C. R. Biologies 333 (2010) 112–118

Contents lists available at ScienceDirect

Comptes Rendus Biologies

www.sciencedirect.com

Evolution / Évolution

Cross- and self-fertilization of plants

Autofécondation et fécondation chez les plantes

Michael Ruse

Department of Philosophy, Florida State University, Tallahassee, Florida, 32306, USA

ARTICLE INFO

Article history:
Available online 18 February 2010

Keywords:
Fertilization
Charles Darwin
Sexuality
Adaptation

Mots clés :
Fécondation
Charles Darwin
Sexualité
Adaptation

ABSTRACT

This essay considers Charles Darwin's late work, *Cross- and Self-Fertilization of Plants*, locating it in the overall context of Darwin's thought and ideas. It is shown how it is part of a long-term interest in the purpose of sexuality, and how it complements Darwin's earlier book on the fertilization of orchids. It is concluded, however, that Darwin had no full solution to his problem.

RÉSUMÉ

Cet essai examine le travail tardif de Charles Darwin *Fécondation croisée et directe chez les plantes*, en le situant dans le contexte général de la pensée et des idées de Darwin. Il est montré à quel point il traduit un intérêt long terme pour la question de la sexualité, et complète le livre précédent de Darwin sur la fécondation des orchidées. On conclut, cependant, que Darwin n'avait pas de solution complète à la question qu'il avait posée.

1. Introduction

The reason why we celebrate Charles Darwin in 2009 on the 200th anniversary of his birth is obviously because of his great book *On the Origin of Species* published in 1859 [1]. In that work, Darwin made the fact of evolution a matter of commonsense—before that many had been evolutionists, most notably the French biologist Jean-Baptist de Lamarck (1809) [2]—but it was Darwin who made the case beyond reasonable doubt, as they say in British courts of law. He also proposed his mechanism of natural selection, arguing that thanks to the struggle for existence, not all organisms can survive and reproduce and that hence there will be a constant winnowing and only (what came to be known as) the fittest will be the generators of future organisms. Importantly, Darwin stressed that change is not random but in the direction of increased adaptation—hands, eyes, teeth, penises, vaginas, bark, leaves, roots, pistils, stamens, they all contribute to the wellbeing of their possessors, they are as if designed for the purpose.

2. Darwin's other books

The *Origin* was published when Darwin was 50. He lived from 1809 to 1882, in other words although he was sick for much of his adult life, he had 20 or more years of mature life before the *Origin* and the same amount after the *Origin*. One thing is true above all about Charles Darwin. He was a compulsive worker. No one had imbibed the Protestant work ethic more than he. With time out for illness, he worked steadily every day, including Sundays. And it showed, because a stream of works issued forth from his pen, from early studies of geology to late studies of earthworms.

Nothing could equal the *Origin*, but there is a natural and perpetual fascination with the other works. Some are fairly easy to assess. Probably the second most important

E-mail address: mruse@mailer.edu.

1631-0691/$ – see front matter
doi:10.1016/j.crvi.2009.11.011

Darwin book is the one on our own species, the *Descent of Man* [3], published some 12 years after the *Origin*. It is a somewhat odd work, because more than half is in fact not on the main topic, but rather on the secondary mechanism of sexual selection (there is a reason for this, namely that Darwin needed a mechanism to counter Alfred Russel Wallace's [1870] [4] objections to a natural origin for humankind, and sexual selection filled this role). It is also a work that draws far more heavily than the *Origin,* on the work of others, and that in respects is much more one of opinion and value judgment than the *Origin* (there is, for instance, lots of material on the natural superiority of Europeans). My sense is that today we rate the *Descent* somewhat higher than we would have done 50 years ago, at the 100th anniversary of the *Origin*. Sexual selection today is given a much bigger role than back then, and Darwin's detailed discussions of the evolution of morality have attracted much (positive) attention. I have just extracted them for a collection I am publishing on Darwin's importance for philosophy (Ruse [2009] [5]).

Among those of us who work on Darwin, my suspicion is that the favorite—perhaps even giving the *Origin* itself a run for its money—is the travel book, *Journal of researches into the natural history and geology of the countries visited during the voyage of H.M.S. Beagle round the world, under the Command of Capt. Fitz Roy, R.N.* (1839) [6], published in a popular version and better known as the *Voyage of the Beagle* (1845) [7]. Much of this is based on Darwin's diaries and his letters home to his family and it surely is a terrific read. We follow a bright and educated young man, literally on a voyage of discovery, both at sea and (for most of the time) on land—just as well the latter, since Darwin suffered dreadfully from seasickness. We stay with him as he discovered exotic flora and fauna in the Southern Hemisphere, as he uncovered the mysteries of the past recorded in the fossil record, and as he learns so much more about his fellow humans, be they slave owners or gauchos or (what he regarded as) "savages" down at the bottom of South America, in Tierra del Fuego. I love the book and I suspect many others do too (it is still available in English in about 10 different editions).

