

An early flowering of genetics

This is an edited version of Richard Dawkins' introduction to a new edition of Charles Darwin's *The Descent of Man*, published by Gibson Square Books, price £10. This piece also appears in *A Devil's Chaplain: Selected Essays* by Richard Dawkins, published by Weidenfeld next week, price £16.99

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Charles Darwin's theory of human evolution was published long before knowledge of genes was available. But Richard Dawkins reveals that an obscure letter found in a library proves Darwin was already doing research into heredity which anticipated the breakthroughs of the next century

Humanity is the missing guest at the feast of Charles Darwin's *Origin of Species*, published in 1859. The famous "light will be thrown on the origin of man and his history" is a calculated understatement matched, in the annals of science, only by Watson and Crick's "it has not escaped our notice that the specific pairing we have postulated immediately suggests a possible copying mechanism for the genetic material".

By the time Darwin finally got around to throwing that light with the publication of *The Descent of Man* in 1871, others had been there before him and the greater part of his book is not about humans but about Darwin's "other" theory, sexual selection. It might have seemed a good idea to separate it into two books: *Sexual Selection* followed by *The Descent of Man*. But Darwin knew what he was doing.

The distinguished American philosopher Daniel Dennett has credited Darwin with the greatest idea ever to occur to a human mind. This was natural selection, the survival of the fittest, of course, and I would include sexual selection as part of the same idea. But Darwin was not only a deep thinker, he was a naturalist of encyclopaedic knowledge and (which by no means necessarily follows) the ability to hold it in his head and deploy it in constructive directions.

He was a master encyclopaedist, who collated huge quantities of information and observations solicited from naturalists all around the world, each gentleman meticulously acknowledged for having "attended to" the subject and sometimes complimented as a "reliable observer". I find an addictive fascination in his Victorian prose style, quite apart from the feeling one gets of having been ushered into the presence of one of the great minds of all time.

Prescient as he was (Michael Ghiselin, author of *The Triumph of the Darwinian Method*, University of Chicago Press, has said that he worked at least a century ahead of his time) Darwin was still a Victorian, and his book must be read in the context of its age, warts and all. What will grate most irksomely on the modern ear is the unquestioned Victorian presumption that animals in general, and humans in particular, are disposed on a ladder of increasing superiority.

Like all Victorians, Darwin happily referred to particular species as "lowly in the scale of nature". Even some modern biologists do this, though they should not, for all living species are cousins who have been evolving for exactly the same length of time since the common ancestor. What educated moderns never do, but equivalent Victorians always did, is think of human races in the same hierarchical way. It requires a special effort for us to read something like the following without distaste: "It seems at first sight a monstrous supposition that the jet blackness of the negro has been gained through sexual selection [ie, is attractive to the opposite sex]..."

But it is a mark of historical infantilism to view the writings of one century through the politically tinted glasses of another. The very title, *The Descent of Man*, will raise hackles among those naively locked into the mores of our own time. It can be argued that reading historic documents that violate the taboos of one's own century gives valuable lessons in the ephemerality of such mores. Who knows how our descendants will judge us?

Less obvious, but as important to understand, are the changes in the scientific climate. In particular,

it is hard to overstate the fact that Darwin's genetics were pre-Mendelian (Gregor Mendel, 1822-84, did not live to see himself revered as the father of genetics). The intuitively plausible blending inheritance theory, that variation disappears over generations, of Darwin's time was not just wrong, it was grievously wrong and especially grievous for natural selection.

The fact that Darwinism could not work under the assumption of blending inheritance was pointed out in a hostile review of the *Origin* by the Scottish engineer Fleeming Jenkin. Variation tends to disappear with every blending generation, leaving not enough for natural selection to get its teeth into.

What Jenkin should have realised is that blending inheritance is incompatible not just with Darwinian theory but with obvious fact. If it were really true that variation disappeared, every generation should be more uniform than the previous one. By now, all individuals should be as indistinguishable as clones. Darwin needed only to retort to Jenkin: whatever the reason, it is obviously the case that there is plenty of inherited variation and that's good enough for my purposes.

It is often claimed that the answer to the riddle of the allegedly disappearing variation lay on Darwin's shelves, in the uncut pages of the proceedings of the Brunns Natural History Society where nestled Mendel's paper on "Versuche über Pflanzen-Hybriden". Unfortunately this poignant story seems to be an urban myth. The two scholars best placed (at Cambridge and at Down House) to know what was in Darwin's personal library can find no evidence that he ever subscribed to the proceedings, nor does it seem likely that he would have done so. They have no idea where the legend of the "uncut pages" originated.

