evidence for stasis is being "thrown away" by paleontologists as non-data. He challenged dissenters to document "gradual change from species to species thus countering the PE hypothesis."

Gould's talk "struck a chord" with Cheetham, although at this stage he was not a convert to punctuated equilibria. Rather he resolved "to find convincing evidence that gradual patterns are common, perhaps even predominant in the taxonomic group" on which he was working. However the taxa he studied "proved to be too sporadic in occurrence to distinguish between alternative patterns" – the data did not fulfil the criteria for a valid punctuated equilibria/phyletic gradualism test. During this research he came across another taxonomic group, cheilostome bryozoa, that he thought would be able to fulfil the criteria. Working with the fossils from this group "changed my way of thinking about evolutionary patterns." After developing new statistical methods to analyse the data he found "overwhelming evidence not only for stasis but also for what Levinton … called the 'persistence criterion' (i.e. the survival of the ancestor after giving rise to the descendant)" and, by 1986, "became convinced that there is something to the PE model after all." (Cheetham 1999a)

Jackson did his Phd at Yale in the 1960s under the supervision of G. Evelyn Hutchinson, one of the most respected ecologists of the time. The subject of his research was Jamaican coral reefs. His professional association with Cheetham began in 1970, when they met after Jackson gained a position at John Hopkins University. Jackson became interested in the bryozoans that Cheetham was studying, and in the mid-1970s he spent about six months doing research in Cheetham's laboratory at the Smithsonian Institution. In the 1980s they jointly supervised the dissertation of Scott Lidgard, who went on to become curator at the Field Museum of Natural History in Chicago. Cheetham credits Jackson with "opening his eyes to the evolutionary biology literature" and lauds his expertise, saying that in terms of having research credentials in ecology, biology and paleontology he is "in a class almost by himself." (Cheetham 1999c)

Cheetham and Jackson wrote their first (formal) proposal for joint research in 1986 after the former had published the results of his research on bryozoans and had found strongly in favour of punctuated equilibria. (Cheetham 1986) Jackson had doubts about Cheetham's results, being unconvinced that that the methods he was using to delineate the fossil species could discriminate between actual species and variants of species. In Jackson's words: "Clearly, the strength of any discovery of punctuated equilibrium – a model of speciation – depends on our ability to recognize species, so I challenged him to submit his methods to biological examination." (paraphrased from (Kerr 1995)) They gathered extant bryozoan species from the Caribbean, used the same morphological criteria that Cheetham had used to delineate the fossil species then double-checked the results with protein electrophoresis (a method of determining genetic species). They found that the morphological species matched the genetic species, vindicating Cheetham's results. ((Cheetham and Jackson 1990) or, for a lay account, see (Kerr 1995))

That first project was an attempt to answer one of the main criticisms of the biologists dissenters of punctuated equilibria – that paleontologists can only recognise morphological change and cannot know when (reproductive) speciation actually took place. Jackson and Cheetham have been undertaking collaborative research ever since and have published numerous joint articles. They have continued to compare living and fossil species and have consistently found punctuated evolutionary patterns, moving on from simple tests of punctuated equilibria to exploration of the nature of the processes at work, attempting to ascertain whether the processes are deterministic or random (see (Cheetham, Jackson et al. 1994) and (Cheetham and Jackson 1995) for instance.) In their most recent article they summarised the significance of their work, asserting that almost all "cases of speciation in the sea over the past 25 My show prolonged morphological stasis punctuated by geologically sudden morphological shifts at cladogenesis [speciation]." They conceded that occasional examples of gradualism did appear but that these only served to "increase confidence in our ability to detect different patterns" and concluded that "prevalence of punctuated equilibria [in the sea], macroevolutionary trends must arise through differential rates of origination and extinction and not by adaptive evolution within single species." (p.76)

As might be expected, considering the strength of Jackson and Cheetham's punctuationist assertions, not everyone agreed with their conclusions. For instance paleontologist Robert Anstey of Michigan State University, co-editor of *New Approaches to Speciation in the Fossil Record*, believes that their exclusive "reliance on phenetic methods clouds the usefulness of their results." (Anstey 1999) Biologist Jeffrey Levinton of the State University of New York, who has followed Jackson and Cheetham's work with interest, made similar criticisms of their research in a letter to the journal *Science*, asserting that the lack of cladistic analysis results in ignorance "of the relatedness of the bryozoan species" and hence that, whilst a general punctuated pattern can be discerned punctuated equilibria "still has not been shown to be a dominant or a necessary mechanism for the generation of morphological diversity." (Levinton 1991)

However almost everyone agreed that their general approach, combining biology and paleontology, is very important. Like Anstey, paleontologist Doug Erwin of the Smithsonian Institution retains some reservations about Cheetham and Jackson's work – for instance he doesn't agree that the trends they found necessitate the existence of higher level selection (as they claimed in their 1999 paper). However he believes that "their work is probably the best anyone has done on speciation in the fossil record" and that "it is studies like Cheetham and Jackson's that will finally convince some evolutionary biologists … that a longer temporal view of the evolutionary process will reveal a broader spectrum of evolutionary phenomena than is evident from studying the past 100 years." (Erwin 2000) And in the introduction to *New Approaches to Speciation in the Fossil Record* Erwin and Anstey described Jackson and Cheetham's research as "ground breaking" (Erwin and Anstey 1995). Biologist John Endler of the University of California agrees that the lack of communication between biologists and paleontologists is a major obstacle to achieving a comprehensive view of evolution. When asked if he knew of any comparable projects to Jackson and Cheetham's he replied that he didn't and added that "it is sad that [such projects are] so rare." (Endler 1999b)

In recent years more research projects combining biological and paleontological approaches have begun to appear. ((Collins, Frazer et al. 1996), (Budd and Johnson 1996)

and (Huber, Bijma et al. 1997) for instance. Of these Collins *et al* is the most well known and like Cheetham and Jackson they found strongly in favour of punctuated equilibria.) This must be seen as a direct consequence of the success of Jackson and Cheetham's research – they have shown that the combined approach can produce quality results. It seems clear that the communication divide between paleontologists and evolutionary biologists is restricting the growth of evolutionary theory. A re-synthesis of evolutionary thought, a modern incarnation of the 1940s synthesis, is necessary and will be possible only via such united research projects.

6.2: The questionnaires.

6.2.1: Description.

During July and August of 1999 over 50 evolutionary scientists were requested to fill in a questionnaire about punctuated equilibria and related topics.[190] A total of 27 responded, twelve paleontologists and fifteen evolutionary biologists (zoologists, population biologists, evolutionary ecologists and evolutionary geneticists). The scientists were mainly from the USA, with a few from Australia and the UK. The questions were grouped into particular topics:

- Questions 1 and 2 asked when and where the scientists first encountered punctuated equilibria.
- Questions 3, 4 and 5 asked for evaluations of the theory. Specifically, 3 asked for an opinion about the value of punctuated equilibria, 4 asked about punctuated equilibria's consistency with the data of evolutionary biology and 5 asked about punctuated equilibria's consistency with neo-Darwinism or the Modern Synthesis.
- Question 6 asked if and how punctuated equilibria had influenced the scientists own research.
- Questions 7, 8 and 9 asked about species selection and species sorting. Specifically 7 asked for an opinion of their value, 8 asked for an opinion about the connection between them and punctuated equilibria and 9 asked whether they were accepted in evolutionary biology[191] and if and how they had influenced the scientist's research.
- Question 10 asked for an opinion about how much punctuated equilibria had affected paleontology's rise in status.
- Question 11 asked for an opinion about if and how socio-philosophers of science had influenced the practice of science.

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[190] A full version of the questionnaire and details regarding the collection process are supplied in the Appendix.

[191] Note that in the field of evolutionary science there is confusion regarding the term 'evolutionary biology'. Some scientists see it as including all disciplines concerned with evolution (including paleontology) others see it as referring only to biological treatments of evolution. At the time that I wrote the questionnaire I was using the former interpretation. This confused some of the respondents who, seeing species selection and species sorting as paleontological theories, did not see that evolutionary biology's acceptance or non-acceptance of said theories as significant. After this I introduced the term 'evolutionary science' to cover the entire field and restricted the term 'evolutionary biology' to biological treatments of evolution.

- Question 12 asked if the scientists thought external factors (political views, social contexts, etc) were an important influence of the practice of science.
- Question 13 asked for an opinion about how such external factors had affected the course of the punctuated equilibria debate.

6.2.2: The paleontologists.

Of the twelve paleontologists seven were practicing scientists when Eldredge and Gould's first punctuated equilibria article was published in 1972 and five were still students (four of the latter completed their doctorates in the 1980s and one in the late 1970s). There was a marked difference in the character of responses between these two groups whom I shall refer to respectively as the 'Scientists' and the 'Students' (note that all of them are now practicing scientists).

***Questions 1 and 2*:**

All the 'Scientists' encountered punctuated equilibria within a year of the publication of Eldredge and Gould's 1972 article either from the article itself (4), from Eldredge and Gould's presentation of punctuated equilibria at the Geological Society of America symposium in the same year (2) or from discussion with Eldredge and Gould (1). All the 'Students' first encountered punctuated equilibria in their undergraduate courses.

***Questions 3, 4, 5, 6 and 10*:**

All twelve of the paleontologists credited punctuated equilibria with having made an important contribution to paleontology. However there was a marked difference in enthusiasm between the 'Scientists' and the 'Students'. The 'Students' gave far more credit to punctuated equilibria for revitalising paleontology and for legitimising paleontological theory and data than did the 'Scientists'. Indeed all five of them were extremely positive in their appraisal of punctuated equilibria in this respect whilst the 'Scientists' were rather ambivalent. I classified three of the 'Scientists' as showing a positive response and four a neutral response.[192] However even the positive responses of the 'Scientists' were generally less enthusiastic than that of the 'Students'. Some excerpts from the questionnaires will illustrate this point[193]:

Positive

Student A: **"**It certainly stimulated much research, even though the idea was not new, it was the restating of the idea at the right time, and was the major paradigm in paleontology for the next 20 years. … It did seem to re-energize the field of paleontology and give shape to much subsequent research."

[192] I did not class any of the responses as 'negative' as, compared to some of the evolutionary biologists, none of the paleontologists were actually hostile to punctuated equilibria. The category 'negative' was thus reserved for the responses of said evolutionary biologists.

[193] Note that all quotes are unedited except for obvious spelling errors. Hence some faulty grammar and slang terms (such as 'punc eq') are evident.