The volumes on geology—*The structure and distribution of coral reefs. Being the first part of the geology of the voyage of the Beagle, under the command of Capt. Fitzroy, R.N. during the years 1832 to 1836* (1842) [8], *Geological observations on the volcanic islands visited during the voyage of H.M.S. Beagle, together with some brief notices of the geology of Australia and the Cape of Good Hope. Being the second part of the geology of the voyage of the Beagle, under the command of Capt. Fitzroy, R.N. during the years 1832 to 1836* (1844) [9], *Geological observations on South America. Being the third part of the geology of the voyage of the Beagle, under the command of Capt. Fitzroy, R.N. during the years 1832 to 1836* (1846) [10]—seem me as more dutiful than exciting, although, of course, they do incorporate Darwin's brilliant hypothesis about the formation of coral reefs. But even this, that the reefs are formed by the sinking of land as the coral grows upwards, is part and parcel of a Lyellian approach to the rocks (for all that, Darwin's hypothesis was correcting an earlier hypothesis of Lyell himself), and ultimately what Thomas Kuhn would have called "normal" rather than "revolutionary" science. The volumes of barnacle taxonomy—*A Monograph of the Sub-Class Cirripedia, with Figures of all the Species. The Lepadidae; or Pedunculated Cirripedes* (1851) [11], *A Monograph of the Fossil Lepadidae; or, Pedunculated Cirripedes of Great Britain* (1851) [12], *A Monograph of the Sub-Class Cirripedia, with Figures of all the Species. The Balanidge (or Sessile Cirripedes); the Verrucidae, and C.* (1854) [13], *A Monograph of the Fossil Balanidae and Verrucidae of Great Britain* (1854) [14]—are detailed and obviously something for the professional in the field, rather than for general reading. Tradition praises the quality of the work, although more recent assessments have been highly critical. It is not yet sorted out whether Darwin provided a foundation on which others could build or if he simply went entirely astray and his work can be and should be ignored (Newman [1993] [15]).

After the *Origin*, I find the big two-volume work on *Variation of Animals and Plants under Domestication* (1868) [16] to be more worthy than exciting, filling out (as promised) the specific claims made (especially in the first chapter) in the *Origin*. I suspect that Darwin felt the same way, because despite promises, he certainly did not spend the rest of his life writing books based on each and all of the individual chapters of the *Origin*. The *Expression of the Emotions in Man and Animals* (1872) [17] likewise does not do much for me, being basically material left on the cutting floor after Darwin had finished the *Descent of Man*. I will say that one book I like very much is the little work that comes next after the *Origin: On the Various Contrivances by which British and Foreign Orchids are Fertilised by Insects* (1862) [18]. Darwin himself told his publisher that he regarded it as an example of how to do biology within the paradigm (as we would say) of the *Origin*. It is to show how thinking about adaptation can be done now. Something I find particularly fascinating is the way in which Darwin wrestles with adaptation, showing that descent with modification often means that things are not done as efficiently as they might if one could sit down and start from scratch whenever faced with a problem or demand. One has to work with what one has and this reflects in the finished product. The English would speak of this as being designed in the "Heath Robinson" mode, after a humorist who used to build fantastical machines, way over-complex, to do simple jobs.

So this then brings us to the books of Darwin's old age. Most of these strike me as fairly straightforward, in the sense that they represent projects that an old naturalist found fascinating—*The Movements and Habits of Climbing Plants* (1875) [19], *Insectivorous Plants* (1875) [20], *The Power of Movement in Plants* (1880) [21], and *The Formation of Vegetable Mould, Through the Action of Worms, with Observations on their Habits* (1881) [22]—that he could work on in a fairly low-tech sort of way, using simple tools and the time of himself and his gardeners. I would certainly not condemn them for being what they are, although equally I would not want to pretend that they are more than they are. In a sense, as many knew, the world of science had started to pass Darwin by in the 1870s—he was not up on the latest laboratory techniques or methods of experimentation. He was coasting down after a long life of effort (I have argued that in respects Darwin was out of

date by the time he published the *Origin*—he was responding rather to the problems of the 1830s—but there I would certainly defend the proposition that it was the world that was out of kilter not Darwin. By the 1870s, I think the story is the other way around. I am not making this claim as the thin end of a very large wedge to belittle the achievements of the *Origin*).

