

8 Postgenomic Darwinism

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Introduction

I might perhaps have better called this chapter post-Darwinian genomics. One point I want to make is that it is time we disconnected our discussions of evolution from an unhealthily close connection with the name of Charles Darwin. Darwin, after all, wrote his most famous work 150 years ago, and rapidly advancing sciences do not generally rest directly on work a century and a half old. Darwin knew nothing of genetics or genomics and, as I shall especially emphasise, there have also been remarkable advances in microbiology that he could not have known about and that fundamentally affect our understanding of evolution.

I do not, of course, have any wish to deny Darwin's greatness as a scientist. It is impossible to read his extensive scientific writings without being struck by the powers of his observation, the encyclopaedic breadth of his knowledge, and a remarkable ability to move between detailed observation and the grand sweep of theory. Moreover, the fact that it was Darwin who convinced the learned world of the fact of evolution, of the common descent of humans and other forms of life, gives him an uncontested place in the history of ideas. This has provided a cornerstone of the naturalistic world view which, if hardly the universal perspective of the human race, has increasingly become the dominant perspective among its most educated and reflective minorities.

But this is not just a quibble about an anomalous degree of deference to a distinguished and influential dead scientist. I think this deference can act as an obstacle to the advance of the science. At its most extreme – and here one cannot help seeing an ironic defeat for biology in its debate with religious creationists – Darwin takes on the role of scriptural

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authority, and his words are subject to detailed exegetical analysis as if this was a way to better understand the biological world. It sometimes seems that Darwin, like God in war, appears on both sides of most major biological debates. One of the great epistemic virtues of science is that it constantly attempts to revise itself and advance its understanding as new information or insight accumulates. Excessive deference or even reverence for past authorities is the antithesis of this epistemic commitment.

But more subtle and specific misunderstandings are also associated with the excessive reverence for Darwin. It is sometimes forgotten that whereas Darwin quite rapidly convinced the learned world of the truth of evolution, the transformation between distinct species, after the publication of the *Origin of Species*, conviction for the process commemorated in his subtitle, natural selection, was not achieved widely until well into the twentieth century, with the synthesis of Darwinian natural selection with Mendelian genetics. The real target of this chapter is not so much with Darwin's own views, but with the view that emerged at that time as the 'New Synthesis', and has evolved today into what is often called neo-Darwinism. There is a popular view that Darwin got just about everything right that was possible for someone deprived of an adequate understanding of genetics, and the New Synthesis filled in this final gap. And it is this vision, lent weight by the towering authority of Charles Darwin, which I suggest is becoming an obstacle to the advancement of our understanding of evolution and its ability to take account of the very remarkable advances in our biological understanding over the last few decades.

Neo-Darwinism

By 'neo-Darwinism' I mean the New Synthesis as modified by the emergence of molecular genetics in the 1950s and beyond. From the New Synthesis it maintains (in addition to the core commitment to natural selection) the Mendelian idea of inheritance as particulate, the concept of genes that are transmitted to offspring in their entirety or not at all, and the concept, following August Weismann, of a sharp division between germ cells, which carry the transmitted genes, and somatic cells. Neo-Darwinism can be defined, for my present purposes, in terms of two core

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theses and one important corollary. The first thesis is that overwhelmingly the most important cause of the adaptation of organisms to their environment, or conditions of life, is natural selection. This is the heart of the Darwinism in neo-Darwinism. The second thesis is that inheritance, at least as far as it is relevant to evolution, is exclusively mediated by nuclear DNA. This thesis could be seen, if a little simplistically, as a blend of Mendel and Weismann seen through the lens of Crick and Watson.

The corollary, especially stemming from the Weismannian ingredient of the second thesis, is the rejection of Lamarckism. Lamarckism here has perhaps less to do with the actual opinions of Jean-Baptiste Pierre Antoine de Monet, Chevalier de la Marck even than do contemporary understandings of Darwinism with the ideas of Charles Darwin. Lamarckism now has come to mean the inheritance, or bequeathal to descendants, of somatic characteristics acquired in the lifetime of an organism, and this has become the ultimate taboo in Darwinian theory. The significance of the taboo is that it presents a powerful restriction on the variations that can be the targets of natural selection, the differences between which Nature selects. These differences are now assumed to be, or to be direct causal consequences of, randomly generated changes in the genes or genome of the organism.

In the following pages I shall describe some developments in recent biology that show that neo-Darwinism, if not entirely obsolete, is at least severely limited in its ability to encompass the full range of evolutionary processes. My suggestion is that the association with a long-dead hero can convey the message that in general outline the problems around evolution have been solved long ago, and only the details, perhaps of evolutionary history, need to be sorted out. This message is sometimes explicitly promoted in opposition, particularly in the United States, to the powerful voices of creationists opposed to the very idea of evolution. As I have already suggested, the response is surely a counterproductive one. We should celebrate the fact that the exploration of evolution is an exciting scientific project and, far from being essentially complete, it is one of which we are still only at the very early stages. Those who insist on having the whole 'truth' whether or not we have any serious grounds for believing it are perhaps closer to the religious fundamentalists they so vehemently oppose than they would like to believe. At any rate, what

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I shall do in the main body of this essay is look at some areas of biological research that are radically altering our views of evolution and challenging neo-Darwinian orthodoxy. As should by now be clear, I take this as illustration of the excitement and dynamism of evolutionary science, certainly not any indication of its vulnerability.