Student B: “To me the greatest contribution of punc eq has been to focus our attention on the predominance of stasis and the mechanisms for stasis and on the implications of stasis for large-scale rates and trends.”

Student C: “I think punctuated equilibria is an important concept that changed the way most paleontologists (and perhaps biologists – I speak from the perspective of paleontology) think about the evolutionary process and how it should be preserved in the fossil record.”

Student D: “It helped give paleontology, specifically the patterns observed in the fossil record a legitimacy, that they tended to lack previously.”

Student E: “… it focused attention on the issue of how good the fossil record really is, and what questions can be asked of it, and when can we get reliable answers to these questions.”

Scientist T: “The punctuated equilibria idea is part of the expansion of an interest in the interaction between philosophy and geology and biology. This is an important development … The model has initiated a large research program, and has made an important contribution to the science.”

Scientist W: This scientist gave a long personal account of how he initially rejected punctuated equilibria and started a research programme to show that “gradual patterns are common, perhaps even predominant in the taxonomic group on which I work.” During the course of this research, however, he apparently found “overwhelming evidence not only for stasis … but also for … the ‘persistence criterion’.” Hence he became convinced that “there is something to the PE model after all.”

Scientist Z: “The punctuated equilibrium idea (PE) provides a plausible answer to one of paleontology's oldest questions: Why are so few forms intermediate between species found in the fossil record? In other words, Why do we not find Darwin's ‘finely graduated chain?’ Ever since Darwin, we have known that species usually appear suddenly in the fossil record and show little morphologic change during their time span. As exploration of the fossil record proceeded, the conventional explanations (gaps in the record or in its study) became less and less credible. Eldredge & Gould suggested a biological explanation which was testable.”

Neutral

Scientist U: “It is useful to the extent that it meshes with ideas about allopatry in speciation. In that it is also readily explicable in the Darwinian paradigm I don't believe it is as 'revolutionary' as originally claimed.”

Scientist V: “…I regard P.E. as a potential pattern that fossil species could display. Investigating actual patterns, however, is a research agenda that regards P.E. as one of many possibilities.”

Scientist X: “Value? To make people think It is probably right in part, it is useful as it made people question gradualism. Necessary? Not any more. It added to knowledge at that time.”

Scientist Y: “I think the theory is one end of a continuum between slow, ‘anagenetic’ change …”

The fact that the ‘Students’ gave more credit to punctuated equilibria for revitalising paleontology than the ‘Scientists’ suggests that Eldredge and Gould’s reconstruction of paleontological history has been effective. Those scientists trained after the creation of punctuated equilibria, the ‘Students’, seemed to take it for granted that paleontology needed to be delivered from the doldrums and that punctuated equilibria had effected that delivery. Those who experienced the period of history in question, the ‘Scientists’, generally agreed that paleontology had come a long way since the early 1970s but were more likely to put the movement down to a combination of events (various research programmes, technical changes, etc.). They did not see punctuated equilibria as causal in the movement so much as part of it. However it should be taken into account that envy may be playing a role in the ‘Scientists’ appraisal of punctuated equilibria. They may resent the attention that punctuated equilibria has received, the credit it had been given for the (apparent) rise of paleontology whereas the ‘Students’, having entered paleontology after the creation of punctuated equilibria would have no such reason to be envious.

It should also be remembered that Eldredge and Gould attempted to construct a certain amount of disciplinary antagonism with punctuated equilibria. That is, they cast population genetics as a dictator to which paleontology was subservient. However there was little evidence in the questionnaire replies that this had entered the typical paleontologist’s state of mind. Indeed only two of the respondents displayed any such antagonism. Still, their replies in this respect are interesting:

Student E: (In response to Q.4) “Population geneticists, an increasingly irrelevant bunch, have developed models which mimic the pattern, so at least some of them are happy.”

Scientist Z: (In response to Q.5) “Population geneticists have been quickest to attack PE – because, I guess, they found no credible mechanisms for stasis over millions of years. … PE is surely at odds with Darwin and with most of the modern synthesis because it postulates long periods (millions of years) of no significant evolutionary change.”

Indeed almost all the paleontologists thought that punctuated equilibria was consistent with synthetic theory. However over half (7 of the 12) also mentioned that stasis was the crucial observation of punctuated equilibria and was something that had not been predicted by the Modern Synthesis. For instance:

Student D: “I don't think evolutionary biology would have predicted stasis, and certainly could not have predicted what the exact distribution of types of change actually are.”

Student B: “If stasis is the rule, then macroevolutionary trends cannot simply be reduced to trends within single lineages.”

Question 10 asked specifically for the respondent’s opinion about punctuated equilibria’s role in paleontology’s rise in status. Opinion was quite polarised, nine of the twelve paleontological respondents believing that punctuated equilibria had been influential in this respect and three (Scientist Y, Scientist X and Student A) believing that

it had had no influence.[194] Of the nine positive responses four could be classed as 'quite positive' and five as 'very positive' about the role of punctuated equilibria in revitalising punctuated equilibria. A few quotes will illustrate this:

Negative

Scientist Y: "I see no special significance of paleontology to PE."

Student A: "I'd like to think that theoretical paradigms like "punk-eek" are responsible for your view that paleo has been ascendent (I'm not sure that is correct? On what do you base this observation?). I tend to think the book and movie "Jurassic Park" have a larger impact on the field than our esoteric theories. If people ever tire of dinosaurs, paleo will fall off the radar screen of public awareness."[195]

Quite positive

Student E: "PE is merely a component of a shift from a largely descriptive field to one developing pattern-based, and now process-based models."

Scientist T: "The shift to "Paleobiology" has been a major development, and punctuated equilibria is an important part of this. (Along with plate tectonics, island biogeography, paleoecology, mass extinctions, computer and statistical tools, and so on.)"

Scientist U: "It helped. It was the first of a number of paleontologically-derived pattern theories …"

Scientist Z: "Probably quite influential."

Very Positive

Student B: "Very. It is now clear that, to understand large-scale patterns in the history of life, it is not enough to study patterns on short time scales and extrapolate."

Student C: "Very influential - helped change image of paleontology from "stamp collecting" to hypothesis testing and demonstrated that paleontology can have a key role in formulating evolutionary ideas."

Student D: "In a deep sense, highly influential, in that it helped catalyze the independence of paleontology, perhaps most importantly in the minds of paleontologists, but also in the minds of those in allied fields."

Scientist V: :[The debate over punctuated equilibria] has allowed the perception that paleontologists have a claim to status as evolutionary biologists."

Scientist W: "I think PE has had a significant impact."

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[194] The latter two questioned whether paleontology had actually risen in status. The question was worded in a leading fashion, assuming that paleontology had achieved a rise in status over the last thirty years. I was actually surprised that more respondents did not question this.

[195] As is apparent, this respondent assumed that I was referring to an external rise in status for paleontology where all the other respondents assumed, correctly, that I was referring to an internal rise in status.

Question 6 asked how punctuated equilibria had influenced the particular scientists research. The responses came in four forms:

- Three respondents credited punctuated equilibria with having directly initiated a major programme of research (2 'Scientists' and 1 'Student').
- Four responded that punctuated equilibria had little or no influence on their research (3 'Scientists' and 1 'Student').
- Two responded that punctuated equilibria had had a moderate influence on their research – that is they had published a few articles on the subject but had not undertaken a major programme of research (2 'Scientists').
- Three of the students credited punctuated equilibria with having cleared the way for their research without having directly initiated it, once again demonstrating that Eldredge and Gould's reconstruction of the history of punctuated equilibria has been most successful with the post-punctuated equilibria generation. For instance:

Student A: "It really hasn't influenced the direction of my research, but it has given me a framework with which to look at my data."

Student B: "Much of my work uses modeling in which species origination and extinction (rather than evolution within lineages) constitute the "raw ingredients." This approach makes sense in light of punctuated evolution (although it makes sense in other ways as well). It's not so much that I decided to use these evolutionary models because of punctuated equilibrium, but I think that the intellectual world in which I work finds this sort of modeling acceptable or sensible at least in part because punc eq paved the way."

Student D: "Not much in detail, but in some sense my own research is the same vein - that the fossil record has its own story to tell independent (but cognizant of) studies in evolutionary biology."

***Questions 7, 8 and 9*:**

In answer to Question 7 eight respondents gave positive opinions about the value of species selection and species sorting, three gave negative opinions and one said he didn't know enough about it. All five of the students were in the positive category, once again showing that the punctuated equilibria 'revolution' has been most influential amongst the new generation. The negative respondents believed species selection and species sorting to be weak effects and/or to be untestable.

Seven of the eight positive responses were fairly vague in nature – they thought the idea sounded good but didn't really know much about it. For example 'Student C' replied "It makes sense to me that there may be some traits of species that are acted upon in a way not reducible to selection at the level of the individual" and 'Scientist X' simply wrote "Sounds sensible". 'Scientist' W was the only one who seemed to have a good working understanding of species selection and species sorting – he wrote that "selection of individuals" cannot explain "long term trends" and that species selection and species sorting, via a "hierarchic structure", are necessary to "preserve the Darwinian model of evolution."

Question 8 asked for the respondents opinion of the connection between punctuated equilibria and species selection. Six of the paleontologists, including two of the students, replied that there was no connection at all, that each can occur independently of the other. Of the six who thought there was some connection only one

actually said that he thought punctuated equilibria implied species selection. The other five gave qualified positive responses, seeing the ideas as connected but believing that species selection (or species sorting) was a natural consequence of punctuated equilibria. For instance 'Scientist' T wrote that the "ideas are linked broadly, but there is not a simple relation", 'Scientist' W thought that stasis was a necessary but not a sufficient condition for species selection and/or species sorting and 'Student' E thought that punctuated equilibria implies species sorting but not species selection.

Question 9 asked whether the respondent thought species selection was generally accepted in evolutionary biology and whether it had influenced their own research. None of the respondents thought that species selection was a generally accepted theory. Three respondents said they didn't know how accepted species selection was, one said she didn't care, seven of the respondents thought it was not generally accepted and one said it was not an issue. In retrospect this half of the question was badly worded. It would have been better to ask whether it was generally believed that species selection was a strong evolutionary force (i.e. strong enough to challenge the domination of individual selection). One suspects that the general response to such a question would have been a categorical no.

Despite the above negative response six of the respondents said that species selection had influenced their own research. However in only one case ('Scientist' W) was species selection a central part of a research programme. The other five had only limited contact with the theory. For instance 'Student' C said "Some of my research has been involved in testing hypotheses related to species selection". Four of the positive responses were from 'Students' which means that five of the seven 'Scientists' said that species selection had had no influence on their research, once again showing that punctuationism has had more influence on the new generation of paleontologists.