Once originated, however, it is easy to see that its very poignancy might speed its proliferation. The whole affair would make a nice little project in memetic research [the theory, outlined in *The Selfish Gene*, that ideas are "viral"] complementing that other popular urban legend, the agreeable falsehood that Darwin turned down an offer from Marx to dedicate *Das Kapital* to him.

Mendel did indeed have exactly the insight Darwin needed. Its relationship to the Jenkin critique, however, would not have been immediately obvious to the Victorian mind. Even after Mendel's work was rediscovered in 1900, it was not until RA Fisher, founder of modern statistics and of British population genetics, came along in 1930 that its supreme relevance to Darwinism was widely understood. If heredity is particulate - if, as Mendel showed, a gene is an indivisible entity such that you either have it or you don't, with no half measures - variation does not disappear but is reconstituted in every generation. Neo-Darwinian evolution precisely means change in gene frequencies in gene pools.

What is genuinely poignant is that Darwin himself came tantalisingly close to Mendel's conclusion. Fisher quotes him in a letter to Huxley of 1857: "I have lately been inclined to speculate, very crudely and indistinctly, that propagation by true fertilisation will turn out to be a sort of mixture, and not true fusion, of two distinct individuals, or rather of innumerable individuals, as each parent has its parents and ancestors. I can understand on no other view the way in which crossed forms go back to so large an extent to ancestral forms. But all this, of course, is infinitely crude."

Fisher cleverly remarked that Mendelism has a kind of necessary plausibility, which could have led to its discovery by any thinker in a mid-Victorian armchair. He might have added that particulate inheritance stares us in the face whenever we contemplate sex itself (as we not infrequently do). All of us have one female and one male parent, yet each of us is either male or female, not an intermediate hermaphrodite. Fascinatingly, Darwin himself made this very point, clearly, in an 1866 letter to fellow naturalist Alfred Wallace, which Fisher would surely have quoted had he known of it.

"My dear Wallace... I do not think you understand what I mean by the non-blending of certain varieties. It does not refer to fertility; an instance will explain. I crossed the Painted Lady and Purple sweetpeas, which are very differently coloured varieties, and got, even out of the same pod, both

varieties perfect but none intermediate. Something of this kind I should think must occur at least with your butterflies & the three forms of *Lythrum*; tho' these cases are in appearance so wonderful, I do not know that they are really more so than every female in the world producing distinct male and female offspring...

Believe me, yours very sincerely Ch. Darwin"

Here Darwin comes closer to anticipating Mendel than in the passage quoted by Fisher, and he even mentions his own Mendel-like experiments on sweet peas. I am extremely grateful to Dr Seymour J Garte of New York University, who found this letter by chance in a volume of correspondence between Darwin and Wallace in the British Library in London, immediately recognised its significance and sent a copy to me.

Another piece of Darwin's unfinished business later sorted out by Fisher was the matter of the sex ratio, and how it evolves under natural selection. Fisher begins by quoting the second edition of *The Descent of Man*, in which Darwin prudently said: "I formerly thought that when a tendency to produce the two sexes in equal numbers was advantageous to the species, it would follow from natural selection, but I now see that the whole problem is so intricate that it is safer to leave its solution to the future."

Fisher's own solution made no appeal to species advantage. Instead he pointed out that, since every individual born has one father and one mother, the total male contribution to posterity must equal the total female contribution. If the sex ratio is anything other than 50/50, therefore, an individual of the minority sex can expect, other things being equal, a greater share of descendants, and this will set up selection in favour of rebalancing the sex ratio.

Fisher rightly used economic language to express the strategic decisions involved: they are decisions over how to allocate parental expenditure. Natural selection will favour parents who spend proportionately more food or other resources on offspring of the minority sex. Such correcting selection will continue until the total expenditure on sons in the population balances the total expenditure on daughters. This will amount to equal numbers of males and females, except in those cases where offspring of one sex cost more to rear than offspring of the other.

If, for example, it costs twice as much food to rear a son than a daughter (perhaps to make sons big enough to compete effectively with rival males) the stable sex ratio will be twice as many females as males. This is because the strategic alternative to one son is not one daughter but two. Fisher's powerful logic has been extended and refined in various ways, for example by WD Hamilton and EL Charnov.