Revisionist Darwinism 1: the tree of life

The first topic I want to address that will indicate the shakiness of the neo-Darwinian orthodoxy is the concept of the tree of life. The tree of life is the standard neo-Darwinian representation of the relatedness of organisms. As a tree, crucially, it constantly branches, and branches always diverge, never merge. Species are represented as small twigs; larger branches represent larger groups of organisms. By following down from the branches towards the trunk of the tree it is possible in principle to work backwards through all the ancestors of a group of organisms to the earliest beginnings of life at the tree's base. Darwin's imprimatur for this divergent evolutionary structure is often secured by a picture in the notebooks that seems to represent a divergently branching structure, accompanied, to the delight of philosophical commentators, by the legend 'I think' (Figure 8.1). More significant still, though, is the sole illustration in the *Origin of Species* representing with a branching diagram the formation of new species through the divergence of varieties within a species, an illustration that follows a chapter adumbrating the benefits of divergence by analogy with the division of labour (Figure 8.2).

But this image of the tree of life has been rendered at least partially obsolete by recent developments, especially in microbiology, where so-called lateral gene transfer, the passage of genetic material not from ancestors, but from sometimes distantly related organisms on widely separated branches of the tree of life, is common. One reason for the importance of this phenomenon is that it threatens to undermine the pattern of explanation of features of biological organisms that is universally mandated by the divergently branching structure of the tree. Neo-Darwinism, it will be recalled, attributes the adaptation of organisms to natural selection, working on variations in the genetic material. These variations are generated endogenously and transmitted within the

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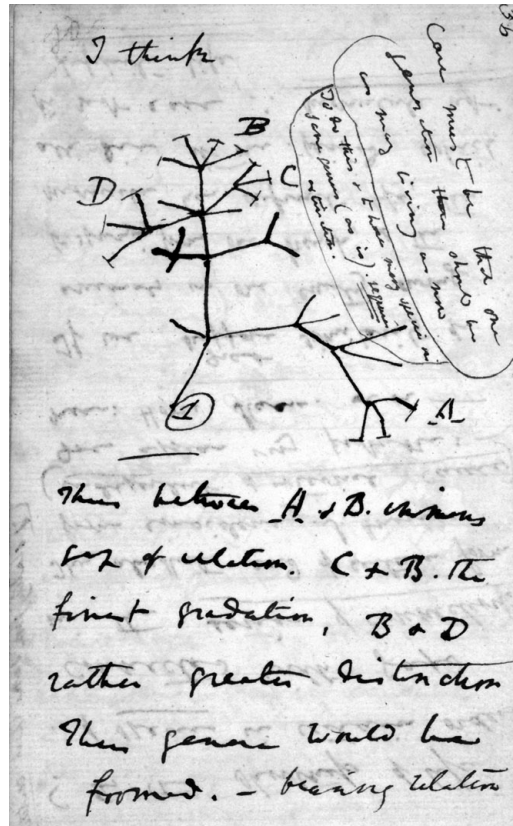


FIGURE 8.1 Darwin's first sketch of an evolutionary tree from Notebook [B], the first notebook on *Transmutation of Species* (1837). Reproduced by kind permission of the Syndics of Cambridge University Library.

narrow confines of the species, understood as groups of organisms sharing access to the same gene pool. Embedding this idea within the wider frame of the tree of life, we can see that the explanations for all the characteristics of an organism are to be sought in the sequence of ancestors traceable down the branches of the tree, and in the evolutionary process, namely natural selection, to which these ancestors had been subject. Explanation of the characteristics of an organism by lateral gene transfer, on the other hand, puts no limit in principle on where in the history of life a particular aspect of a lineage may have originated. This is

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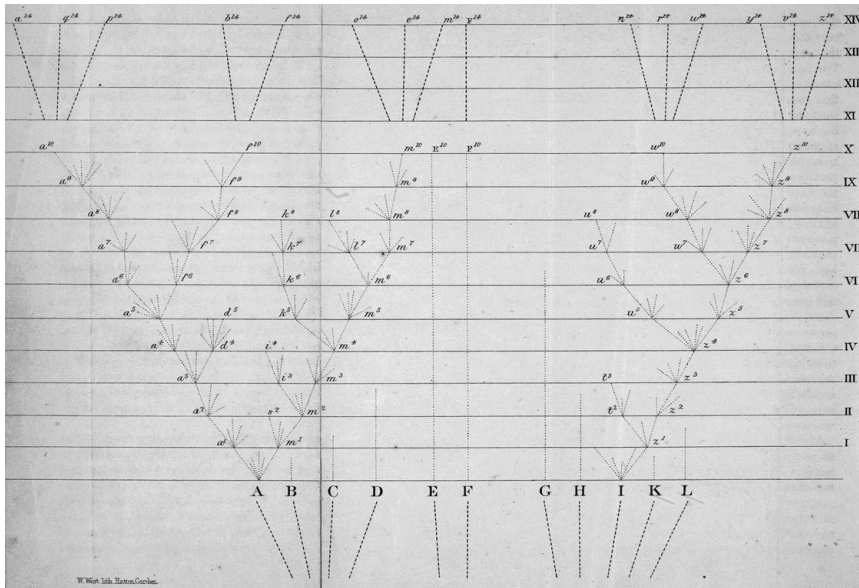


