

Backwards in Retrospect

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1. Is the *Origin* Backwards?

It is a pleasure and an honour to contribute to this symposium on Elliott Sober's recent book.¹ Much of my own research can be construed as a series of responses to, or elaborations of, Sober's own writings. His general approach to the subject is a model for how to remain simultaneously committed to philosophical and biological seriousness. *Did Darwin Write the Origin Backwards?* is an unusual and unfashionable enterprise. Unlike many historical works it treats Darwin's arguments from a perspective that often breaks free of Darwin's own texts and contexts to ask, in a more general logical and epistemological manner, about how evolutionary argumentation is best structured. Moreover, unlike many philosophical works, it pays very close attention to precisely how Darwin's thinking is laid out, on a variety of topics that include the levels of selection, sex ratios, and common ancestry. The book is especially unusual because its method presupposes that we can come to understand historical facts about Darwin's cases for evolution by asking questions of a more philosophical, generalising style regarding confirmation, causation and so forth. That sort of approach is, as I have indicated, unfashionable in both historical and philosophical circles, but it can be defended by a straightforward appeal to charitable interpretation. If you want to understand what Darwin probably did mean, it is helpful to think about what it would

¹ These comments were first presented at a roundtable session on *Did Darwin Write the Origin Backwards?* at the ISHPSSB Conference, Montpellier, in July 2013. For valuable discussion of these ideas I am grateful to Elliott Sober, Samir Okasha, Jean Gayon, Jim Moore, Greg Radick and Jon Hodge. This work has received funding from the European Research Council under the European Union's Seventh Framework Programme (FP7/2007-2013)/ERC Grant agreement no 284123.

have been sensible for him to have meant. Sober's book amply demonstrates the ongoing virtues of this type of approach.

This paper offers a critical reading of just one chapter of Sober's *Did Darwin Write the Origin Backwards?*, namely its long title chapter. We should note immediately that Sober does *not* argue here that the *Origin* is fundamentally mis-structured. Instead, he makes a series of observations about the logical and evidential relationships between Darwin's claims about common ancestry and his claims about natural selection. So let me first offer a reconstruction of Sober's argument, before moving on to make some critical comments.

Darwin began the *Origin* by making a case for the existence and efficacy of natural selection. Only in the later chapters did he turn to making a case for common ancestry. Sober's claim is that in one sense (but only in one sense) this means the *Origin* is written backwards. That is because Darwin could have begun by making a case for common ancestry. After all, the claims that the species we see around us are all descended from a small number of common ancestors, and that those ancestors' lines of progeny have expanded in tree-like fashion over large amounts of evolutionary time, entail nothing about selection. It is possible to imagine that life might form a tree-like structure, in spite of the fact that natural selection is never an important evolutionary force. One could imagine that use-inheritance, for example, is the sole process acting to produce arboriform divergence from a single group of related organisms.

Sober does not merely make the point that Darwin had a choice about how to present his argument. He also adds that there is an important asymmetry between facts about selection and facts about common ancestry. Roughly speaking, the idea is that facts about genealogy often contribute important evidence to claims about selection; conversely, facts about genealogy are themselves most easily established when selection is not at play. That is why it is not merely a possible option, but an attractive option, to structure the *Origin* in a manner that Darwin refused. Darwin could have established a tree-like genealogy for our planet's species independently of claims about selection, before going on to use that genealogy to inform plausible claims about the action of selection.

Sober sets this in the context of his important claim that Darwin himself appeals to ‘Tree Thinking’—i.e. to facts about the structure of genealogical trees—when he addresses hypotheses about selection. On Sober’s view Darwin, too, uses genealogy to constrain selective hypotheses. Consider, for example, Darwin’s discussion of cranial sutures in the *Origin*. Darwin points out that cranial sutures facilitate parturition in mammals such as ourselves. They allow the head of the baby to squash up as it passes through the birth canal. And so, we might be tempted to think that these structures have been shaped by selection for the facilitation of parturition. Darwin points out that this inference is unwise, because baby birds also have cranial sutures. Sober thinks that Darwin employs tree thinking here. On Sober’s view, Darwin is casting doubt on an adaptationist hypothesis by raising the possibility that both mammals and birds have inherited their cranial sutures from a common ancestor.