2.1. Cross- and Self-Fertilization

Where then does one fit in the book *Cross- and Self-Fertilization of Plants* [23], first published in 1876 with a second edition (virtually a reprint of the first edition) in 1878? It was not a big seller, although 1500 copies of the first edition did get sold in the first year, necessitating the reprint. In his *Autobiography* Darwin wrote [24]:

> "During this autumn of 1876 I shall publish on the *Effects of Cross- and Self-Fertilisation in the Vegetable Kingdom*. This book will form a complement to that on the *Fertilisation of Orchids*, in which I showed how perfect were the means for cross-fertilisation, and here I shall show how important are the results. I was led to make, during eleven years, the numerous experiments recorded in this volume, by a mere accidental observation; and indeed it required the accident to be repeated before my attention was thoroughly aroused to the remarkable fact that seedlings of self-fertilised parentage are inferior, even in the first generation, in height and vigour to seedlings of cross-fertilised parentage. I hope also to republish a revised edition of my book on Orchids, and hereafter my papers on dimorphic and trimorphic plants, together with some additional observations on allied points which I never have had time to arrange. My strength will then probably be exhausted, and I shall be ready to exclaim 'Nunc dimittis'"(Darwin [1958] [24: 133]).

One should say that even from the volume itself, one gets the feeling of a little bit of an ugly duckling, for Darwin did not bother to co-ordinate the spelling on the spine (Self-Fertili**z**ation) with the spelling on the title page (Self-Fertili**s**ation). And certainly, in his correspondence, Darwin is not much more encouraging. It is worth starting by quoting Francis Darwin, Darwin's son and biographer and a botanist in his own right, on his father's work [25].

"THIS book, as pointed out in the 'Autobiography', is a complement to the 'Fertilisation of Orchids', because it shows how important are the results of cross-fertilisation which are ensured by the mechanisms described in that book. By proving that the offspring of cross-fertilisation are more vigorous than the offspring of self-fertilisation, he showed that one circumstance which influences the fate of young plants in the struggle for life is the degree to which their parents are fitted for cross-fertilisation. He thus convinced himself that the intensity of the struggle (which he had elsewhere shown to exist among young plants) is a measure of the strength of a selective agency perpetually sifting out every modification in the structure of flowers, which can affect its capabilities for cross-fertilisation.

The book is also valuable in another respect, because it throws light on the difficult problems of the origin of sexuality. The increased vigour resulting from cross-fertilisation is allied in the closest manner to the advantage gained by change of conditions. So strongly is this the case that in some instances cross-fertilisation gives no advantage to the off spring, unless the parents have lived under slightly different conditions. So that the really important thing is not that two individuals of different *blood* shall unite, but two individuals which have been subjected to different conditions. We are thus led to believe that sexuality is a means for infusing vigour into the offspring by the coalescence of differentiated elements, an advantage which could not follow if reproductions were entirely asexual.

It is remarkable that this book, the result of 11 years of experimental work, owed its origin to a chance observation. My father had raised two beds of *Linaria vulgaris*—one set being the offspring of cross- and the other of self-fertilisation. These plants were grown for the sake of some observations on inheritance, and not with any view to cross-breeding, and he was astonished to observe that the offspring of self-fertilisation were clearly less vigorous than the others. It seemed incredible to him that this result could be due to a single act of self-fertilisation, and it was only in the following year, when precisely the same result occurred in the case of a similar experiment on inheritance in Carnations, that his attention was "thoroughly aroused," and that he determined to make a series of experiments specially directed to the question. The following letters give some account of the work in question" (Darwin [1887] [25]: 3, 290).