It thus seems that the punctuationists (specifically Eldredge, Gould and Stanley) attempts to challenge the hegemony of natural selection with species selection has not really been a success. The paleontologists surveyed here expressed generally positive opinions about species selection and species sorting but none of them thought that either idea was widely accepted and only one has made species selection a central part of his research. Also it must be said that punctuationist attempts to convince their peers that species selection is implied by punctuated equilibria has not been a success – only one respondent ('Student' B) agreed that such was the case and this was not the same individual ('Scientist' W) that was actually doing research with species selection!

***Questions 11, 12 and 13*:**

Questions 11, 12 and 13 sought respondents' opinions about the influence of socio-political forces on science. All but two of the respondents had read at least some sociology or philosophy of science literature and a few had read quite widely. Of the ten who had read some sociology of science two professed it to have had no influence on their work. The other eight thought that reading Kuhn and/or Popper had in some way clarified their reasoning. Popper's idea of science as hypothesis testing was particularly popular, with five citing his ideas as being particularly influential. The newer Sociology of Scientific Knowledge movement was less popular, with only two referring to it. 'Scientist' T wrote that he "is not in favour of extreme relativism" but is also against

"dogmatism" while 'Student' E wrote that he thinks "sociology of science … to be drivel written by people who neither understand science or how to write."

Ten of the twelve respondents did believe that socio-political factors have a significant impact on the development and/or practice of science, but interestingly only eight thought that this was the case with the punctuated equilibria debate. A wide variety of social effects were identified by the latter. Four said that Gould and his professed Marxism had hampered the acceptance of punctuated equilibria, although one of these pointed out that there are Marxists on both sides of the debate (Maynard Smith has a Marxist background). One thought Eldredge and Gould's challenging presentation of punctuated equilibria had polarised the community to the detriment of the science while another thought the same style of presentation was an important factor in spurring research. One scientist identified Eldredge and Gould's declaration of independence as an important step forward for paleontology. Last but not least, one thought that the philosophy of reductionism, which he believed was predominant in science, had delayed a general acceptance of punctuated equilibria.[196]

6.2.3: The evolutionary biologists.

All fifteen of the scientists in this section are 'evolutionary biologists' (the term 'evolutionary biologist' is used here in a broad sense to mean 'using the study of extant organisms to investigate evolution'). The scientists' sub-disciplines were not as easy to categorise however. I counted four zoologists, four population biologists, five evolutionary ecologists and two geneticists but almost all of them could just as easily have been put into any of several categories. It seems that contemporary evolutionary biologists are integrating many different approaches in their attempts to come to terms with the complex phenomena of microevolution. (For example Biologist G, whom I placed as an evolutionary ecologist, has a Phd in Zoology and described his research interests as: "evolutionary biology, adaptation, functional ecology, evolutionary ecology, the interface between ecology, evolution, behaviour and genetics.") This fact, perhaps better than any other, demonstrates the extent to which evolutionary biology matured as a science - different approaches from different disciplines are respected as valid and scientists are attempting to incorporate them in order to assemble coherent descriptions of the processes of evolution.

***Questions 1 and 2*:**

Of the fifteen biologist respondents seven were practicing scientists when Eldredge and Gould's 1972 article was published and all of them had either read the paper or discussed it with colleagues within a year of its publication. Of the remaining eight, four received their doctorates in the 1970s, two in the 1980s and two in the 1990s. All of them became aware of punctuated equilibria as undergrads, through a combination of exposure in evolution courses, reading literature, seminars and discussions with other students. Unlike the paleontologists there was no conspicuous difference in responses between those who were practicing scientists in 1972 and those who joined the ranks at a

[196] Interestingly 'Student' E, who was very dismissive of the Sociology of Scientific Knowledge movement, was not one of those who thought that social factors have no influence.

later date. In any event it seems that punctuated equilibria is not an obscure theory to biologists but rather has become part of their general consciousness. Biologist H, for instance, described his introduction to it thus:

> "I am not sure when I first heard of it. However, it was being discussed in the literature, and was part of the general dialogue amongst faculty and grad students. With external speakers, widespread trading of literature, and grad student seminars, we tended to be pretty current on all the major issues."

***Questions 3, 4, 5, 6 and 10*:**

Overall 8 of the biologists were generally positive in their appraisal of punctuated equilibria, 4 were neutral and 3 were negative. In general the eight pro-punctuated equilibria biologists credited the theory with having stimulated new approaches to evolutionary research, whilst the three who spoke against punctuated equilibria thought that it hadn't added anything new and had only served to confuse both scientists and the public. The four 'neutral' respondents' did not offer an opinion either way, only commenting on the empirical value of the theory. A few quotes will illustrate these trends:

Positive

Biologist A: "Yes, I feel that PE is quite useful. It produced a major paradigm shift in the way that the fossil record is regarded as well as giving us new perspectives on the nature of adaptation in stable ecosystems. Finally it made evolutionary biologists & paleontologists treat stasis as data."

Biologist D: "Eldredge and Gould showed that one cannot legislate empirical data away. … Eldredge and Gould simply said, 'The appearance of episodic changes is due to episodic changes.' In opposition to the standard, 'The appearance of episodic changes is due to missing data which must have existed because to think otherwise is to question the received view.'"

Biologist E: "I think PE (to coin a phrase) was over-hyped, but it contains an essential 'truth' about stasis. The hype was mostly about rapid transitions, which are really a non-issue. But the apparent prevalence of stasis is surprising, and may hint at some macro-level phenomena that we don't understand."

Biologist F: "I think it is a very valuable concept, and clearly describes the uneven tempo of evolutionary change. In fairness, the concept certainly had it seeds in Simpson's "Tempo and Mode" book, but E and G [brought it to everyone's attention] … Ultimately, the reality appear to lie somewhere between absolute punctuated equilibrium (where no change occurs between bursts of change) and steady gradualism."

Biologist H: "It is certainly meritorious from a heuristic standpoint, in the sense that it has directed our thinking and investigations in ways they otherwise would not have gone."

Biologist M: "It is a useful heuristic device for forcing us to think about problems in new ways. … It remains a useful teaching device and is also continuously useful in research applications."

Biologist N: "I think it was an exceedingly important concept, and it certainly stimulated research on evolutionary rates and patterns of evolutionary change."

Biologist P: "I think it is very useful, particularly as it caused the scientific community to rethink various matters."

Neutral

Biologist B: "It is an hypothesis that requires more testing before it is unequivocally accepted."

Biologist C: "Requires no special mechanisms but useful observation of empirical pattern."

Biologist K: "The theory is valid if properly defined. Either I or any other evolutionist could spend several pages explaining what we think should be included."

Biologist L: "I have no problem with it, but I do not think it added much."

Negative

Biologist G: "Most evolutionary biologists view it as verging on the silly and others as trivial. Speaking for myself it seems trivial to say that evolutionary rates are not constant in time and that there may be periods of slow and periods of rapid evolution. No one that I know (who isn't a paleontologist, and even many paleontologists) can imagine why evolutionary rates of morphology should be constant so the whole thing seemed like a non-problem."

Biologist I: "PE was entirely anticipated by Darwin and is in no way novel."

Biologist J: "I think the idea has served only to confuse and to generate misunderstanding between paleontologists and population biologists."

Fourteen of the fifteen biologists thought that punctuated equilibria did not in any way question the basic tenets of neo-Darwinism or the Modern Synthesis. Some typical opinions on this: *Biologist B*, from the 'neutrals', wrote simply: "I don't see a conflict."; *Biologist I*, from the 'negatives', asserted that punctuated equilibria had been anticipated by Darwin and was thus always part of Darwinism; *Biologist F*, from the 'positives', wrote: "… the concept certainly had its seeds in Simpson's 'Tempo and Mode' …"; *Biologist P*, also from the 'positives', placed punctuated equilibria's roots with Mayr's work on speciation.

Eight of these fourteen felt the need to explicitly express disapproval about the 'hype' or 'rhetoric' associated with punctuated equilibria. That is they displayed an interest in deconstructing the punctuationist version of the history of evolutionary science and replacing it with their own history, in which punctuated equilibria is simply a new horse in the neo-Darwinian stable. They seemed prepared to give paleontologists a higher spot in the pecking order, but did not want to radically alter the authority structure of the field. This kind of deconstruction might be expected from those in the 'negative' category. However six of the eight came from the 'positive' category. Hence it seems that

whilst evolutionary biologists are prepared to accept punctuated equilibria as an interesting theory they reject the rhetorical constructions that revolve around it.

A few excerpts will be sufficient to illustrate this trend:

Biologist G, from the 'negatives', was the most disparaging - "No one that I know (who isn't a Paleontologist, and even many paleontologists) can imagine why evolutionary rates of morphology should be constant so the whole thing seemed like a non-problem. We were flabbergasted to hear that "most" paleontologists (to whom Eldredge and Gould were talking) thought that rates were constant." He thus rejected the idea that phyletic gradualism has dominated perspectives on macroevolution, which is a keystone of the punctuationist version of the history of evolutionary science.

Biologist E from the 'positives' was more circumspect but still rejected the punctuationist authority-challenge: "I don't think people see it as a major challenge to orthodoxy, in the way that Steve Gould would clearly like us to view it. … It's an interesting idea, its derivation from allopatric-isolate speciation was clever, and the observation of stasis is intriguing. I see its current role as 'Darwin told us that rates are variable .. Eldredge and Gould told us that they are VERY variable, sometimes almost dichotomous'." So, PE is an extension, not a challenge to the main structure."

Biologist H, also from the positives, explicitly rejected any notion that punctuated equilibria placed doubt upon the basic tenets of neo-Darwinism. He asserted that those who had claimed this were more interested in pursuing their personal agendas than their science: "I do not believe it in any way challenges the modern synthesis. US creationists like to claim otherwise, but they have a political agenda and do not understand the issues. Some proponents of the theory also sometimes claim it challenges the modern synthesis, but they too have an agenda, and that aspect of their views has not been accepted."

Biologist D was the only one to break with this trend. He totally embraced the punctuationist version of the history of evolutionary science. Part of his response to question 4 reads: "The question is not how it stands up to the data, or even how it stands up to Darwin, but how it stands up to the 1940's New Synthesis and the 1960's Evolutionary Ecology revolution, which represent two episodes of dumbing down Darwinism. Evolutionary biologists became afraid of diversity, and became bigots. As Gould has pointed out … Darwin had a much more inclusive view of evolution, much more robust than what we had at the end of the 1970's."