FIGURE 8.2 The sole illustration from *The Origin of Species*, showing the divergence of ancestral species, first into varieties and eventually species. Species G and H, for instance, have gone extinct, whereas species I eventually gives rise to six descendant species. Reproduced by kind permission of the Syndics of Cambridge University Library.

immediately obvious when we note that if lateral gene transfer is common, the overall structure of relations between organisms will take the form not of a tree, but of a web, or net. And in a web, unlike a tree, there are many paths from one point to another.

Lateral gene transfer is widely recognised to be endemic among microbial life forms (see, for example, Doolittle, 1999). Microbes transfer bits of DNA from one to another by a process sometimes likened to sex called *conjugation*, in which a tube down which the genetic unit passes is inserted by one cell into another; by *transformation*, the uptake of free DNA from the environment; and by *transduction*, in which the transfer is mediated by viruses. These processes can result in genetic transfers between the most distantly related organisms, even organisms from different domains, the threefold classification now taken to be the most fundamental division of living organisms.¹ This, in short, removes the presupposition that the evolutionary exigencies of linear ancestors explain

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the features of their living descendants. Lateral gene transfer allows features to have come from, more or less, anywhere in the biosphere.

Questioning the tree of life remains, none the less, a controversial business.² Although many microbiologists have accepted that there is no unique tree for microbes, some still resist this conclusion, and insist that there is a core genome, resistant to lateral transfer, and in terms of which a microbial phylogenetic tree can be reconstructed (Lawrence and Hendrickson, 2005; but see Charlebois and Doolittle, 2004). There are serious problems with this, however. First we might wonder, even if the claim can be sustained in some sense, whether the tree based on the core genome is very useful. Or in other words, what is the tree of life for? If, as I have been suggesting, its function is to underpin evolutionary explanations of organismic features, then the more prevalent is lateral transfer, the less will any tree be able to serve this end. This is even more so as the genes that are likely to form the constant core will inevitably be ones with fundamental, and therefore substantially invariant, functions across a very wide range of organisms. They will, for that reason, be the least useful in tracking differences between organisms. This leads naturally to the question, why track phylogeny using these genes rather than some others. Because of lateral transfer not all trees of genes will coincide. And it may be that different gene trees will be useful for answering different questions. Perhaps the defenders of the core genome have in mind that what they should attempt to construct is the cell tree, the tree that traces the sequence of (vertical) cell divisions back to the beginning of cellular life. The trouble then is that this seems just to assume what is at issue, that vertical inheritance is what really matters. If this position is to be maintained regardless how much the contents of the cells may be changed by other interacting, non-vertical processes, one might wonder in the end whether it would end up as little more than a fetishism of the cell membrane.

Eukaryote³ biologists are generally much more confident of the tree of life, and with good reason.⁴ Lateral gene transfer seems less common among eukaryotes, and there is little question that the tracing of vertical ancestral relations is a powerful and useful way of classifying these organisms.⁵ Even here, though, there is reason to be cautious. For a start, hybridisation seems to be much more common than was once

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thought (Mallet, 2008). But perhaps more important, the transfer of genetic elements by viruses certainly does continue in eukaryotes, and may well prove to be an important factor in evolution. About half of the human genome, for instance, consists of material that is thought to have originated in transfers from viruses. Much of this, it is true, consists of highly repetitive sequences that have seemed unlikely to be functionally significant. When the idea of 'junk DNA' was fashionable, these were prime candidates for junk. However, it now appears that at least 70% of the genome is transcribed into RNA, and investigation of the roles of various kinds of RNA fragment in regulating the genome is one of the fastest growing fields in molecular biology. It would be premature to assume that sequences of viral origin may not play crucial roles in such regulatory systems. And finally, there are examples of significant functional features of cells that do appear to involve protein-coding sequences of viral origin. The best example here is of the evolution of placental mammals. The tissue that provides the barrier between fetal and maternal circulations, the syncytium, is believed to be coded for by genes of viral origin (Mallet *et al.*, 2004). There may surely be other equally significant cases. It is at any rate clear that, even among eukaryotes, lateral origins play some role in explaining the current features of organisms. The always branching, never merging, tree of traditional phylogeny is not enough.