In a rare endorsement of pluralism, Sober notes that there are ‘many good ways to write a book.’ *Causally* the book is the right way around, because natural selection is (for Darwin) the primary agent of organic change. That is why Darwin begins his book by telling us about the causal principle of selection, before moving on to tell us about its consequences. *Evidentially* Darwin’s book is the wrong way around, because (Sober says) the establishment of claims about selection relies on prior claims about genealogy. In sum, Darwin chose one good way to write his book—the cause-first way—but he could have chosen another, the evidence-first way.

My critical comments will focus on three main areas. First, I am doubtful that Darwin is so consistent a tree-thinker as Sober believes. Second, I suggest (adapting a case made by Jon Hodge) that we can understand why Darwin structures the *Origin* as he does by casting the argument as a species of inference to the best explanation, in the style advocated by Herschel. This perspective also enables us to understand the manner in which Darwin conceives of natural selection, and how natural selection is thought to explain the phenomena exhibited in the second half of the *Origin*. Third, I note a tension between Sober’s claims about the manner in which very strong selection would undermine our ability to reconstruct the past, and his own understanding of what it means to say that the force of selection is strong.

2. Was Darwin a Tree-thinker?

Sober is right to draw our attention to the important ways in which genealogies can constrain hypotheses about selection. That said, Sober is somewhat tentative about the question of Darwin's own tree thinking, and with good reason. On 4th January 1835, while sailing off the Chilean coast, Darwin remarked in his *Beagle Diary* that:

The number of the Seals, was quite astonishing; every bit of flat rock or beach was covered with them. They appear to be of a loving disposition & lie huddled together fast asleep like pigs: but even pigs would be ashamed of the dirt & foul smell which surrounded them. Often times in the midst of the herd, a flock of gulls were peaceably standing: & they were watched by the patient but inauspicious eyes of the Turkey Buzzard. — This disgusting bird, with its bald scarlet head formed to wallow in putridity, is very common on this West Coast. Their attendance on the Seals shows on the mortality of what animal they depend. (Darwin 1988: 277-8)

Later in the *Origin* Darwin implicitly scolded his younger self for such a rash inference regarding the Turkey Buzzard, also known as the Turkey Vulture, a species of New World vulture:

The naked skin on the head of a vulture is generally looked at as a direct adaptation for wallowing in putridity; and so it may be, or it may possibly be due to the direct action of putrid matter; but we should be very cautious in drawing any such inference, when we see that the skin on the head of the clean-feeding male turkey is likewise naked. (Darwin 1859: 197)

This example of Darwin's caution regarding hypotheses about selection *may* involve 'tree thinking', but then again, it may well not. Darwin is arguing here that we cannot assume (even though it may be true) that selection has been responsible for shaping the bald head of the vulture, for clean-feeding turkeys are also bald. The problem for the tree-thinking interpretation is that Darwin's reasoning here is rather sparse: all Darwin

does in all these examples is point to the lack of correlation between adaptive pressure and anatomical structure. He does not tell us in these passages of the *Origin* that the shared trait is most likely inherited from a common ancestor.

We see exactly the same pattern of reasoning when Darwin discusses cranial sutures. Mammals and birds both have them, even though only mammals give birth to live young. We should, therefore, question whether selection for assistance in parturition is responsible for the structure in question. At this point Darwin says nothing about common ancestry as an alternative hypothesis. Instead, he says that 'laws of growth', may be responsible instead:

...as sutures occur in the skulls of young birds and reptiles, which have only to escape from a broken egg, we may infer that this structure has arisen from the laws of growth, and has been taken advantage of in the parturition of the higher animals. (Darwin 1859: 197)

In general, when Darwin discusses 'laws of growth' he is interested in the ways in which organic development is set up such that selective action on one trait can bring with it a further response in some developmentally correlated trait. He introduces the term 'correlation of growth', explaining that:

I mean by this expression that the whole organisation is so tied together during its growth and development, that when slight variations in any one part occur, and are accumulated through natural selection, other parts become modified. (Darwin 1859: 143)

On the face of things, Darwin is not contrasting a hypothesis about selection with a hypothesis about common ancestry. Instead, he is contrasting one selective hypothesis with another. The existence of cranial sutures in birds and mammals should alert us to the possibility that mammals may be subject to selection for some feature, also present in birds and subject to selection in them, too, that happens to be developmentally linked to the appearance of these sutures. Tree thinking does *not* feature here explicitly.

