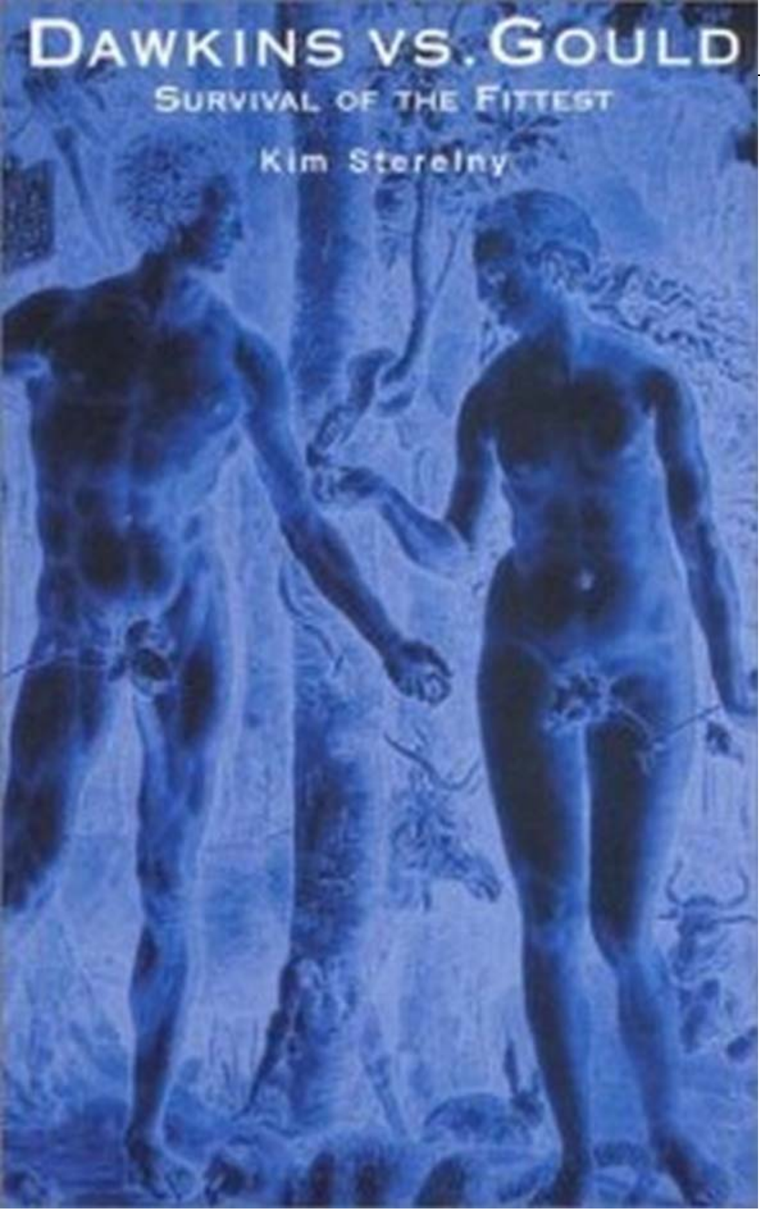
DAWKINS VS. GOULD
SURVIVAL OF THE FITTEST
Kim Sterelny

REVOLUTIONS IN SCIENCE

Dawkins vs. Gould

Survival of the Fittest

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Series editor: Jon Turney

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Dedication

For Peter: Friend and colleague

Part I
Battle Joined

1 A Clash of Perspectives

Science in general, and biology in particular, has seen its fair share of punch-ups. In the 1930s and 1940s, Britain's two greatest biologists, J.B.S. Haldane and R.A. Fisher, feuded so vigorously that their students (John Maynard Smith tells me) were hardly allowed to talk to one another. But their behaviour was civilised compared to the notorious feuds in biological systematics between cladists – notorious for wielding unintelligible terminology and vituperation in equal measure – and their opponents. Mostly these fights are kept more or less in-house, often because the issues are of interest only to the participants. Almost no one except systematicists are interested in the principles by which we tell that *Drosophila subobscura* is a valid species. But sometimes these disputes leak out into the open. Richard Dawkins and Stephen Jay Gould have different views on evolution, and they and their allies have engaged in an increasingly public, and increasingly polemical, exchange.

At first glance, the heat of this exchange is puzzling. For Dawkins and Gould agree on much that matters. They agree that all life, including human life, has evolved over the last 4 billion years from one or a few ancestors, and that those first living things probably resembled living bacteria in their most crucial respects. They agree that this process has been wholly natural; no divine hand, no spooky interloper, has nudged the process one way or another. They agree that chance has played a crucial role in determining the cast of life's drama. In particular, there is nothing inevitable about the appearance of humans, or of anything like humans: the great machine of evolution has no aim or purpose. But they also agree that evolution, and evolutionary change, is not just a lottery. For natural selection matters too. Within any population of life forms, there will be variation. And some of those variants will be a touch better suited to the prevailing conditions than others. So they will have a better chance of transmitting their distinctive character to descendants.