Revisionist Darwinism 2: evolution by merger

Lateral gene transfer can be seen in a rather different light as an example of something much broader, evolution by merger. This gets to one of the most general points I want to make about the limitations of neo-Darwinism. The first thesis mentioned above, the overwhelming emphasis on natural selection, has encouraged neo-Darwinian evolutionists to think a great deal about competition, but very little about cooperation. Indeed, the latter appears mainly in the guise of a problem – the 'problem of altruism'. The problem of altruism is, crudely put, the problem of understanding why it is that, in a 'Darwinian' world in which the only survivors are the most ruthless and self-interested competitors, some organisms are actually nice to one another. But looked at from

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a quite different perspective, life is a massively cooperative enterprise and 'altruism' should hardly be surprising. The elements in a cell or the cells in a multicellular organism must obviously work in a highly coordinated way and subordinate their own 'interests' to those of the whole of which they are part. It will be objected at once that this is cooperation within an organism, not between organisms, and so of course not a problem. But this reply assumes that we know exactly what constitutes an organism and what is merely a part of an organism, an assumption I shall suggest is highly problematic.

It is perhaps hardly controversial to note that natural selection will frequently select the organisms that are best at cooperating with the organisms with which they interact. This is just one way of adapting to the environment, the most salient part of which is typically the other organisms that inhabit it. I want to go a step beyond this, however, and suggest that merger with other organisms (or suborganismic biological entities) is a central process by which biological organisms evolve. Such a process is referred to as endosymbiosis, and is most widely familiar from the ideas of Lynn Margulis (1970) about the origins of the eukaryotic cell.⁶ It is now universally acknowledged that the mitochondria that provide the energy source for all eukaryotic cells, and the chloroplasts that effect photosynthesis in plants, were both originally free-living organisms but are now more or less independently reproducing but wholly dependent constituents of larger cells. Although the details are much more controversial, it is also believed by many that the eukaryotic cell itself derived from a merger between two prokaryotes, perhaps a bacterium and an archaeon.

The examples just mentioned are instances of fully obligate endosymbiosis: mitochondria are parts of eukaryotic cells, and there is no more question of why they are acting altruistically towards the containing cell than of why my liver acts altruistically towards me. However, it is important to note that endosymbiosis is something that may evolve over a long period of time, and in the mean time may consist of a range of degrees of interdependence from conditional and reciprocal cooperation to full endosymbiosis. There are, for example, well studied cases of varying degrees of endosymbiosis between insects and bacteria. *Buchnera aphidicola*, endosymbionts of aphids, have been associated with

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their partners for up to 200 million years, and have lost the ability to carry out various essential metabolic functions on their own. *Wolbachia*, on the other hand, a genus of bacteria associated with a very wide range of arthropod species including perhaps half of all insect species, is generally referred to as a parasite. *Wolbachia* are particularly interesting for their ability to control the reproductive behaviour of their hosts. Some can kill or feminize males, or induce parthenogenesis. They can also induce reproductive incompatibility between insects infected with different *Wolbachia* strains, possibly playing a determinant role in speciation.

It is generally supposed that the manipulation by *Wolbachia* of their hosts' reproduction contributes to their own rather than their hosts' reproductive interest. However, as some host species appear unable to reproduce without the assistance of *Wolbachia*, and as *Wolbachia* are obligatorily symbiotic, it is not always clear how these interests are to be separated. *Wolbachia* are involved in transfers of DNA between insect species, raising questions about genetic differentiation of insect species (Whitworth *et al.*, 2007), and a whole *Wolbachia* genome has been found embedded within a *Drosophila* genome (Dunning Hotopp *et al.*, 2007). It has also been found that *Wolbachia* may reduce the vulnerability of their hosts to viral infections (Texeira *et al.*, 2008). It would be difficult to assess the ratio of costs and benefits to the parties in these intimate associations, but it seems likely that this balance will vary from case to case, and that in some cases the relationship has moved to full mutualism or even symbiosis.

One reason I have spent a little time on this example is that it begins to introduce a fundamental question, namely how we determine the limits of an organism. No one doubts that mitochondria are parts of the organisms in which they are found whereas, on the whole, everyone takes *Wolbachia* and their insect hosts to be distinct organisms. But what is the basis of this different treatment? It will be recalled that discussions of altruism tend to assume that this question is unproblematic. If, as I shall suggest, it is a thoroughly indeterminate matter, settled as much by our interests as investigators as by anything in Nature, it will clearly be necessary to rethink the question of altruism or, more broadly, competition and cooperation.

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What is an organism?⁷

Although philosophers have for many years questioned some of the key concepts of biology, such as the species or, more recently, the gene, on the whole they have not seen much to worry about with the concept of an organism. According to the orthodox view, there are two kinds of organisms: single-celled, or microbes, and multicellular, or (as I have elsewhere suggested we call them (O'Malley and Dupré, 2005)) macrobes.⁸ In the former case the cell is the organism. In the latter case all the cells derived from a fertilised egg, or zygote, constitute the one organism. We might summarise the view as 'one organism, one genome'. This concept of the organism could be seen as the microlevel reflection of the macroscopic tree of life: both within and between organisms we find orderly and always divergent branching. But we might also want to approach the question of what constitutes an organism from a functional perspective: what are the systems of cells that interact with the surrounding environment as organised and generally cooperative wholes? From this starting point we would note that microbes do not typically function as isolated individuals but rather in complex associations often composed of highly diverse kinds of cells. Typical of such associations are biofilms, the generally slimy coatings that develop on practically any moist surface. Consider, for instance, one well studied class of biofilms, those on the surfaces of our teeth known as dental plaque. Over 500 different bacterial taxa have been found living in the human mouth (Kolenbrander, 2000) and, according to one authority, 'Oral bacteria in plaque do not exist as independent entities but function as a coordinated, spatially organized and fully metabolically integrated microbial community, the properties of which are greater than the sum of the component species' (Marsh, 2004). Why would we not consider this community, the organized functional whole, to constitute an organism?