The (extracted) letters follow:

> "*C. Darwin to Asa Gray*
>
> September 10, [1866?]
>
> ... I have just begun a large course of experiments on the germination of the seed, and on the growth of the young plants when raised from a pistil fertilised by pollen from the same flower, and from pollen from a distinct plant of the same, or of some other variety. I have not made sufficient experiments to judge certainly, but in some cases the difference in the growth of the young plants is highly remarkable. I have taken every kind of precaution in getting seed from the same plant, in germinating the seed on my own chimney-piece, in planting the seedlings in the same flower-pot, and under this similar treatment I have seen the young seedlings from the crossed seed exactly twice as tall as the seedlings from the self-fertilised seed; both seeds having germinated on same day. If I can establish this fact (but perhaps it will all go to the dogs), in some fifty cases, with plants of different orders, I think it will be very important, for then we shall positively know why the structure of every flower permits, or favours, or necessitates an occasional cross with a distinct individual. But all this is rather cooking my hare before I have caught it. But somehow it is a great pleasure to me to tell you what I am about.
>
> Believe me, my dear Gray,
>
> Ever yours most truly, and with cordial thanks,
>
> CH. DARWIN".

C. Darwin to G. Bentham

April 22, 1868

"... I am experimenting on a very large scale on the difference in power of growth between plants raised from self-fertilised and crossed seeds; and it is no exaggeration to say that the difference in growth and vigour is sometimes truly wonderful. Lyell, Huxley and Hooker have seen some of my plants, and been astonished; and I should much like to show them to you. I always supposed until lately that no evil effects would be visible until after several generations of self-fertilisation; but now I see that one generation sometimes suffices; and the existence of dimorphic plants and all the wonderful contrivances of orchids are quite intelligible to me.
With cordial thanks for your letter, which has pleased me greatly,
Yours very sincerely,
CHARLES DARWIN"

[An extract from a letter to Dr Gray (March 11, 1873) mentions the progress of the work: "I worked last summer hard at Drosera, but could not finish till I got fresh plants, and consequently took up the effects of crossing and self-fertilising plants, and am got so interested that Drosera must go to the dogs till I finish with this, and get it published; but then I will resume my beloved Drosera, and I heartily apologise for having sent the precious little things even for a moment to the dogs"]. The following letters give the author's impression of his own book:

C. Darwin to J. Murray

Down, September 16, 1876

"MY DEAR SIR,—I have just received proofs in sheet of five sheets, so you will have to decide soon how many copies will have to be struck off. I do not know what to advise. The greater part of the book is extremely dry, and the whole on a special subject. Nevertheless, I am convinced that the book is of value, and I am convinced that for many years copies will be occasionally sold. Judging from the sale of my former books, and from supposing that some persons will purchase it to complete the set of my works, I would suggest 1500. But you must be guided by your larger experience. I will only repeat that I am convinced the book is of some permanent value...".

C. Darwin to Victor Carus

Down, September 27, 1876

"MY DEAR SIR,—I sent by this morning's post the four first perfect sheets of my new book, the title of which you will see on the first page, and which will be published early in November.
I am sorry to say that it is only shorter by a few pages than my 'Insectivorous Plants'. The whole is now in type, though I have corrected finally only half the volume. You will, therefore, rapidly receive the remainder. The book is very dull. Chapters II to VI, inclusive, are simply a record of experiments. Nevertheless, I believe (though a man can never judge his own books) that the book is valuable. You will have to decide whether it is worth translating. I hope so. It has cost me very great labour, and the results seem to me remarkable and well established.
If you translate it, you could easily get aid for Chapters II to VI, as there is here endless, but, I have thought, necessary repetition. I shall be anxious to hear what you decide...
I most sincerely hope that your health has been fairly good this summer.
My dear Sir, yours very truly,
CH. DARWIN"

C. Darwin to Asa Gray

Down, October 28, 1876

"MY DEAR GRAY,—I send by this post all the clean sheets as yet printed, and I hope to send the remainder within a fortnight. Please observe that the first six chapters are not readable, and the six last very dull. Still I believe that the results are valuable. If you review the book, I shall be very curious to see what you think of it, for I care more for your judgment than for that of almost any one else. I know also that you will speak the truth, whether you approve or disapprove. Very few will take the trouble to read the book, and I do not expect you to read the whole, but I hope you will read the latter chapters.
... I am so sick of correcting the press and licking my horrid bad style into intelligible English" (Darwin [1887] [25]: 3, 290–293).

3. Putting the book into perspective

Well, we can certainly say that Darwin is not wrong in his estimation of much of the book. It is grindingly dull! Page after page of results of experiments. One prays for the coming of the Internet, when the empirical information can be put on the net, for those who want to look at it, and put on the net, for the avoidance by those who do not want to look at it. Having said this, and therefore recognizing that line by line this is not a work for the ages, what about the work in perspective, as it were? Here it does become more interesting. It is part of an overall programme, one which indeed starts back even before Darwin discovered natural selection, just about at the time when he became an evolutionist. It seems to have been something at least in part spurred by reading his grandfather's, Erasmus Darwin's, evolution-mentioning work *Zoonomia* [26]. It is part of the quest for the understanding of sexuality. Why do we have two sexes? What is the biological reason for this, or since Darwin never asks a question without wanting to know the purpose—the final cause as Aristotle (and Darwin often) would say—what is sex for? Why go to the bother of having sex, when it would be so much simpler just to reproduce asexually?