Natural selection was one of the great discoveries in Darwin's *Origin of Species* (1859). If a population of organisms vary one from another; if the members of that population differ in fitness, so one is more likely than another to contribute her descendants to the next generation; if those differences tend to be heritable, so the fitter organism's offspring share her special characteristics, then the population will evolve by natural selection. Australia is renowned for its poisonous snakes and of these the taipan is the most famously venomous. Let's consider the mechanism through which it became so impressively lethal. If a population of taipans differ in the toxicity of their venom; if the more venomous snakes survive and reproduce better than less venomous ones, then taipans will, over time, evolve more toxic venom. Gould and Dawkins agree that complex capacities like human vision, bat echolocation, or a snake's ability to poison its prey evolve by natural selection. And they agree that in human terms, natural selection works slowly, over many generations. Bacteria and other single-celled organisms whip through those generations at speed, and that is why drug resistance outpaces new drugs. But for larger, more slowly reproducing organisms, significant changes take tens of thousands of years to build.

Adaptive change depends on cumulative selection. Each generation is only slightly different from the one that precedes it. Perhaps, very occasionally, a major evolutionary change appears in a single generation, as the result of one big mutation. But the parts of an organism are delicately and precisely adjusted to one another, so almost all large, random changes are disasters. Adding a horn to a horse's head might seem to provide it with a useful defensive weapon, but without compensating changes to its skull and neck (to bear the extra weight) it would be not only useless but detrimental. So large single-step changes, Gould and Dawkins agree, must be very rare. The normal history of an adaptive invention is a long series of small changes, not a short series of large changes.

Yet Dawkins and Gould have clashed heatedly on the nature of evolution. In two notorious articles in *New York Review of Books*, Gould scathingly reviewed *Darwin's Dangerous Idea*, a work of Dawkins' intellectual ally Daniel Dennett. In 1997, there was a better tempered but no more complimentary exchange in *Evolution*, as they traded reviews of each other's most recent creation.

Dawkins and Gould are representatives of different intellectual and national traditions in evolutionary biology. Dawkins' doctoral supervisor was Niko Tinbergen, one of the co-founders of ethology. Ethology aims to understand the adaptive significance of particular behavioural patterns. So Dawkins' background sensitised him to the problem of adaptation; of how adaptive behaviours evolve in a lineage and develop in an individual. Gould, in contrast, is a palaeontologist. His mentor was the brilliant but notoriously irascible George Gaylord Simpson. The match, if it exists, between an animal's capacities and the demands of its environment is less obvious with fossils than with live animals. A fossil gives you less information on the animal and its environment. So it is tempting to suppose that the passion of these exchanges reflects nothing deeper than competition for the same patch of limelight, magnified by different historical and disciplinary perspectives. I think that suspicion would be misplaced, and it's my aim in this book to explain why. Despite real and important points of agreement, their clash is of two very different perspectives on evolutionary biology.

For Richard Dawkins, the fit between organisms and environment – adaptedness, or good design – is the central problem evolutionary biology must explain. He is most struck by the problem Darwin solved in his *Origin*: in a world without a divine engineer, how can complex adaptive structures come into existence? In his view, natural selection is the only possible answer to this question. Natural selection is the only natural mechanism that can produce complex, co-adapted structures, for such structures are vastly improbable. Hence natural selection plays a uniquely important role in evolutionary explanation.

Moreover, and most famously, Dawkins argues that the fundamental history of evolution is the history of gene lineages. The molecular biology of genes – the chemical details of their action, interaction and reproduction – is alarmingly complex. But fortunately Dawkins does not allow himself to be bogged down in these details, and we can follow his lead. He argues that the critical agents in life's drama must persist over long periods *precisely because* the invention of adaptation requires a long series of small changes. Hence the target of selection is a lineage that persists over many generations. Gene lineages and only gene lineages satisfy this condition. Genes are replicated: there are mechanisms that copied some of my genes into my daughter's genome; and those same mechanisms are capable of copying those same genes generation by generation. So genes form lineages of identical copies. These lineages can be very deep in time. You have genes that you share with yeasts and other single-celled organisms; organisms that have been evolving separately for billions of years. Perhaps with the exception of those organisms that clone themselves, organisms do not form lineages of identical copies. Reproduction is not copying. My daughter is not a copy of me. An organism disappears at the end of its life. But an organism's genes may not disappear. If that organism, or a relative carrying a similar complement of genes, reproduced, then copies of the organism's genes will persist. They may do so for many generations.