If we concede that biofilms comprise a kind of multicellular organism, then the argument is also over as far as traditional monogenomic multicellular organisms are concerned. For all known such multicellular wholes exist in symbiotic relations to often enormous and diverse communities of microbes. In the human body, for instance, it is estimated that 90% of the total number of cells are in fact microbial (Savage, 1977), living mainly in our gut, but also on the surface of the skin and in all the

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bodily orifices. These microbes contain perhaps 100 times as many genes as those found in the more traditional human genome (Xu and Gordon, 2003), which has led to the launch by the US National Institutes of Health of the Human Microbiome Project, which will explore this missing 99% of the full human genome. The importance attached to this project reflects an increasing awareness that these symbiotic microbes have a fundamental influence on human health. They are known to be involved in digestive processes, and hypothesized to have a significant role in causing obesity. For model organisms it has been demonstrated that microbial symbionts are necessary for normal physiological development (Bates *et al.*, 2006), that they affect gene expression in the 'host' cells (Hooper *et al.*, 2001), and that they are involved in the maturing of the immune system (Umesaki and Setoyama, 2000).⁹ There is every reason to expect similar findings in humans.

I propose then that the typical organism is a collection of cells of different kinds, organised cooperatively to maintain its structure and reproduce similar structures. As Maureen O'Malley and I have put it (forthcoming), an organism is a metabolically integrated community of lineage segments. It will immediately strike evolutionists that this conceptually separates the organism (functional whole) from the evolving entity (part of a lineage). But this, of course, is the point. The assimilation of these concepts obscures the empirical reality that evolution requires both (directly) reproducing lineages and the assembly of organisms from components of these lineages, and that these are in principle quite independent processes. While most of these lineage segments will have little chance of reproducing themselves except in so far as they are able to form parts of appropriate communities, this is nevertheless a contingent matter.¹⁰ One consequence of this proposal is that what is an organism, and whether something is part of an organism or not, are not questions that necessarily admit of definitive answers. Whether a group of microbes is a closely connected ecological community or an organism may be a matter of biological judgement. The important point is that it, or most of it, will share an evolutionary fate. If its constituent cells are to send descendants off to participate in new biofilms it will be because the parental biofilm is thriving. What I have been calling organisms are units of selection, objects between which natural selection selects.

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Cooperation again

I can imagine a frustrated reader complaining that I have yet to address the kind of cooperation that is of real interest to evolutionary biology, cooperation between conspecifics. Cooperation with other organisms is just adaptation to the environment, of which they are part. Some of them are to be eaten, most can be ignored, others are more useful as collaborators, and so on. Conspecifics, on the other hand, are always competitors for representation by their descendants in subsequent generations. So let me say something about this topic.

The orthodox neo-Darwinian view is that the only circumstance that brings about cooperation between conspecifics is kin selection. Here it is time to distinguish between some degrees of cooperation. If two lions can kill a wildebeest that neither could handle alone, and moreover it will provide plenty of food for both, they will do well to cooperate. Evolutionists tend rather to speak of 'altruism' in a technical sense according to which an act is altruistic only if it not only confers a benefit on the recipient but is also more costly to the donor than refraining from action. Any animal that acted in this way would lose out to natural selection in competition with others that avoided such acts of kindness. The only exception would be the case where the beneficiary is kin, perhaps one's offspring, as described by so-called inclusive fitness theory. Here the fundamental principle is said to be Hamilton's rule: $rB > C$. B is the benefit to the recipient, C the cost to the donor and r the so-called coefficient of relatedness. This coefficient is $\frac{1}{2}$ for offspring or full siblings in sexual species, and is thought of as the proportion of genes that two organisms share by virtue of their relations of descent.¹¹ If $rB > C$, for example if I make a sacrifice that provides more than double the benefit to my child, evolution will favour such behaviour. I don't want to deny that this is a powerful tool for analysing important aspects of evolutionary processes and their potential stability or instability. One very impressive example is its application to theoretical discussions of the evolution of eusociality, the often vast and complexly articulated social system characteristic of many ants, wasps and bees (Hymenoptera), termites and, alone among mammals, the naked mole rat. These arguments have shown that only under conditions of strict monogamy for an exclusive breeding couple

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is such a social arrangement likely to evolve. Recent work (Hughes *et al.*, 2008) has confirmed that such strict monogamy was indeed the ancestral condition in a large number of Hymenoptera species studied, giving convincing support to inclusive fitness theory.