Once again, and notwithstanding the quotation above from the second edition, Darwin himself, in the first edition, came remarkably close to anticipating Fisher, although without the economic language of parental expenditure:

"Let us now take the case of a species producing, from the unknown causes just alluded to, an excess of one sex - we will say of males - these being superfluous and useless, or nearly useless. Could the sexes be equalised through natural selection? We may feel sure, from all characters being variable, that certain pairs would produce a somewhat less excess of males over females than other pairs. The former, supposing the actual number of the offspring to remain constant, would necessarily produce more females, and would therefore be more productive. On the doctrine of chances, a greater number of the offspring of the more productive pairs would survive; and these would inherit a tendency to procreate fewer males and more females. Thus a tendency toward equalisation of the sexes would be brought about."

Sadly, Darwin deleted this remarkable passage when he came to prepare the second edition, preferring the more cautious paragraph later to be quoted by Fisher. Darwin's partial anticipation of Fisher in the first edition of *Descent* is all the more impressive because, as my colleague Alan

Grafen points out to me, Fisher's argument depends crucially on a fact that was not available to Darwin, namely that the two parents make an equal genetic contribution to every offspring. Indeed, in historical times, different schools of thought (the spermists and the ovists respectively) had held that the male, or the female, sex had a monopoly on heredity.

Now, to the descent of man itself. Darwin's guess that our species arose in Africa was typically ahead of his time, amply confirmed today by numerous fossils, none of which was available to him. We are African apes, closer cousins to chimpanzees and gorillas than they are to orang-utans and gibbons, let alone monkeys.

Darwin's "quadrumana" were defined so as to exclude humans: they were all the apes and monkeys, with a hand bearing an opposable digit on the hindlegs as well as the forelegs. The early chapters of his book are concerned to narrow the perceived gap between ourselves and the quadrumana, a gap that Darwin's target audience would have seen as yawning between the top rung of a ladder and the next rung down. Today we would not (or should not) see a ladder at all. Instead, we should hold in our minds the branching tree diagram, which is the only illustration in *The Origin of Species*. Humanity is just one little twig, nestling among many others somewhere in the middle of a thicket of African apes.

Darwin went to town on sexual selection in *The Descent of Man* because he thought it was important in human evolution, and especially because he thought it was the key to understanding the differences among human races. The topic is prominent in Darwin's book and especially germane to the unification of its two parts.

Darwin, like all Victorians, was intensely aware of the differences among humans but he also, more than most of his contemporaries, emphasised the fundamental unity of our species. In *Descent* he carefully considered, and decisively rejected, the idea, rather favoured in his own time, that different human races should be regarded as separate species.

Today we know that, at the genetic level, our species is more than usually uniform. It has been said that there is more genetic variation among the chimpanzees of a small region of Africa than among the entire world population of humans (suggesting that we have been through a bottleneck in the past 100,000 years or so). Moreover, the great majority of human genetic variation is to be found within races, not between them. This means that if you were to wipe out all human races except one, the great majority of human genetic variance would be preserved. The variance between races is just a bit extra, stuck on the top of the greater quantity of variation within all races. It is for this reason that many geneticists advocate the complete abandonment of the concept of race.

At the same time - the paradox is similar to one recognised by Darwin - the superficially conspicuous features characteristic of local populations around the world seem very different. Why did such pronounced superficial differences evolve in different geographical areas, while most of the less conspicuous variation is dotted around across all geographical areas? Could Darwin have been right all along? Is sexual selection the answer to the paradox? The distinguished biologist Jared Diamond thinks so, and I am inclined to agree.

What sexual selection explains, better than natural selection, is diversity that seems arbitrary, even driven by aesthetic whim. Especially if the variation concerned is geographical. And also especially if some of the features concerned, for example beards and the distribution of body hair and subcutaneous fat deposits, differ between the sexes.

Most people have no problem in accepting an analogue of sexual selection for culturally mediated fashions like headdresses, body paint, penis sheaths, ritual mutilations or ornamental clothes. Given that cultural differences such as those of language, religion, manners and customs certainly provide resistance to interbreeding and gene flow, I think it is entirely plausible that genetic differences between peoples of different regions, at least where superficial, externally prominent features are concerned, have evolved through sexual selection.

Our species really does seem to have unusually conspicuous, even ostentatious, superficial differences between local populations, coupled with unusually low levels of overall genetic variation. This double circumstance carries, to my mind, the stamp of sexual selection.

In this, as in so much else, I suspect that Darwin was right. Sexual selection really is a good candidate for explaining a great deal about the unique evolution of our species. It may also be responsible for some unique features of our species that are shared equally by all races, for example our enormous brain. It is starting to look as though, despite initial appearances, Darwin really was right to bring together, in one volume, *Selection in Relation to Sex* and *The Descent of Man*.

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