Moreover, the chance that a gene will be copied is not independent of the character of that gene. It is true that some genes are *silent*, and just seem to be hitching a ride. But often genes influence their own replication prospects. They do so most overtly by their influence on the characteristics (the *phenotype*) of the organism that bears them. So genes influence their own prospects of being copied. Dawkins conceives of the fundamental struggle of evolution as the struggle of genes in lineages to replicate. Moreover, success for one gene lineage can mean failure for another. Dawkins' opponents often portray him as a crazed reductionist, thinking that only genes matter in evolution. That is not his view. Organisms are important, but primarily as a weapon in the struggle between gene lineages. Gene lineages usually compete with other gene lineages by forming alliances. Rival alliances build organisms. Successful organisms replicate the genes in the alliance that builds them. Thus macaw-making genes which build macaws suitable to the bird's circumstances become more common over time. The conflict between two macaws for a safe hollow in which to nest influences evolution by determining which lineages of macaw-making genes will be represented in the next generation, and in what numbers. The ecological struggle between organisms to survive and reproduce is translated into differential success for the genes that build the organisms.

In short, for Dawkins, the history of life is a history of a mostly invisible war between gene lineages. The beautiful biological mechanisms that we see on so many natural history documentaries are the visible products of that war. They are its weapons. For rival gene alliances are engaged in a perpetual arms race. In human arms races, weapons improve over time. So too will biological weapons, though that improvement has from time to time been disrupted by catastrophic and unforeseeable changes to the battlefield: episodes of mass extinction when many species disappear. These changes may be caused by the geology of the earth itself, as continents divide, mountains erupt, seas and ice fields advance or retreat. And they may be caused by forces external to the earth: by impact or by changes in the sun's behaviour. But between these episodes, selection is omnipresent and effective, sifting gene teams, building adaptive improvements in the organisms that are their *vehicles*, as Dawkins puts it.

Gould sees the living world very differently. Life today is fabulously diverse. But many forms of life that used to dominate their environments are no longer with us. Gould is a palaeontologist, and so much of his professional life concerns extinction: from the spectacular extinction of the dinosaurs, pterosaurs and huge marine reptiles, to the less obtrusive, and yet in Gould's eyes more fundamental, extinctions of weird marine invertebrates 500 or more million years ago. The first multi-celled animals in the fossil record lived, then disappeared, 600 million years or so ago. This 'Ediacara fauna' is so enigmatic that there is debate as to whether they were animals at all. The fossils consist of the remains of frond- and disc-shaped organisms, and interpretations of these fossils vary widely; some think they are more like lichen than animals. After the Ediacaran disappearance, in the so-called Cambrian era 530 million years or so ago, the main modern lineages came into existence. *Arthropods* (insects, crabs, and their kin) evolved. So did *bivalves* (oysters, clams and the like) and *molluscs* (snails and their relatives). *Jellyfish* and *sponges* were around too, though they may have appeared a little earlier than the others. A horde of the different kinds of worms appeared. So too did the first *chordates*; our group. But at the same time, many other lineages came into existence, only to go extinct again. Extinction, and its causes, is one of Gould's fundamental concerns.

Dawkins is impressed by the power of selection to build adaptations. Gould is equally struck by conservative aspects of the history of life. In their most fundamental ways, animal lineages do not seem to change over enormous stretches of time. There are hundreds of thousands, perhaps millions, of species of beetle. Every single one is built on the same basic plan. They vary in size, colour, sexual ornamentation and much else. But they are all recognisably beetles. The same is true of the other great lineages of animal life. The main division of the kingdom of animals is into *phyla*. There are thirty odd: the exact number is in dispute. Some are scarcely known as fossils at all. But all of those that have decent fossil records appeared early. That leads Gould to the view that the main ways of building an animal were all invented at roughly the same time, and no new ones – no new fundamental body organisations – have been invented since. Evolution has certainly not ground to a halt when it comes to inventing new adaptations. But if Gould is right, it does seem to have ground to a halt in inventing new phyla of animals. Gould sees this as the most striking fact evolutionary theory must explain.