I want to make two somewhat more sceptical comments on this topic, however. First, it is often said that altruism outside the narrow confines of kin selection theory will be subverted by competition from less altruistic rivals. The assumption that there are indeed such rivals seems sometimes to be a matter of pure dogma. Consider, for instance, an example that seems to contradict standard kin selection theory, also from the Hymenoptera. The Argentine ant (*Linepithema humile*), while known for its inter-colony aggression in its native land, has now taken to behaving in a non-aggressive, cooperative way with relation to other colonies of conspecifics, in a range of newly colonized areas in Europe, North America, Japan and Australia. Contrary to a speculation that this must be due to genetic relatedness between the recently landed colonists, colonies in the European case, at least, were found to be genetically diverse. There is considerable dispute about how to explain or even describe this phenomenon, though one thing that seems to be widely agreed is that the ants as a whole do very well out of the arrangement. As humans have also discovered, warfare may benefit a few, but it is hardly good for the species. Unsurprisingly, it is also speculated that the arrangement will be unstable. A mutant aggressive colony would perhaps do extremely well cutting a swathe through its amiable neighbours. But even if this could happen, it doesn't imply that it must. Perhaps eventually the system will collapse, and perhaps it is bound to do so in the very long run. But, to paraphrase Keynes, in the long run we are all extinct. The existence of cooperation between non-kin is sufficient to show that there are evolutionary processes capable of creating it. The most widely discussed such process is of course group selection, though this does remain controversial, if less so after the extremely influential work of Sober and Wilson (1998). Even if it is demonstrated that there are circumstances that would undermine these cooperative systems, this hardly shows that they could not, after all, have come into being in the first place. It is a contingent matter how long more or less cooperative, even altruistic, systems last.

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This brings me conveniently to my second point, the one that has been the main focus of this paper. It is that arguments about what entities can be expected to cooperate or compete with what others presuppose that we know what the individuals are that are cooperating or competing. Group selection is taken to be problematic because it is assumed that the members of the group are real, robust, indisputable individuals, whereas we see the group itself as a fragile coalition, a thoroughly dubious individual. But what I have been suggesting is that in fact there is no sharp line between the group of more or less cooperative individuals on the one hand, and the unified self-contained individual on the other. Indeed, it may well be that there is a tendency for the former to evolve into the latter, and that in the course of this process the individuals will act increasingly as parts subordinate to a larger whole. Presumably something like this must have happened in the evolution of multicellularity, and indeed is thought to have happened many times (Buss, 1987).

There is even a bigger picture here. The idea that life is hierarchically structured is an ancient and obvious one. Molecules comprise cells; cells make organs and organ systems; organisms are composed of organs and the like; and organisms in turn make up larger social or ecological units. This is a useful picture in focusing the investigating mind on particular aspects of the biological world, but it can easily be taken too literally. Cells, organs, and even organisms are, in Nature, embedded in larger systems, and their separate existence requires either a scalpel or a process of abstraction. Two further points reinforce both the significance and the plausibility of this observation. First, or so I would also argue, a full understanding of a biological entity at any of these intermediate levels is impossible without taking account both of its composition from smaller constituents, and the influences exerted on it by the larger system of which it is part, though that is an argument beyond the scope of the present paper (see Powell and Dupré, 2009). Causal explanation runs both from smaller to larger and from larger to smaller. Second, we should recall that our hierarchy of entities is already itself an abstraction from a hierarchy of processes. It may be that many forms of scientific reasoning require descriptions of entities as if they had a set of static properties definitive of such entities. But the reality, as best we understand it, is of a series of nested processes at timescales ranging from

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nanoseconds for intercellular chemical reactions to hundreds of millions of years for some macroevolutionary processes (Dupré, 2008). The illusion of an objectively distinct and unique hierarchy of objects is much less compelling when this abstraction is borne in mind.

Lamarck redux

I turn now to the strictest taboo in neo-Darwinism, Lamarckism.¹² Lamarckism, here, must be understood in an even less historically grounded sense than Darwinism, and has little to do with the great French naturalist. The taboo concerns the inheritance of characteristics acquired during the lifetime of the organism. According to strict neo-Darwinists only genetic mutations within the germline and the recombination of genetic resources brought about by sexual reproduction provide the resources on which selection acts. Curiously, however, though mention of Lamarckism can still bring a shudder to many evolutionary biologists, almost no one still believes in the strict form of the taboo. Or so, anyhow, I shall attempt to demonstrate.