In response to question 6 eight of the respondents said that punctuated equilibria has had no influence on their research. Five said that punctuated equilibria had a small influence on their work, meaning that they have at some point in their careers published a paper or two on the subject but had not used it in a major research programme. Two credited punctuated equilibria with having had a large impact on their work: *Biologist H* has specialised his studies on the evolution of a particular feature of a particular taxonomic group.[197] He wrote that without punctuated equilibria "we would have entirely overlooked the means by which [the particular feature] evolved."; *Biologist M* wrote "I am very interested in stasis and have written quite a bit about evolutionary causes and consequence of the phenomenon."

In response to question 10 five of the respondents said they didn't know how much punctuated equilibria had influenced the rise in status of paleontology. Three said

[197] I do not want to reveal the particular feature or group as this might disclose the identity of the scientist.

they thought it had had no influence whilst seven thought it had played at least some role. Of the latter seven only two thought that punctuated equilibria had been a major influence. The other five thought paleontological developments such as cladistics and mass extinction theories had been equally or more important,

***Questions 7, 8 and 9*:**

Ten of the fifteen biologists gave species selection and/or species sorting a rather negative appraisal. A few said that species selection was just natural selection extrapolated and that Stanley and company were just playing with semantics. Others said it was untestable or was too weak a force to be the subject of meaningful research. Some embraced the idea that selection could occur at different levels but claimed that this was already part of the Modern Synthesis, citing Sewall Wright. The five who gave species selection and/or species sorting a positive appraisal did not offer anything more than vague justifications for their appraisal. Three simply said that they thought it sounded like a good idea whilst two cited a belief that evolution can only be explained by a hierarchy of levels. It seems that species selection and species sorting are not very well understood theories amongst evolutionary biologists.

Only three of the biologists saw any connection between punctuated equilibria and species selection (two 'positives' and one 'negative'). All three of these considered the link to be a probabilistic one – that punctuated equilibria makes species selection more likely. None of the biologists saw species selection and/or species sorting as widely accepted ideas in evolutionary biology and none of them credited the theories with having any influence on their own work.

***Questions 11, 12 and 13*:**

All but one of the biologists said that they had read at least some literature from History and Philosophy of Science. These fourteen were evenly split over whether it had influenced their practice. *Biologist B,* for example, wrote "It helps me to understand the way I do research.". *Biologist I*, by contrast, wrote "Sure, I've read them. It has had zero influence on the day-to-day work that I do."

In response to question 12 fourteen of the respondents wrote that they thought external political and social factors affected the practice of science. *Biologist E,* for example, wrote "One's science is intimately tied up with one's own personality and experiences." Five of the fourteen, however, believed that such external factors affected the journey but not the destination, that the internal logic of the scientific process eventually prevails over social influences. *Biologist C,* for example, wrote that "fashion can dictate which [theories] are studied at any given time" but that "the scientific method ultimately weeds out the weaker ideas leaving the more robust ones standing."

Interestingly however, only ten of the biologists thought that such external factors had had a major influence on the progress of punctuated equilibria. Four of the nine who gave an unqualified 'yes' to question 12 then wrote 'not really' or 'don't know' in response to question 13. Amongst the others the social and political influences identified as affecting the punctuated equilibria debate were similar to those identified by the paleontologists – Marxism, the independence of paleontology, the egos of the principal protagonists. The five who thought social factors influenced the journey but not the destination of science applied the same principle to punctuated equilibria. *Biologist G,* for

example, identified “Gould, and to a much lesser extent Eldredge” with “pure careerism” but thought that scientists “don’t get very far unless they honestly test their ideas with real data” and that “their work only lasts if it is based on sound science”.

In summary, it seems that whilst punctuated equilibria is not a vital theory for evolutionary biologists it is not one whose use is shunned either. It is simply seen as a strong theory that is useful in particular situations. Also, and perhaps more importantly it is apparent that the first objective of the punctuated equilibria revolution in respect of evolutionary biology has been met – the paleontological voice is now respected amongst evolutionary biologists. It is not so clear that punctuated equilibria itself was the facilitator of this change; rather it seems that it was one of many influences in this respect. Indeed it seems that a myriad of approaches to evolution are now considered equally valid amongst evolutionary biologists and that, as compared to thirty years ago, evolutionary biology is a considerably more democratic institution.

6.3: Correspondence.

There were several topics disregarded in the questionnaire that, in retrospect, it would have been appropriate to enquire about. In particular, a question regarding the relationship between punctuated equilibria and notions of adaptation would have been most relevant. Some questions about evolutionary hierarchies would also have been pertinent. Some of the respondents to the questionnaire agreed to be involved in further correspondence, during which it was thus possible to address some of the subjects neglected by the questionnaires.

In total six of the respondents to the questionnaires agreed to further correspondence. Four of these were paleontologists (*Student E and Scientists V, W and Z*) and two were evolutionary biologists (*Biologists G and P)* This group represented a fair, if small, cross-section. Of the paleontologists, *Scientist V* did not profess to be supporters of punctuated equilibria. *Student E* and *Scientist Z* were mild supporters, believing punctuated equilibria to be a valuable theory despite not using it in their own research. *Scientist W* was fully immersed in punctuationism, having done much research based on punctuated equilibria and finding heavily in favor of it. Of the evolutionary biologists, *Biologist P* was classed amongst those having a positive attitude to punctuated equilibria and *Biologist G* a negative attitude.

The *relationship between punctuated equilibria and perspectives on adaptation* was probably the most important topic not to have been directly addressed in the questionnaire. Hence this was one of the first things that I brought up with the correspondents. A wide range of views were expressed. Each correspondent’s view seemed to mirror their general attitude to punctuated equilibria.

Scientist V had much to say on this topic. He agreed with Gould and Lewontin that most “adaptive scenarios” from evolutionary biology are “just-so stories” that “are not rigorously testable” and thought that “it is wrong to assume that a bodily feature is necessarily adaptive.” However he was more ambivalent about the apparent implications of punctuated equilibria for adaptation. Firstly he noted that for paleontologists it is often very difficult to know which traits are heritable and which are ecophenotypic and hence

which features are actually subject to selection. Secondly he was not a supporter of punctuated equilibria, believing it to be only one pattern amongst many in the fossil record, and not even the most common pattern at that. Thirdly he pointed out that historically the metaphysics of the situation was reversed, that in Darwin's time and earlier there was a "tension in evolutionary biology/paleontology between extreme adaptationists, who emphasised the stability of species, and extreme transmutationists … who envisioned species as highly plastic, if indeed real at all." Thus, he wrote, in the context of those times the idea of stasis supported rather than negated adaptationism. Thus, he implied, it is very difficult for paleontologists to make any assertions about adaptation and the relationship between ideas like punctuated equilibria and adaptationism are more a function of personal agendas than 'hard facts'.

Student E thought that punctuated equilibria's "most interesting implication" was "the suggestion that intra-specific adaptation may not be relevant to long term trends". He believed it to be "an issue of relative frequency" but he did not think that punctuated equilibria was predominant, holding the opinion that "many intra-specific trends do scale up to large scale trends … while others don't."

Scientist Z thought that the pre-punctuated equilibria conception of the "adaptation process was pure neo-Darwinian dogma." However he thought that the initial formulation of punctuated equilibria "did not … offer any challenge to conventional wisdom" on the subject and that it wasn't until it was suggested that "long-term adaptive trends might be effected more by species sorting or selection" that neo-Darwinian notions of adaptation were challenged. He did not see natural selection as the focus of debate, asserting that the "PEists are not denying adaptation by normal neo-Darwinian mechanisms. Rather, he wrote, the conflict "between the PEists and the POP GENs is over whether species selection (and other macroevolutionary processes) are necessary to explain the history of life." His own personal position was ambivalent. He believed that the punctuationists had a legitimate point but that species selection had proved difficult to verify: "The documentation [of species selection] is truly lousy."

Scientist W held a punctuationist perspective on adaptation. Before punctuated equilibria he had maintained an orthodox, neo-Darwinian perspective on adaptation. It was the phenomenon of stasis, he wrote, that caused him to change his mind: "my acceptance of the probability that stasis is pervasive … caused me to rethink my position on adaptation." He was able to reconcile his old views on adaptation with his conviction of the pervasiveness of punctuated equilibria via species selection: "Species selection or sorting is the mechanism that has allowed me to reconcile my conflicting thoughts to some extent."

It thus seems clear that amongst paleontologists there is widespread agreement that punctuated equilibria in some way challenges the neo-Darwinian perspective on adaptation. Even *Scientist V*, who was not a supporter of punctuated equilibria, agreed with the punctuationist assertion that many biological adaptive scenarios were 'just-so' stories. That is, whilst he did not accept the details of the punctuationist assertions (specifically that punctuated equilibria challenges the centrality of adaptive processes to evolution) he did accept their debasement of the syntheticist perspective on adaptation. However there was less agreement that this challenge actually stands up to analysis – that the theory of punctuated equilibria really did affect the way adaptation should be considered. Only *Scientist W* had totally accepted the punctuationist assertions about

adaptation, *Scientist V* rejected the idea that punctuated equilibria had anything to say about adaptation while *Student E* and *Scientist Z* accepted some aspects and not others.

Both biological correspondents rejected the idea that punctuated equilibria had anything to say about adaptation. *Biologist P* was very succinct, saying that "the claims simply failed to pan out" and that they were mostly "PR and hot air." *Biologist G* had more to say and was even more disparaging.. Firstly he said that there had been no studies done to investigate whether speciation was associated with morphological change[198] and that it was "absurd .. to argue in the absence of hard data." He also pointed out that paleontologists can only detect speciation when there is morphological change and that "the whole thing becomes tautological."[199] He could not see any relationship between punctuated equilibria and notions of adaptation: "I don't see how it [punctuated equilibria] is relevant to how adaptations occur."

I suggested to *Biologist G* that the punctuationists were not addressing how adaptation occurs but rather what happens to such adaptations in the (geological) long term, that they were asserting that in macroevolutionary time-scales population genetic processes, including adaptation, become 'instant' events. He agreed with my suggestion ("I think you got it right") but as he went on to explicate his opinion it became clear that he did not really understand the nature of it: "I personally think that long term trends are real, but they may be explained by adaptations to long-term trends in climate, habitat, and concomitant changes in complete communities – adaptation is to both the physical and biological environment." He still maintained that long term evolutionary trends were an extrapolation of basic population genetic processes and hence did not really agree that adaptive processes were singular events in macroevolutionary time.