3. Pattern, Process and Explanation

Sober is right to stress that Darwin's presentation in the *Origin* is cause-first. Why? Perhaps the answer lies in the fact that the *Origin's* argument is an inference to the best explanation (see Lewens 2007). Darwin frequently appeals to the explanatory power of his theory as an argument for its veracity. Consider this example of the link between selection and systematics, which Darwin remarks on at the end of Chapter 4 of the *Origin*:

Natural selection...leads to divergence of character and to much extinction of the less improved and intermediate forms of life. On these principles, I believe, the nature of the affinities of all organic beings may be explained. It is a truly wonderful fact...that all animals and all plants throughout all time and space should be related to each other in group subordinate to group...On the view that each species has been independently created, I can see no explanation of this great fact in the classification of all organic beings; but, to the best of my judgement, it is explained through inheritance and the complex action of natural selection, entailing extinction and divergence of character... (128-9)

Natural selection, Darwin claims, explains why it should be that we are able to classify species in a hierarchical manner.

Jon Hodge has argued that Darwin's case in the *Origin* is modelled on Herschel's *vera causa* principle (e.g. Hodge 1977, 2012). To establish selection as a 'true cause' Herschel tells us that we need to show (paraphrasing somewhat) that it is real, that it can conceivably bring about the effects it is alleged to bring about, and that it is in fact responsible for these effects. And so the *Origin* begins by establishing the reality of selection by securing the conditions required for its existence. This explains the stress in these opening chapters on the wide availability of variation, the intensity of the struggle for existence, the exposition of the nature of selection by means of a series of analogies with artificial selection, and so forth. The *Origin* moves on to counter worries that selection could not possibly explain various phenomena (such as 'organs of extreme perfection', among others). Finally, in the later chapters, Darwin shows that

selection better explains several broad classes of phenomena, including facts about biogeography, comparative morphology and so forth, than its special creationist rival.

On this view, Darwin's theory gets evidential support from the explanatory fit between the cause it posits—natural selection—and the alleged effects of that cause. It is possible, of course, to lay out an inference to the best explanation by beginning with the effects and then showing how the cause makes sense of them. That said, it would be hard for a reader to appreciate the explanatory relationship between selection and its effects unless one is familiar with what natural selection is supposed to be, and how it is supposed to act, when one comes to review the diverse phenomena Darwin thinks it can account for. That is why, even considered as an evidential exposition, Darwin's book has a cause-first structure.

There is a significant worry about this interpretation. Is it plausible to think there is much by way of explanatory fit between selection and the diverse classes of facts relating to morphology, embryology, biogeography etc. laid out in the second half of the *Origin*? One sometimes gets the impression that the second half of the *Origin* constitutes a case for common ancestry alone, not a case for the action of selection. Here we might follow Sober in pointing out that hypotheses about the *process* of natural historical change are logically independent of hypotheses about the *pattern* of natural historical change. Commentators such as Waters (2003) have then gone on to argue that while Darwin succeeds in making a case for common ancestry in the second half of the *Origin*, he does so in a way that remains neutral on the cause of change.

It is true, of course, that many different processes might give rise to tree-like genealogies: even some intelligent design theorists have tried to accommodate the evidence for evolution by pointing out that an evolutionary genealogy for all of life is compatible with the notion that intelligent intervention is responsible for some especially complex adaptations (e.g. Behe 1996). It is also true that Darwin managed to convince his contemporaries of his views on common ancestry, while they remained far cooler about natural selection (Bowler 1983). Even so, I am sceptical of very strong ways of isolating Darwin's achievement in the second half of the *Origin* from his case for selection in the first half, in large part because I am sceptical of whether the

pattern/process distinction is as salient for Darwin as it may be for us (see also Hodge 2012).

As Jean Gayon has pointed out (this issue), the single illustration that features in the *Origin*, which to modern eyes looks like a genealogical tree, and hence an illustration of evolutionary *pattern*, does not appear in the second half of the *Origin* (where modern commentators tend to note that the primary focus on establishing common ancestry lies) but instead it appears in Chapter Four. That chapter is entitled ‘Natural Selection’, and it is concerned with presenting what is, for Darwin, the primary agent of organic change. Natural selection is usually understood today as a *process*. We should not conclude that Darwin is confused about the process/pattern distinction, or that he failed to think properly about where in the *Origin* his diagrammatic representation of the pattern of common ancestry should feature. If we ask ourselves how we might go about producing a diagrammatic representation of the *process* of selection, we see that the sort of *pattern* illustrated by arboriform divergence is the answer.