The topic with which I began, lateral gene transfer, is one generally acknowledged qualification of strict anti-Lamarckism. Genes transferred laterally into the genome of an organism are certainly acquired, and may certainly be inherited. The reason that Lamarckism is such a profound potential challenge to traditional Darwinism is that somatic traits acquired during the lifetime of the organism may often be adaptive, constituting the organism's response to the environment. An animal may run as fast as it can to escape speedy predators or in pursuit of fleet-footed prey, for example, and in doing so it may develop stronger leg muscles. But the inheritance of such adaptive acquired characteristics would threaten the first principle of neo-Darwinism, the monopoly of natural selection in producing adaptation.¹³ Here it may be thought that lateral gene transfer offers little threat of this kind. Perhaps we should see it as no more than the equivalent of a very big mutation. But first, there is a growing consensus that lateral gene transfer has been of fundamental importance, at least in microbial evolution. Boucher and colleagues (2003) review the evidence for its role in 'photosynthesis, aerobic respiration, nitrogen fixation, sulfate reduction, methylotrophy, isoprenoid

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biosynthesis, quorum sensing, flotation (gas vesicles), thermophily, and halophily'. Moreover, second, a large number of researchers suggest that lateral gene transfer is indeed often an adaptive response to the environment. According to Pal and colleagues (2005) 'bacterial metabolic networks evolve by direct uptake of peripheral reactions in response to changed environments'. And 'lateral gene transfer provides the bacterial genome with a new set of genes that help it to explore and adapt to new ecological niches' (Marri *et al.*, 2007). Note the similarity with the kind of cooperative ventures I discussed earlier in this paper. Whole microbial cells (or indeed macrobial cell systems) adapt to their environment by recruiting, or being recruited by, coalitions of cooperating cells. More complex organisms may recruit conspecifics or even members of other species to form social collectives that enhance their ability to cope with environmental challenges. And, finally, cells may sometimes recruit adaptively useful genetic fragments from their environments. All very Lamarckian.

One response to the issue of lateral gene transfer may be to downplay the importance of microbial evolution. Perhaps microbes are really rather insignificant little beasts? To this, however, it is sufficient to respond that 80% of evolutionary history is a history solely of the evolution of microbes; the vast majority of organisms alive today are microbes; and all known macrobes are dependent for their existence on symbiotic relations with microbes. As I have briefly mentioned above, the importance of lateral gene transfer in macrobial evolution is itself a matter of active debate. But anyhow, an account of evolution that doesn't apply to microbes is one that ignores the overwhelmingly dominant manifestation of life on Earth.

Varieties of inheritance

The Lamarckian aspects of the topic just considered at least do not violate the idea that the vast majority of inheritance passes through the nuclear genome. Lateral gene transfer may be very important in evolution, but it is very rare by comparison to the routine passage of genetic material from parents to offspring. However, there are other reasons to recognize that the neo-Darwinian restriction of inheritance to transmission of the nuclear genome provides a thoroughly impoverished

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picture.¹⁴ The most widely discussed form of inheritance that is excluded is cultural inheritance. Much of this discussion is directed specifically to human evolution (e.g. Richerson and Boyd, 2005). Although this work is very important in many ways, including in showing the inadequacy of the orthodox neo-Darwinian treatments of human evolution offered by evolutionary psychologists, in the present essay I shan't discuss the special problems of human evolution. There is still heated debate about whether human evolution raises unique issues, and every aspect of human evolution has been discussed and debated by numerous authors, including myself (Dupré, 2001). In this essay I shall avoid these very specific issues.

I mentioned in passing above the perspective of developmental systems theory (DST) (see note 10). DST abandons the myopic focus on the nuclear genome typical of much neo-Darwinism, and looks at the entire cycle of events by which the organism is reproduced. The fundamental unit of analysis is the life cycle of the organism and, given this unit of analysis, it should be clear from the preceding discussion that the requisite concept of an organism must also be the multigenomic, multi-lineage one advocated above. From a DST perspective a large body of work on the cultural transmission of behaviour can be seen as fitting fully into an evolutionary framework. Some fairly arbitrarily selected recent examples are the learning of frog calls by bats (Page and Ryan, 2006), the use of sponges in foraging by bottle-nosed dolphins (Krutzen *et al.*, 2005), or, perhaps the best studied example, the transmission of bird songs (Slater, 1986). The process of learning behaviour by immature individuals, and the behaviour of mature individuals involved in mating and in rearing offspring, are clearly crucial parts of the developmental cycle, and potentially evolving aspects of the life cycle.

Less familiar, but perhaps even more important, is the fact that far from the idea occasionally suggested in popularisations of neo-Darwinism (e.g. Dawkins, 1976) that the genome is the only significant material thing transmitted in reproduction, the minimal material contribution in any form of reproduction is an entire maternal cell. This is an extremely complex object with a great deal of internal structure and a bewildering variety of chemical constituents. For asexual organisms (most organisms, that is), it seems perverse to think of anything other than the cell as the

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basic unit of inheritance. For sexual organisms the issue is more complex, because each individual begins life with a new, generally unprecedented, inheritance, at least genetically. But of course there is a vast number of other materials that are passed on with the maternal cell (and a few even with the paternal sperm) that form a major part of the (inherited) developmental system.

It is sometimes supposed that all the non-DNA material passed on in reproduction is unimportant because it is the DNA that carries the inherited differences on which natural selection can act. But this seems to be a dogmatic assertion rather than anything for which there is empirical evidence. Why, for example, might not changes in the chemistry of the cell membrane be inherited in the process of cell division? But we do not need to speculate. There is a rapidly developing field of biological research, epigenetics, which may be seen as answering a fundamental question, but one that can seem mysterious from the radically DNA-centred perspective – why do different cells with the same genome do different things? Why do my liver cells differ so radically from my brain cells, for instance? Central to epigenetic research is the understanding of how other chemicals in the cell act on the genome to determine which parts of it are expressed (i.e. transcribed to RNA and (sometimes) translated to a protein).