Another important topic of discussion was *the concept of evolutionary hierarchy*. It was immediately evident that a wide range of perspectives existed as to both the meaning and significance of evolutionary hierarchy. This is perhaps a symptom of the fact that the concept is not a testable theory as such but rather an attempt to combine many ideas and theories into a complete metaphysic of evolution. In a practical sense it is a research programme that aims to articulate three evolutionary disciplines – population studies, ecology and paleontology. The way that this articulation is to be achieved, however, has remained vague and hence open to individuals interpretation. It is thus to be expected that each scientist would see different aspects of it as important.

Scientist V for instance, saw the most important question as what effects different levels have on each other. This issue was actually having a strong influence on his research – he and his colleagues were investigating the relationship between the incidence of speciation and the production of higher taxa in particular lineages.[200] He saw punctuated equilibria as being an important influence in redirecting paleontologists' attention to such hierarchical questions but did not think that the theory itself was important to the programme of research.

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[198] Which he correctly identified as a crucial aspect of the assertion that punctuated equilibria challenges the centrality of natural selection to adaptive change.

[199] He means that because paleontologists con only detect speciation when there is morphological change the punctuationist assertion 'speciation is associated with morphological change' becomes 'morphological change is associated with morphological change'.

[200] Interestingly they found, contrary perhaps to intuition, that the rate of production of higher taxa was inversely related to the number of speciations. This was because the lineages they studied "evolved most [in morphological terms] when they had the fewest species hanging around."

Scientist W, by contrast, thought that punctuated equilibria and particularly stasis were crucial to any concept of evolutionary hierarchy. The important question for him was at which levels some form of selection analogous to natural selection in populations were applicable. He professed to be "persuaded by Gould's and Eldredge's arguments that applying the concept of selection to a hierarchy of entities expands, rather than denigrates, the Darwinian model."

Biologist P held some very idiosyncratic views on the subject. He thought the important assertion to arise from evolutionary hierarchy was that species are individuals whose interactions can be studied without recourse to the properties of the individuals therein, asserting that the "individuality of species is axiomatic in modern evolutionary biology." He alleged that, in this respect, many modern biologists "are in denial." However he did not accept much of what the punctuationists had written on the subject either, asserting that a lot of what they had written on the subject is "hype and hope."

Biologist G thought that the whole idea made some sense but that it was too vague to be treated as a serious research programme: "I actually do think that there might be some higher order processes, but they are not actually identified yet, so it is more of a religion than science. As I mentioned in an earlier letter, the only higher order process that has a workable mechanism is the one involving the gene flow and dispersal distance--species with greater gene flow distances will speciate at a slower rate and go extinct at a slower rate and this will yield very different cladogenesis patterns than those species with smaller gene flow distances. And there is paleontological evidence for this in addition to good biology and well established theory. But aside from this it is all hope, faith, and charity."

The nature of communication between paleontologists and biologists was a subject on which all parties expressed a similar view –that there is not enough communication between the disciplines and that when discussions do take place they are marred by a lack of understanding of the others concerns. In general the paleontologists thought that most biologists did not take enough interest in their discipline. Of the two biologists one basically said that he thought that most paleontological research was not of a high enough standard to be taken seriously by biologists whilst the other was more philosophical, identifying the structure of universities as the source of the problem.

Scientist V was particularly vocal on this issue. He felt that there were two reasons for the lack of communication. First was the simple physical barrier that "we belong to different departments, and sometimes different divisions of our colleges". Secondly, and more importantly, that biologists did not give paleontologists ample respect.:

> "Neontology[201] itself is psychologically fragmented into 'organismal' versus 'molecular', with the former considered antiquated and subscientific. Geologically oriented paleontologists are perceived as even less 'scientific' than organismal biologists. … My laboratory is adorned with computers, microscopes, and thin-section equipment, but no fancy stuff for automated analysis of DNA or other biochemical/molecular high-tech gadgets. So we are also low-tech, as well as fundamentally unscientific.

[201] The word 'neontology' refers to the study of living animals.

> Fossils themselves are seen as inadequate materials for biological study. Even some Neocladists claim that fossils cannot be used in phylogenetic analysis, and certainly no data from stratigraphy. It takes an unusually unbiased neontologist to admit paleontologists to their exalted company. … To call our problems a lack of communication is an understatement. Active hostility requires a measure of respect; it is far more common just to be ignored."

I then asked *Scientist V* whether he thought it was possible for evolutionary biologists and paleontologists to find some kind of common language by which they could communicate. In this case he was more circumspect, identifying the barriers of different "time-scales and wildly different analytical techniques" as the origins of misunderstanding between the disciplines. However he was not optimistic that the barriers could be overcome. Science, he wrote, tends towards "increasing specialization and increasing technical competence within those specialities" and thus the only way to have inter-disciplinary communication is to have someone in your department who is technically competent in both areas, although even this "doesn't solve much."[202]

Biologist P professed to have a strong interest in crossing disciplinary boundaries. He expressed concern that his colleagues from the 'selfish gene' school were trying "to get evolution out of Darwinism". He saw this movement as a product of a split between "population ecology and the historical, natural history sciences" rather than between evolutionary biology and paleontology as such (that is he saw it as a metaphysical divide rather than a dispute over authority between the disciplines). He maintained that it was not "particularly difficult" to combine approaches from different disciplines but conceded that it was "a lot of work." The "real problem", he thought, was not producing the work as such but "finding people who are open to such interaction". He blamed the structure of universities for the lack of communication between the sub-disciplines of evolutionary science, contending that "the academic economy is set up so as to create barriers to entry."

Biologist G thought that the lack of communication between evolutionary biologists and paleontologists was "because biologists don't know enough paleontology and vice-versa" and that "being in different departments" exacerbated the problem. He contended that from a biologist's point of view most paleontological data are unacceptable, saying that they paleontologists do not produce enough "hard data" and do virtually "no quantitative analysis." Later he was more generous to the paleontologists. I suggested to him that macroevolution was a subject of common concern for biologists and paleontologists but that in inter-disciplinary discussions on the topic the two sides had been "talking past one another."[203] He agreed that this was true but said that he didn't "know what can be done about it" because the kinds of data the disciplines produced are

[202] In terms of Bourdieu's struggle *Scientist V* is thus citing the problem of ever increasing capital – that the more established a discipline becomes the more capital one needs to even enter discussions let alone argue from a position of authority.

[203] Ie that whilst they had been ostensibly discussing the same issues they had not been able to establish any real empathy with one another and thus strictly speaking had not managed to communicate.

"entirely different" due to the different time-scales being used, with "the only common ground" consisting of "what is being explained."

One of the concerns of this thesis has been the *punctuationist version of the history of evolutionary science* (i.e. the way that Eldredge, Gould and the other punctuationists have attempted to reconstruct the history of evolutionary science in their own interest). In general the paleontologists were in complete agreement with the punctuationist history. *Scientist W*, for instance, wrote that "one of the greatest contributions that Gould and Eldredge made with PE was in causing people like me to realize we were under the spell of such [gradualist] dogma." *Student E* thought that the most important aspect of punctuated equilibria was "the revolution it inspired", which he identified as "a rejection of the blinders imposed by microevolution (population genetics in particular)". Even *Scientist V*, who was antipathetic to punctuated equilibria, thought that "there was a psychological barrier to be overcome" by paleontologists in the early 1970s and that punctuated equilibria had contributed to "a diminished feeling among paleontologists that they are a variety of geologist" even though it had "failed" as a theory.

6.4: Textbooks.

Textbooks are the bastion of orthodoxy. The information given by textbooks generally represents the status quo of any scientific field. It is this information that the students who will become the leaders of the next generation are asked to absorb, to believe, to accept without misgiving. Hence the best indicator of the acceptance of any particular theory, idea, research programme or worldview is the context of its presentation in this literature. In the following section eighteen textbooks are surveyed, six from paleontology and twelve from biology.

6.4.1: Paleontological textbooks

The treatment of punctuated equilibria in the surveyed paleontological textbooks was quite a mixed bag. Two had very short sections dealing with punctuated equilibria - only a paragraph or so. Two devoted sections of the order of five pages to the theory. One had an entire chapter devoted to punctuated equilibria and one (written by Eldredge) made punctuated equilibria central to the entire presentation. The range of presentations provides a good summary of the range of paleontological attitudes towards punctuated equilibria:

1. *Life of the Past* (Lane 1992) is aimed at first year undergraduates. It has only a one paragraph discussion of punctuated equilibria, within a section about the origin of species. Punctuated equilibria is characterised as currently controversial. This is perhaps accurate although the author clearly didn't understand the terms of the debate. (e.g. "Phyletic evolution is also called phyletic gradualism because this kind of evolution leads to true speciation, or splitting of lineages through time." (p.82)) Stasis is presented as a phenomenon that is fairly common.

2. *History of Life* (Cowen 1995(1990)) is aimed at first year undergraduates and is, of all the textbooks reviewed, the only one with the traditional phone-book format. This traditional format also coincides with a traditional treatment of the subject matter of paleontology – the book focusses on the history of each of the main biological groups (i.e.mammals, reptiles, eukaryotes, flowering plants, etc) and the major events in evolutionary history (such as the initial migration to land, the evolution of flight in insects and birds). There is very little mention of paleontological perspectives on the causes and processes of evolution. (e.g. Possible causes of speciation are not discussed.) The only allusion to punctuated equilibria is in a section outlining the debate about interpretation of Burgess shale fossils. Cowen leans towards the gradualists: "This argument [about interpretation of the Burgess shale fossils] is important because it reflects the division between paleontologists who expect to find evolutionary processes operating at fairly 'reasonable' rates all the time (Briggs) and those who are willing (perhaps eager) to envision revolutionary times at which extraordinary events occur very quickly (Gould)." (pp.86-87)
3. *Basic Paleontology* (Benton and Harper *1997*) is also aimed at paleontological beginners. It contains a five page section on punctuated equilibria and species selection. (pp.51-55) A good understanding of the basic issues under debate is displayed. The authors outline some the punctuationist claims then discuss some of the studies that both support and refute these claims. They conclude that both punctuated equilibria and phyletic gradualism occur (p.53) but that species selection is probably erroneous ("evolution occurs by natural selection, as Darwin said in 1859" (p.55))
4. *Fossils: The Evolution and Extinction of Species* (Eldredge 1991) also targets undergraduates. It is, quite literally, a punctuationist textbook. Punctuated equilibria is presented as an accepted fact derived from the fossil record and all subsequent analysis is centred on the theory. (e.g. "Most species actually remain pretty much the same throughout their existence. New species arise and, while they may not differ greatly from their ancestors, neither do they grade back into them as we trace their ancestry through time. Evolution is relatively abrupt …" (p.55) and "Punctuated equilibria take the real pattern of great stability that fairly leaps from the fossil record and puts it together, not with the old picture of gradual transformation of species, but with the newer picture of the emergence of new species through the fragmentation of lineages. It tells us that adaptive transformation does not occur to any significant degree unless speciation is involved." (p.58)) The apparent consequences of punctuated equilibria for adaptation – that adaptation only occurs at speciation and that it is hence random re the direction of long term trends – is also presented as an accepted fact (e.g. "[Assuming punctuated equilibria] there is no necessary accumulation of anatomical change in any specific direction.") Species selection is presented as a consequence of punctuated equilibria - "Species selection is one of the additional theoretical notions that follows as an implication from the general idea of punctuated equilibria." (pp.85-86)
5. *Fossils and Evolution* (Kemp 1999) is a more advanced textbook. It focusses on paleontological considerations of the patterns and processes of evolution and contains a whole chapter on punctuationism v gradualism: 'Speciation: gradual, punctuated, or what?' (pp.129-155) Kemp states that punctuated equilibria is central to