On Darwin’s view (even if not on ours), natural selection is an essentially gradual process. Hence his well known assertions that: ‘If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down’ (1859: 189), or later his claim that ‘As natural selection acts solely by accumulating slight, successive, favourable variations, it can produce no great or sudden modification; it can only act by very short and slow steps’ (471). Darwin also thinks of the ‘divergence of character’ as a primary corollary of how selection works. Since selection is a competitive process, producing increasingly refined adaptations, Darwin reasons that it tends to promote division of labour and diversification in order to capitalise on unexplored niches. The *Origin*’s single diagram appears in Chapter 4, and it is initially used as an illustration of divergence of character. A *process* such as natural selection—a gradual one, which tends to promote diversification—is best illustrated by the very diagram that we usually think represents a genealogical *pattern*.

Darwin asserts a very tight relationship between natural selection understood as process, and tree-like genealogy, in his remarks that summarise the account of selection offered in Chapter 4:

Natural selection...leads to divergence of character; for more living beings can be supported on the same area the more they diverge in structure, habits, and constitution...Therefore during the modification of descendants of any one species, and during the incessant struggle of all species to increase in numbers, the more diversified these descendants become, the better will be their chance of succeeding in the battle of life. This the small differences distinguishing the varieties of the same species, will steadily tend to increase till they come to equal the greater differences between species of the same genus, or even of distinct genera. (127-8)

In the later chapters of the *Origin*, Darwin sometimes draws our attention to phenomena that are well explained if we assume that adaptation to novel environments proceeds through the gradual accumulation of such 'numerous, successive, slight modifications':

Oceanic islands are sometimes deficient in certain classes, and their places are apparently occupied by the other inhabitants; in the Galapagos Islands reptiles, and in New Zealand gigantic wingless birds take the place of mammals. (391)

A process which, on the one hand, works to fit species to their local environments, while on the other hand being constrained to make use of slight variations wrought on existing forms, can explain these odd phenomena of convergence. Natural selection is (for Darwin at least) just such a process.

4. Natural selection and common ancestry

I now move on to a third and final line of criticism. Sober devotes considerable discussion to something he calls 'Darwin's Principle':

Darwin's Principle. Adaptive similarities provide almost no evidence for common ancestry while similarities that are useless or deleterious provide strong evidence for common ancestry.

Sober does not endorse this principle without qualification; even so, a little later Sober draws the following consequence from it:

Darwin's claim that selection is not the exclusive cause of evolution plays an essential role in allowing him to develop his evidence for common ancestry. His conjunction—common ancestry and natural selection—would be unknowable, according to Darwin's Principle, if the second conjunct described the only cause of trait evolution.

The thought that lies behind this is that if every trait were caused by selection, then we wouldn't be able to figure out whether species have common ancestors, because we'd always be confronted by traits that might owe their similarities to common adaptive pressures. The plausibility of this principle depends on how we understand the idea that selection is the only cause of evolution. Suppose we agree with 'Darwin's principle': we cannot draw good inferences about common ancestry based on similarity with respect to shared adaptive features. Still we can deny that all similarities would be of this adaptive variety if selection were the only important evolutionary force. Darwin thinks that the existence of morphological similarity in spite of significant difference in function is good evidence for common ancestry:

The framework of bones being the same in the hand of a man, wing of a bat, fin of the porpoise, and leg of the horse—the same number of vertebrae forming the neck of the giraffe and of the elephant,—and innumerable other such facts, at once explain themselves on the theory of descent with slow and slight successive modifications. The similarity of pattern in the wing and leg of a bat, though used for such different purposes,—in the jaws and legs of a crab,—in the petals, stamens, and pistils of a flower, is likewise intelligible on the view of the gradual modification of parts or organs, which were alike in the early progenitor of each class. (Darwin 1859: 479)

Does this genealogical inference rely on selection not being the ‘only cause of trait evolution’? That depends, in part, on what it means to say that selection is the only cause, or the most important cause, of trait evolution? Sober himself understands this claim as follows: ‘When selection is the only force guiding a population’s evolution, the fittest of the available phenotypes evolves.’ (Sober 1998: 73) So if drift, or heterozygote superiority, are widespread, then selection is not the only cause of trait evolution, because these forms of influence can result in the fittest trait not going to fixation. But there is no conflict between the fittest available trait going to fixation and the availability of traits being highly constrained. So even if the fittest available trait always went to fixation, we might still find that the limbs of men, horses, bats and porpoises were variations on a common historical theme. These facts of structural resemblance in spite of radically differing functions would still be well explained by common ancestry, and we could still infer common ancestry on the basis of that explanatory relationship. The lesson here is that even if, in one sense, selection turned out to be the only cause of trait evolution, this would not undermine our ability to spot common ancestry.

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