Epigenetics is important in part for breaking the hold of the so-called ‘central dogma’ of molecular genetics, that causality, and hence information, runs only in one direction, from DNA to RNA to protein.¹⁵ Epigenetics could be described, with a little hyperbole, as the study of the falsity of the central dogma. But, secondarily and consequently, it reveals the potential diversity of inheritance at the molecular level. In the first place, once it is seen that the surrounding cell acts on the genome, not merely the other way around, it is clear that the inter-generational transmission of any part of the cellular system may embody significant heredity. Second, one of the crucial ways in which epigenetic effects on the DNA occur is through actual modifications to the structure of the DNA chain. The best studied of these is methylation, in which a methyl group is attached to one of the bases, cytosine, that comprise the DNA sequence. This has the effect of inhibiting the transcription of the sequence of which the methylated cytosine molecule is part. It is

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an obvious possibility that these modifications could be inherited. The claim that they are indeed inherited has been highly controversial. In part this was because it had been understood that a process of demethylation took place during meiosis, the formation of sex cells. If this demethylation was total, then the epigenetic changes would not be transmitted. Recently, it has become increasingly widely agreed that demethylation is not complete, and hence that methylation is to some degree inherited (Chong and Whitelaw, 2004). This has been a remarkably heated controversy, and it is impossible to avoid the suspicion that this is in significant part because if methylation patterns, something that can be acquired in the lifetime of an organism, can be inherited, this will raise the possibility of violating the taboo against Lamarckian inheritance.

It is very interesting to note that epigenetic changes might still be inherited even if they had proved to be entirely erased at meiosis. This is because when they are induced by external, environmental influences they may also contribute to the production of those same influences. The classic example substantiating this possibility derives from a series of experiments on maternal care in rats, carried out by Michael Meaney and colleagues. Grooming, especially licking, by mother rats appears to be very important for the proper development of rat pups, and rats that do not receive sufficient such maternal care grow up generally fearful and, most significantly, less disposed to provide high quality maternal care to their offspring (Weaver *et al.*, 2004; Meaney *et al.*, 2007). It has been demonstrated that these effects are mediated by maternal grooming causing changes of methylation within cells in the brain, which in turn affect the production of neurotransmitters. Thus, the trait of high quality maternal care appears to be transmitted through the induction of methylation patterns in young female rats through exposure to such maternal care. This might also be seen as an adaptive and heritable epigenetic switch: in a stressful and dangerous environment, perhaps, it is best to be fearful (even the paranoid can be right) and too risky to devote more than the minimum effort to caring for the young. It is, of course, possible, and a possibility that might be very widely significant, that this modestly Lamarckian mechanism could be an adaptation acquired by Darwinian means. As mentioned above, inheritance mechanisms are among the more interesting features of organisms that evolve.

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Conclusion

I conclude very much as I began. With absolutely no disrespect to Darwin, biological insights gained over the last few decades have profoundly altered the way we can and should think about evolution. It appears that evolutionary processes may be more diverse than we had imagined, including Lamarckian mechanisms as well as neo-Darwinian, cooperative and symbiotic as well as competitive and individualistic.¹⁶ The evolutionary histories of the entities that make up biological wholes may also be multiple. Genomes have different histories from the organisms in which they reside, both because they assimilate material from other sources, and because they have their own history within the organism – for example, of intragenomic duplications. And organisms, at least when understood as the functional wholes that interact with the rest of the world, are coalitions of entities with diverse evolutionary histories. Neo-Darwinism has much to say about the divergent processes that push biological entities apart, much less about the convergent processes in which the whole is constantly more than the sum of the parts.

None of this should be remotely shocking. But for some reason or reasons we have buffered an outdated view of evolution with a thicket of surrounding dogma and presumption that stands in the way of advancing the theory in line with the stunning insights that are being gained in other parts of biology. Part of this story surely is that this dogma has developed as an unintended response to competition with thoroughly anti-scientific perspectives (creationism, ‘intelligent design’) that have somehow positioned themselves as rivals to scientific evolutionism. And I suspect the links with creationist views may be more complex than that. Extreme neo-Darwinists sometimes share with creationists the yearning for an all-encompassing scheme, a single explanatory framework that makes sense of life.¹⁷ One thinks, for instance of Daniel Dennett’s (1995) paean of praise for natural selection, which he then deploys as the essential resource to explain everything from the breeding behaviour of bees to the deliberative processes of the human mind. But evolution is a mosaic of more or less related processes, producing a motley collection of outcomes. Just because one has a hammer, one should be careful not to suppose that everything is a nail.

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If one of the things that needs to be done to remedy this partial paralysis of our evolutionary thinking is that we detach our view of evolution a little from our reverence for Charles Darwin, then I am sure he won't mind.

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