Moreover, Gould has a different conception of the mechanism of evolution. He argues that selection is constrained in important ways by the limits of variation in lineages. For selection can act only to magnify and sculpt variations found in the population. Moreover, he thinks chance has played a pivotal role in the history of life. In times of mass extinction, many species disappear. Surviving, in Gould's view, depends more on luck than on fitness. So in explaining evolutionary history, Gould places less weight on selection than does Dawkins. Moreover, he has a different view of the way selection works. He is very sceptical of gene selection, for he doubts that particular genes usually have a consistent enough effect on the fitness of their bearers for Dawkins' story to make sense. The effect of a particular gene on a body depends on the other genes in that body and on many features of the environment in which the organism develops. So Gould thinks that when selection acts, it typically acts on individual organisms. But this is only part of the story. Gould is sympathetic to theories of 'species selection'. Species themselves may have properties which make them more, or less, apt to go extinct or to *speciate*; that is, to give rise to daughter species. For example, there are very few species of asexual vertebrates; just the odd species of lizard, fish and frog. Moreover, those few seem not to have long evolutionary histories. A mutation is a copying error that takes place when a gene replicates. Most mutations are neutral or bad, but sometimes they cause a beneficial change. And in an asexual species, if two good mutations occur in separate mother–daughter clones, they cannot combine their luck. If they could mate, they could combine their advantages. So perhaps asexual species are vulnerable to extinction as a consequence of their evolutionary inflexibility.

These differences within evolutionary theory are exacerbated by different assessments of science itself. As *Unweaving The Rainbow* shows, Dawkins is a wholehearted son of the Enlightenment. We should embrace the scientific description of ourselves and our world, for it is true (or the nearest approach to truth of which we are capable), beautiful and complete. It leaves nothing out. Gould, on the contrary, does not think that science is complete. The humanities, history and even religion offer insight into the realm of value – of how we ought to live – independent of any possible scientific discovery. And while Gould has never embraced the view that science is just one of many equally valid perspectives on the world, he has often written of social influences on scientific views. Scientific orthodoxy *does* respond to objective evidence about the world, but often slowly, imperfectly, and in ways constrained by the prevailing ideology of the times. In short, Dawkins, but not Gould, thinks of science as a unique standard-bearer of enlightenment and rationality.

Part II
Dawkins' World

2 Genes and Gene Lineages

The Selfish Gene begins with a creation myth. Dawkins asks us to imagine a primitive, pre-biotic world – a world in which physical and biochemical processes make available a soup of chemical and physical resources. In this soup, nothing lives, nothing dies and nothing evolves. But then, Something Happens. A *replicator*, by chance, comes into existence. A replicator is a molecule (or any other structure) that in the right environment acts as a template for its own copying. Active replicators have characteristics which determine their prospects of being copied, though their chances will always depend as well on their environment. A replicator that is highly copy-worthy in one environment might, for example, be too unstable and hence have very poor prospects in a hotter chemical soup, or one composed of different compounds.

The formation of the first active replicator is a world-shaking event. It is truly something new under the sun, for it introduces natural selection and hence evolution into the world. No copying process is perfect. Hence at some stage, after some number of copyings, the copies of the prime replicator will begin to vary from one another. A population of variants comes into existence. Within the population of variant replicators, some will have better prospects than others. Some will have a higher propensity to be copied. Others will have a lower propensity; they are less stable, or require a less common ingredient in the soup. That creates the conditions for natural selection. For resources are not infinite: the replication of one lineage will have consequences for other lineages. And thus evolution driven by selection begins:

Competition + variation + replication =
natural selection + evolution.

The replicators that descend from the original are weeded by natural selection: the variants with features that promote replication will become common; the variants with features that make replication less likely will become rare or extinct.

It would be hard to exaggerate the differences between a world in the first stage of evolution, and our world. Today's genes are made from DNA: specifically, they are sequences of the four bases *adenine*, *guanine*, *cytosine*, and *thymine* (usually abbreviated to A, G, C and

T) attached to a sugar and phosphate spine. Some genes do nothing at all. But most that do anything code for a protein. Indeed, when biologists speak of genes (for instance, when talking of the number of genes carried by particular organisms) they usually have in mind the base sequence that specifies a particular protein. This specification is implemented by an almost universal code. The base sequence is read in groups of three, each of which (aside from a stop signal) specifies one of twenty amino acids. Hence long base sequences specify amino acid sequences, and such sequences are the 'primary structure' of proteins. The process by which genes produce proteins is indirect, requiring two RNA intermediaries – known as messenger and transfer RNA – and it depends on complex cellular machinery.

The upshot is that genes, and the gene-to-protein system, are themselves complex products of evolution. The first replicators were certainly not DNA sequences. They may have been RNA sequences (in which *uracil* replaces thymine) though even that is very controversial. Moreover, this was a world of the 'Naked Replicator'. In our world, the genes are replicated, and the organism interacts with the environment both to protect the genes and to secure the resources for their copying. Hence biologists distinguish the *genotype* of an organism (the complement of genes it carries) and the *phenotype* (its developed form, physiology and behaviour). But in this