paleontological analysis of speciation: “All modern consideration of fossils and speciation begins with Eldredge and Gould’s (1972) paper on punctuated equilibria.” After introducing punctuated equilibria and the inferences stemming from it (such as species selection and the decoupling of macroevolution from microevolution) he gives a long summary of the debate over it: ‘The debate and the synthesis’ (pp.139-155) He tries to give a balanced perspective and does not present any perspective as favorable to any other.

6. *Systematics and the Fossil Record* (Smith 1994) is also for advanced students, the focus being the different methods for interpretation of fossils (i.e. systematics).It contains a five page section on ‘punctuated evolution’ (pp.183-187) Smith doesn’t bother to cite Eldredge and Gould or outline punctuated equilibria – he simply assumes that the student is already familiar with it. He discusses the way some scientists, such as Cheetham and Fortey, have attempted to approach the problem, stating that “there is evidence that both rapid and gradual modes of evolution occur” and that it often comes down to a matter of differing interpretations – that gradual evolution is stasis to the punctuationist where punctuations are evidence of breaks in fossilisation to the gradualist.

6.4.2: Biological textbooks.

Punctuationists, as we have seen, have continually asserted that punctuated equilibria and its peripheral extensions have consequences for the biological perspective on evolution. These assertions have varied over time and from actor to actor. However there has always been one common theme – that microevolution cannot be directly extrapolated to macroevolution with the consequence that biologists should reassess the importance of their microevolutionary assumptions. It is interesting therefore to see how much and in what form punctuated equilibria has infiltrated the textbooks of biology.

Twelve textbooks were surveyed.[204] They were published over the period 1985 to 1996 and aimed at undergraduate students. Of these twelve all but one contains a discussion of punctuated equilibria. The discussions are generally short, perhaps a page or two, and are basically presented as an aside to the main text or as an introduction to speciation. The general feeling generated by this presentation is that the debate over punctuated equilibria is of interest to the student but is not something he or she need be overly concerned about. In general punctuated equilibria is presented as a deductive theory from paleontology[205] whose consequences for evolutionary biology are still being debated. This debate is characterised as being entirely internal to neo-Darwinism – none of the twelve mention that punctuated equilibria could circumscribe the centrality of natural selection to evolutionary explanation or that it challenges the extrapolation of population biology to macroevolution.

A brief survey of the twelve texts will explicate the above points:

1. *The Cambridge Encyclopedia of Life Sciences* (1st edition) (Friday and Ingram 1985) offers a two page appraisal of gradualism v punctuated equilibria. Arguments from

[204] Actually, 11 textbooks proper and one biological encyclopaedia.
[205] That is, derived from fossil data.

both sides are given and neither view is presented as more widely accepted than the other. Rather, the section leads into a discussion of the different modes of speciation (i.e.allopatric, sympatric, parapatric). Neither Gould nor Eldredge are mentioned at all. Stanley's *Macroevolution* is the only punctuationist literature suggested for further reading.

2. *Biological Science* (Keeton and Gould 1986) has a section devoted specifically to punctuated equilibrium.(905-907). Identifies Eldredge and Gould as the source of the theory. Says that punctuated equilibria is "[b]ased on a careful study of certain fossil records" That is, punctuated equilibria is presented as if it were empirically derived rather than theoretically implied. Presents punctuated equilibria as a currently debatable issue but definitely leans towards the punctuationists: "The evolution of some organisms is evidently less uniform and gradual than many present-day biologists have supposed … The usual tempo of speciation may turn out to lie somewhere between the gradual-change and punctuated-equilibrium models."
3. *Biology* (Campbell 1987) has a three page section on punctuated equilibrium titled 'The theory of punctuated equilibrium has stimulated research on the tempo of speciation.' (pp.449-451). Cites Eldredge and Gould's 1972 article as the source of the theory. States that stasis is due to stabilising selection in an unchanging environment. Presents punctuated equilibria v gradualism as an ongoing debate that has had and continues to have positive effects: "Whatever the outcome of research on the pace of speciation, there is no question that the theory of punctuated equilibrium has stimulated research and catalyzed a new interest in paleontology. In the next chapter, we will see how this investigation of the fossil record extends beyond the issue of speciation to major patterns in the history of life." This textbook also has a discussion of species selection. Punctuated equilibrium is mentioned in the introduction to species selection, but no causal link between the two is identified (i.e.they are simply presented as related research programmes).
4. *Biology* (Barret, Abramoft et al. 1986) has a three paragraph section titled 'Gradualism versus punctuationism in evolution.' (pp.767-768) Basically just mentions punctuated equilibria - neither Eldredge nor Gould nor any other punctuationist is mentioned at all. First punctuated equilibria is summarised, then the assertion is made that punctuated equilibria is not contrary to neo-Darwinism: "… rapid speciation itself is not contradictory to the concept of evolution by natural selection." Seems like the authors wanted to make sure students saw the controversy as internal to neo-Darwinism.
5. *Biology: The common threads.*(Swanage 1991) has a one page subsection with the title 'Is evolutionary change gradual or by jumps?' (p.348). Basically says that science is Popperian and that challenges to accepted ideas are an important part of science. Adds that the controversy over punctuated equilibria does not cast doubt on the existence of evolution.
6. *Biology* (Knox, Ladiges et al. 1994) has a two page section titled 'Rates of Evolution' (pp.712-714, p.713 is filled with an unrelated diagram) The authors do not seem to understand punctuated equilibrium or the issues being debated. They characterise punctuated equilibrium as arguing for very rapid speciation without specifying that it is rapid only in geological time. Suggest that the question "What use is half an eye or

lung?" is still topical and that punctuated equilibrium and saltationism was offered as an answer.

7. *Biology* (Arms and Camp 1987) has a three page section titled 'How quickly do new species form?' (pp.385-387) Locates punctuated equilibria as entirely internal to neo-Darwinism by identifying Mayr, Simpson and Verne Grant as the founders of punctuated equilibria: "As long ago as the 1940s, Ernst Mayr, George Gaylord Simpson, and Verne Grant proposed that at least some species arise according to a pattern now known as punctuated equilibrium. In the 1970s many evolutionists came to agree." Does not even mention Eldredge and Gould. Says that punctuated equilibrium definitely occurs but has debatable importance. Lists extensive further reading, but neither Eldredge nor Gould are represented. The only punctuationist literature listed is Stanley's *The New Evolutionary Timetable*.
8. *Life: The Science of Biology* (Purves and Orions 1987) has an entire chapter devoted to macroevolution. (pp.1059-1086) The abstract to the chapter describes punctuated equilibrium without naming it or sourcing anyone. "During the history of various taxa, periods of rapid evolution alternated with periods of stasis, when changes were relatively slow", then links this to mass extinction. Places more emphasis on mass extinction and adaptive radiation than punctuated equilibrium as general pattern of fossil record. Describes stasis as an indisputable fact of the fossil record and sources of the idea with Wright and his adaptive landscape. Neither Eldredge nor Gould are listed in the further reading. Stanley's *Macroevolution* and Stanley and Raup's *Principles of Paleontology* are listed.
9. *Biology: The Science of Life* (Wallace, King et al. 1986) has a very short section titled 'Gradualism versus Punctuated Equilibrium.' (pp.388-389) Says that punctuated equilibria is basically accepted by biologists. Further reading includes Eldredge and Gould's 1972 article.
10. *Advanced Biology* (Simpkins and Williams 1989) was the one textbook that did not mention punctuated equilibria. Has a chapter on evolution that is only 26 (out of 750) pages long. Contains no discussion of the tempo of evolution let alone punctuated equilibrium. Says geographical isolation is the cause of speciation.
11. *Biology: The Unity and Diversity of Life* (Starr and Taggart 1989) has a short section on punctuated equilibria ((p.557), less than one page). Says strong natural selection can cause speciation in hundreds to thousands of years and that stabilising selection causes stasis. States that punctuated equilibria describes the fossil record better than gradualism.
12. *Biology* (Raven and Johnson 1996) has a three page section titled 'The Tempo and Mode of Evolution.' (pp.490-492) Presents punctuated equilibrium as a moderately strong fact: "…[taxonomic] groups *apparently* have rapid periods and relatively slow periods in their evolution." (my italics) Does not provide a time-frame for speciation. Describes punctuated equilibrium as a "useful perspective for considering the mode of evolution." Deconstructs Eldredge and Gould's rhetoric: "Eldredge and Gould contrasted their theory of punctuated equilibrium with that of gradualism, or gradual evolutionary change, which they claimed was what Darwin and most earlier students of evolution had considered normal. Whether they did so or nor is debatable."

In summary, it is apparent that amongst the authors of these textbooks punctuated equilibria is considered to be a moderate to strong fact. However they also consider it to have only limited relevance to evolutionary biology – it is presented as an object that is of interest value only. Furthermore they see the debate about the theory as entirely internal to neo-Darwinism – none of them mentioned that the importance of natural selection to macroevolutionary patterns is being challenged. This represents a good model for the general attitude of evolutionary biologists to punctuated equilibria in the 1990s. They basically accept it as a strong theory for paleontology but one that has little or no relevance to evolutionary biology and definitely does not negate the importance of natural selection.

6.5: Ego clashes.

I have claimed that three major movements have marked the history of punctuated equilibria in the 1990s. The first two of these were paleontological and biological research into the frequency and consequences of punctuated equilibria. The scientists involved in this research accepted that punctuated equilibria is a common macroevolutionary pattern and that aspects of it (particularly stasis) require cross-disciplinary investigation, and amongst them there was little of the heated argument that marked discussions over punctuated equilibria in the 1980s. Particularly strong evidence for this comes from the citation history, where it can be seen that the frequency of negative appraisals of punctuated equilibria in the 1990s decreased markedly.

Indeed it seems that most negative appraisals of punctuated equilibria in the 1990s came from a small group of high profile scientists and philosophers who, for a variety of reasons, continued to take exception to punctuationism (foremost among this group were John Maynard Smith, Richard Dawkins, Daniel Dennett, Michael Ruse and Robert Wright). Their criticisms of punctuationism were also often combined with personal attacks on its most famous proponent, Stephen Gould. It seems they had lost patience with Gould, had tired of the fact that he continued to present his own ideas as accepted scientific fact in his popular writings, and rather than attempting to criticise his ideas they sought to debase his scientific reputation.

In a 1995 review of philosopher Daniel Dennett's book *Darwin's Dangerous Idea* John Maynard Smith had this to say about Stephen Gould:

> "Gould occupies a rather curious position, particularly on his side of the Atlantic. Because of the excellence of his essays, he has come to be seen by non-biologists as the preeminent evolutionary theorist. In contrast, the evolutionary biologists with whom I have discussed his work tend to see him as a man whose ideas are so confused as to hardly worth bothering with, but as one who should not be publicly criticised because he is at least on our side against the creationists." (Maynard Smith 1995)

This kind of personal criticism makes a sharp contrast with Maynard Smith's earlier treatments of Gould and his ideas, when he had often been critical but always scrupulously impersonal (see Section 5.4.2). As Gould himself later pointed out, in a 1984 *Nature* article Maynard Smith described Gould as "a leading figure" amongst a group of paleontologists whose work had been influential in bringing paleontology out of the theoretical doldrums. ((Gould 1997a) – Gould was quoting from (Maynard Smith 1984))

Evolutionary psychologist Robert Wright was another scientist to be engaged in disputes of a personal nature with Gould during the 1990s.[206] In 1996 he wrote an article titled 'Homo Deceptus: Never Trust Stephen Jay Gould' and declared publicly that he was "involved in a bitter dispute with no less a personage than Stephen Jay Gould." The context of this declaration was a reply to a review Gould had written about Wright's book *The Moral Animal*. Gould had condemned evolutionary psychology as "pop science" and described Wright's book as "the most noted and most absurd example". Wright argued that Gould's review of his book was simple retribution for Wright's own 1990 review of Gould's *Wonderful Life* in which he "argued, basically, that Gould is a fraud" who "has convinced the public that he is a not merely a great writer, but a great theorist of evolution" and yet "among top-flight evolutionary biologists" he is "considered a pest – not just a lightweight but an actively muddled man who has warped the public's understanding of Darwinism." (Wright 1996)

The personal attacks on Gould by Maynard Smith and Wright pale into insignificance, however, when compared to the fifty page deconstruction of Gould given by Daniel Dennett in his book *Darwin's Dangerous Idea: Evolution and the Meanings of Life* ((Dennet 1995), pp.262-312). The book itself, which runs to over 500 pages, is an attempt at a neo-Darwinian manifesto. In it Dennett argues that Darwin's theory is a "universal acid" that "eats through just about every traditional concept, and leaves in its wake a revolutionized world-view, with most of the old landmarks still recognizable, but transformed in fundamental ways." (p.63) He then applied this 'universal acid' to large range of modern ideas, from biology to ethics.

In the chapter devoted to the ideas of Gould, Dennett sought to completely debase every aspect of Gould's scientific worldview, beginning with a section titled 'The Boy Who Cried Wolf' (pp.262-267) in which he made a similar allegation to that of Maynard Smith and Wright – that Gould, despite his high public profile, is not highly thought of within evolutionary science and that his writings have been misleading the public:

> "This chapter is about another myth – Stephen Jay Gould, Refuter of Orthodox Darwinism. Over the years Gould has mounted a series of attacks on aspects of contemporary neo-Darwinism, and although none of these attacks has proven to be more than a mild corrective to orthodoxy at best, their rhetorical impact on the outside world has been immense and distorting." (p.263)

[206] Evolutionary psychology is one modern incarnation of sociobiology.

The next section, 'The Spandrel's Thumb' (pp.267-282) was a deconstruction of Gould and Lewontin's ideas about adaptation, as expressed in 'The Spandrels of San Marco and the Panglossian Paradigm.' (Gould and Lewontin 1979). The third section, confrontationally titled 'Punctuated Equilibrium: A Hopeful Monster' (pp.282-299), was an analysis of punctuationism. The fourth section, 'Tinkers Ever to Chance': The Burgess Shale Double-Play Mystery' (p.299-312) criticised Gould's ideas about the role of contingency in the history of life, as expressed in *Wonderful Life*. Analysis of Dennett's criticism will be restricted to the section on punctuationism.

Dennett's tactics were to deny most of punctuated equilibrium any importance (to debase it) and to absorb the rest into standard neo-Darwinism (via reconstruction). First he analysed the punctuation part of the theory, denying that the breaks in the fossil record refute gradualism. He asserted that even if speciation occurs instantaneously in geological time, it is still gradual and quoted a section from Richard Dawkins in which it is claimed that it is possible for an animal the size of a mouse to evolve to one the size of an elephant, by imperceptibly small steps, in only 12,000 generations or about 60,000 years. ((Dawkins 1986), p.242) He then stated that since each step is imperceptible to human methods of measurement this change is gradualism at work, even though the fossil record would not record the transition. Even Gould, he said, "would not call such a locally imperceptible mouse-to-elephant change a violation of gradualism".[207] He made the rather fatuous suggestion that punctuated equilibrium is thus more gradual than gradualism - periods of slow transition between periods of no change at all.

Dennett then went on to analyse the equilibrium, or stasis, part of the theory. He claimed that the apparent stability of species in the fossil record is a retrospective fallacy, in that paleontologists will only be able to find evidence of the existence of species when they are stable for a decent period of time. The question to be answered, he asserted, is not the stability of species but why there are species at all, a question easily answered by neo-Darwinism - "neo-Darwinism has several obvious adaptationist explanations for why stasis should often occur in a lineage. …every species is - must be - a going concern, and going concerns must be conservative; most deviations from the time-tested tradition will be quickly punished by extinction".(p.293)

After debasing both punctuations and stasis Dennett discussed species selection. He described it as "a powerful proposal worth taking seriously", as an idea that "neither refutes nor supplants gradualism" but rather "builds on it". The phrasing of the next sentence revealed his intentions: "…it is clear that however large a role species selection comes to play in the latest versions of neo-Darwinism…". He did not see species selection as a challenge to the centrality of natural selection but as a valid assertion which thus must be incorporated into neo-Darwinism. Rather than admitting that the punctuationists might have a good point he attempted to absorb the theory, to show that it is a natural part of his own worldview.

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[207] One suspects that Gould would demur rather strongly. Punctuated equilibrium is a theory about macroevolution. It has nothing to say about transitions in time that are not geologically measurable. In saying that a speciation event that occurs in 60, 000 years is gradual, Dennett is using the word in a different sense from the way that Gould and Eldredge do. The gradualism that they refute is the idea that the transition from one species to the next is one that is constantly occurring in geological time. Dennett is using the word in its everyday sense, that speciation is so gradual in ecological time we can't measure it as it happens.

Gould replied to the attacks of Maynard Smith, Wright and Dennett by publishing a stinging diatribe of his own in the *New York Review* (Gould 1997a). In this essay (which runs to about 5,000 words) Gould defended himself against the aforementioned criticisms of Maynard Smith and others, and in turn attempted a complete debasement of their worldview. As the title ('Darwinian Fundamentalism') suggests, Gould cast his foes as fundamentalists, ultra-Darwinian extremists blinded to the facts of evolution by their faith in the omnipotence of natural selection. By contrast he portrayed himself as a pluralist willing to accept many different perspectives as valid (except of course those of Maynard Smith and company).

Gould's debasement of his foes began with the delineation of their position and the identification of precisely who they were. He described their "movement" as a "self-styled form of Darwinian fundamentalism" that encompassed the biological work of Maynard Smith, the "uncompromising ideology (albeit in graceful prose) of his compatriot Richard Dawkins", "the equally narrow and more ponderous writing of … Daniel Dennett" and "the study of human behaviour along a Darwinian straight and narrow under the name of evolutionary psychology". At the core of their beliefs, he wrote, these "ultra-Darwinists share a conviction that natural selection regulates everything of any importance in evolution, and that adaptation emerges as a universal result and ultimate test of selection's ubiquity."

Gould then argued that this 'ultra-Darwinian' movement was concurrent with an "invigoration" of evolutionary science that was due to the emergence of "exciting nonselectionist and nonadaptationist data from the three central disciplines of population genetics, developmental biology and paleontology". These three 'data' are the "mathematical account of the large role that neutral, and therefore nonadaptive, changes play in the evolution of nucleotides", the "stunning" discovery that there is "close similarity of basic pathways of development of phyla that have been evolving independently for at least 500 million years"[208] and, of course, punctuated equilibria. Gould portrayed the latter movement as pluralist, contrasting it with the narrow-minded ultra-Darwinian perspective. He also attempted to marginalise the latter, the 'pluralist' view being presented as if it were the status quo with the comment that it was "an odd time to be a fundamentalist about adaptation and selection" giving the impression that that ultra-Darwinians dwelt on the fringes of evolutionary science.

In the latter half of the article Gould responded to the criticisms of Dennett and Maynard Smith more directly. He was extremely disparaging about Dennett and *Darwin's Dangerous Idea*, describing the latter as "a limited and superficial book" that "reads like a caricature of a caricature" and labelling Dennett as "Dawkins' lapdog"[209] He responded to Maynard Smith's comments about his scientific stature (as quoted above) by describing them as "empty of content" and "based only on comments by anonymous critics". Gould then provided a chronicle of the "numerous articles" Maynard Smith had written about his work and, responding to Maynard Smith's charge that he was a scientific lightweight, asked why "he has been bothering about my work so intensely, and for so many years?" Gould concluded that Maynard Smith's "once genuinely

[208] Which, apparently, confirms the proposition that developmental constraints restrict the range of adaptive possibilities.

[209] This is a pun on the famous 'Darwin's bulldog' tag given to Thomas Huxley, a great friend and defender of Darwin.

impressive critical abilities seem to have become submerged within the simplistic dogmatism epitomized by Darwin's Dangerous Idea, a dogmatism that threatens to compromise the true complexity, subtlety (and beauty) of evolutionary theory and the explanation of life's history."

Eldredge was not silent in the 1990s – indeed he was equally as outspoken as Gould when it came to statements about the significance of punctuationism. His book *Reinventing Darwin* (Eldredge 1995) summarised his perspective. Self-consciously "partisan", the book was intended both as a "contribution to evolutionary discourse" and as an historical account of the "arguments and dialogues" within evolutionary science from 1959 to the time of writing. Eldredge saw dialogue about punctuationism as having taken place between two "opposing camps" – the exponents of "ultra-Darwinism" and the "naturalists". Eldredge identified Maynard Smith, Dawkins and George Williams as core protagonists of the former camp and himself, Gould, Vrba and Stanley as the core group of the latter. (p.x-xi)

Eldredge saw the debates between the camps as revolving around their differing perspectives on the significance of natural selection. The ultra-Darwinists, according to Eldredge, saw natural selection as the center of all evolutionary explanation, a view that he cast as short-sighted and extremist. The naturalists, by contrast, held much more reasonable views. They did not deny that natural selection was a powerful phenomenon, simply seeing it as part of a greater whole. Naturalists, he wrote, "are convinced that there are processes relevant to understanding evolution that go on within .. [a number of levels] … - from genes right on up through populations, species and ecosystems."

Eldredge's punctuationist statements, before and during the 1990s, were no weaker than those of Gould. However he managed to avoid attracting the kind of personal attacks that Gould suffered. Partly this was because he does not have the public profile of Gould - his public audience, whilst large for a scientist, is small compared to Gould's. He was also careful to profess admiration for his rivals and repeatedly stated that the dialogue between them was indispensable to the attempt to understand evolution.

The intensity of the personal attacks between Gould, Dennett, Maynard Smith and company suggests a clash of egos. Indeed it seems that the 'ultra-Darwinians', as Gould and Eldredge dubbed them, had tired of Gould presenting his own ideas as representative of the status quo in his popular (in both senses of the word) writings and sought to erode his authority in the eyes of the scientifically informed lay readers of such literature.[210] Gould in turn defended his own (public) authority and attempted to erode that of his opponents. However the focus of their arguments, the centrality of natural selection, was the same as it was in the 1980s, when debate was equally as heated but of a less personal nature. The punctuationists continued to attempt the removal of natural selection from the center of evolutionary explanation and thus to debase the authority of the syntheticists. The syntheticists attempted to maintain the position of natural selection and thus their own authority, and sought to debase the punctuationist challenge.

[210] The notion that Gould indulges in such action - presenting his own ideas as status quo science, does seem to have some veracity - indeed his popular writings are replete with statements revealing such. For instance consider this premise to a logical deduction from one of Gould's recent essays: "Since organic species are independent and stable units (after the brief moment of their branching origin), the Linnean system …" ((Gould 1998), p.92) He has simply assumed that punctuated equilibria is ubiquitous.

6.6: Conclusion.

In Sections 6.2, 6.3, and 6.4 it was shown that by the end of the 1990s punctuated equilibria was generally (though not universally) accepted as an important paleontological theory with possible applications in other areas of evolutionary science. To most paleontologists punctuated equilibria was an important macroevolutionary model and to a notable few it was the basis of entire research programmes, whilst the idea of stasis was of research interest to some evolutionary biologists. This was a major change from the state of affairs in the early 1980s, when punctuated equilibria was the focus of controversy for many evolutionary scientists. However, as discussed in Section 6.5 of this thesis, by the late 1990s there was still resistance to punctuated equilibria amongst a handful of notable scientists (and some philosophers). This resistance continued mainly in response to the continued anti-neo-Darwinian claims of Gould, Eldredge, Stanley and other punctuationists.

In summary then it can be said that by the late 1990s punctuated equilibria the theory was no longer controversial but punctuationism, the research programme constructed to break the hegemony of population genetics in evolutionary science, was still the focus of significant argument. Dispute over the latter had by this time been going on for over twenty years and amongst the principal protagonists there was little sign that resolution was forthcoming. However there were signs of reconciliation amongst the grassroots of evolutionary science. For example, the research programme of Jackson and Cheetham had shown that it was possible to combine biological and paleontological data and others were beginning to follow suit (Section 6.1.4).

In Chapters 3 and 4 the rhetorical process by which Eldredge and Gould constructed the ‘revolution’ of punctuationism was analysed in detail. The principal objective of this revolution was to make paleontology the chief authority of macroevolution, thereby raising its status within evolutionary science, and it can now be said that by the late 1990s this objective had been met. The patterns and processes of macroevolution are now the exclusive property of paleontologists – only they are considered to have the authority to form theories about evolution in geological time scales. The creation of a rift between paleontology and evolutionary biology was an important part of this independence movement, and the fact that a reconciliation process has begun is another clear indication that the revolution has succeeded.

Eldredge, Gould and Stanley, supported by other lesser known punctuationists have continued to push forward, seeking to claim even more territory for paleontology. Utilising notions of evolutionary hierarchy they have sought to reverse the original syntheticist extrapolation from microevolution to macroevolution by claiming that the only significance of microevolutionary processes are as instantaneous macroevolutionary events. Syntheticists such as Maynard Smith, Dawkins and Ruse have not been convinced and have continued to resist this punctuationist push The stakes are sufficiently high for both camps to ensure that the argument has at times spilled over into what can only be described as personal invective, an interesting commentary on the manner of scientific debate. No doubt the debates will continue, but the fact that these further objectives have not yet been met does not devalue the punctuationists’ achievement in realising their initial goal.

As one method of making sense of this particular scientific debate, the ideas of Pierre Bourdieu (discussed in Section 1.2.1) were utilised. Bourdieu proposed that cultural fields are constituted by the actions of agents who do no more than pursue their individual interests, but that each field has a specific logic that generates its unique properties. He observes that in scientific fields the producers of knowledge are also the consumers of knowledge and thus to become a high status scientist one must attain a certain level of technical competence, as judged by one's peers. This specificity, argues Bourdieu, allows a *systematic diversion of ends* whereby a *progress of reason* can be realised.

I would argue that the debate over punctuated equilibria has caused such a 'progress of reason'. If 'progress' in the field is equated with democratisation then it can be unequivocally stated that evolutionary science has progressed in the last thirty years and that punctuated equilibria has been a major part of the process. In 1970 the only scientists considered to have the authority to make assertions about evolution were evolutionary biologists. Thirty years on the perspectives of a diverse range of disciplines (paleontology, ecology and embryology to name a few) are considered to be more or less equally valid to the perspective of evolutionary biology. Concomitant with this democratisation is a rise in the technical competence of all these sub-fields of evolutionary science. Punctuated equilibria's challenge to the status quo was a major factor in this movement as it broke the hegemony of the tenets of population genetics in evolutionary theory, allowing the development of a wider range of approaches to evolutionary theory. I would also argue that this progress occurred by a process akin to Bourdieu's systematic diversion of ends.' At no stage did the actors in the drama do anything more than pursue their own personal and group interests: the punctuationists wanted to achieve a raised status for paleontology; the syntheticists wanted to protect their territory. The fact that their debates eventually created a vacuum that allowed other sub-disciplines of evolutionary science to become equal members of the field was not on either of their agendas.

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Appendix – The questionnaire

Requests to fill out questionnaires were made to the scientists via e-mail in the second half of 1999. The process for selection of suitable candidates was random in that it was essentially haphazard – I simply searched the internet home-pages of university biology and paleontology departments and asked scientists with listed e-mail addresses if they would be interested in taking part. I also asked those who responded positively if they could recommend other scientists who would be interested in taking part. Ultimately over 50 scientists were asked to take part, of which 27 responded. The questionnaire, as presented to the scientists, is given below for reference.

Punctuated Equilibria Questionnaire

The debate over the theory of punctuated equilibria has been going on for almost thirty years now. My research aims to follow the progress of this debate, and other related issues, like adaptation and species selection. I am interested in how much the theory has influenced scientists, in their ideas about how evolution operates and in the direction of their own research.

Hence the information that you supply via this questionnaire will be invaluable to me. I may wish to quote some of the comments that you make. All comments will remain confidential. Please put your replies on separate paper and attach to cover sheet. I do not expect respondents to spend more than an hour on this, so please, there's no need for extended replies. Just a paragraph or so for each question will be ample.

Replies can be sent to me by e-mail as an attached document, as text in an e-mail, or by mail to: Andrew Grimshaw, 1700 Colac-Gellibrand Rd, Kawarren 3249, Victoria, Australia. If you do send your replies electronically please number them and don't forget your answers to the cover sheet.

1. When did you first become aware of the theory of punctuated equilibria?

2. How and from whom did you learn of it?

3. What is your opinion of the value of punctuated equilibria? Do you think it is 'right'? Is it useful? Necessary? Does it add anything to previously existing knowledge?

4. How does it stand up to the data of evolutionary biology?

5. Is punctuated equilibria generally accepted in evolutionary biology? Where does it fit in with standard neo-Darwinism or the modern synthesis?

6. How has the it influenced the direction of your own research?

7. Steven Stanley and Elizabeth Vrba came up with some evolutionary models of their own to explain the form of the fossil record. They call their models “species selection” or “species sorting”. They claim that selection at the level of the individual or the gene is not sufficient to explain all of evolution. What is your opinion of this claim?

8. Gould and Eldredge claim that species selection is a natural consequence of punctuated equilibria. What do you see as being the connection between these two theories? (i.e. Are they linked or independent?)

9. Is species selection a generally accepted theory in evolutionary biology? How has it influenced your own work?

10. The status of paleontology as a science has certainly risen in the last thirty years. How influential has punctuated equilibria been in this respect?

11. Recently it seems that scientists have become more aware of work in the philosophy and sociology of science, especially that of Thomas S Kuhn and Karl Popper. Have you read much in this area, or attended lectures, seminars, etc.? Has it had any influence on the way you go about your work?

12. In general do you think external factors, like social context, political views, etc., have a significant impact on the formation of scientific ideas?

13. In particular, do you think external factors have had a significant influence on the formation or acceptance of punctuated equilibria or species selection?

Thank you for your time.