The answer seems to be that somehow organisms need shaking up. If they just continue along the same path, without stresses and strains and changes, they seem to run out of steam. Hence, they need new conditions just to tone them up as it were, and more particularly they need sex to bring together two lines and shake things up internally. But it cannot be just two lines, indifferently. It has to be two

lines coming in from different circumstances. Coming from the same background cuts the worth of the mating.

This means that as Darwin says in his *Autobiography*, we have a two-part project. In the first place, we need proof that organisms have adaptations for sexuality, and moreover for making sure that they do not cheat and fertilize themselves. I presume that humans are not particularly interesting here, for it is not that easy to see how humans could fertilize themselves. Plants, however, are more interesting and pertinent, because often they carry both male and females organs—they are hermaphrodites—and thus have the potential for self-fertilization. It was the task of the little book on orchids to show that nevertheless plants have adaptations making self-fertilization difficult if not impossible. This is a very Darwinian project, because natural selection would have been at work here, as Darwin shows in abundance.

In the second place, we need proof that self-fertilization is indeed bad for you, and this is the job of *The Effects of Cross- and Self-Fertilisation in the Vegetable Kingdom*, a job that Darwin prides himself on having done well and successfully.

"The first and most important of the conclusions, which may be drawn from the observations given in this volume, is that cross-fertilisation is generally beneficial, and self-fertilisation injurious. This is shown by the difference in height, weight, constitutional vigour, and fertility of the offspring from crossed- and self-fertilised flowers, and in the number of seeds produced by the parent-plants. With respect to the second of these two propositions, namely, that self-fertilisation is generally injurious, we have abundant evidence. The structure of the flowers in such plants as *Lobelia ramosa*, *Digitalis purpurea*, etc., renders the aid of insects almost indispensable for their fertilisation; and bearing in mind the prepotency of pollen from a distinct individual over that from the same individual, such plants will almost certainly have been crossed during many or all previous generations. So it must be owing merely to the prepotency of foreign pollen, with cabbages and various other plants, the varieties of which almost invariably intercross when grown together. The same inference may be drawn still more surely with respect to those plants, such as Reseda and Eschscholtzia, which are sterile with their own pollen, but fertile with that from any other individual. These several plants must therefore have been crossed during a long series of previous generations, and the artificial crosses in my experiments cannot have increased the vigour of the offspring beyond that of their progenitors. Therefore the difference between the self-fertilised and crossed plants raised by me cannot be attributed to the superiority of the crossed, but to the inferiority of the self-fertilised seedlings, due to the injurious effects of self-fertilisation.

With respect to the first proposition, namely, that cross-fertilisation is generally beneficial, we likewise have excellent evidence. Plants of Ipomoea were intercrossed for nine successive generations; they were then again intercrossed, and at the same time crossed with a plant of a fresh stock, that is, one brought from another garden; and the offspring of this latter cross were to the intercrossed plants in height as 100 to 78, and in fertility as 100 to 51. An analogous experiment with Eschscholtzia gave a similar result, as far as fertility was concerned. In neither of these cases were any of the plants the product of self-fertilisation. Plants of Dianthus were self-fertilised for three generations, and this no doubt was injurious; but when these plants were fertilised by a fresh stock and by intercrossed plants of the same stock, there was a great difference in fertility between the two sets of seedlings, and some difference in their height. Petunia offers a nearly parallel case" (Darwin [1876] [23]: 436–437).

Note, as insisted, the cross-fertilization only works effectively if the organisms have been brought up in different circumstances. Presumably Darwin had use and disuse in mind as important operative factors here, since this was always a mechanism he endorsed and as is well known in the light of criticisms made of the arguments of the *Origin* (for instance about heredity), he grew to rely more on it rather than less as he grew older.

"It is obvious that the exposure of two sets of plants during several generations to different conditions can lead to no beneficial results, as far as crossing is concerned, unless their sexual elements are thus affected. That every organism is acted on to a certain extent by a change in its environment, will not, I presume, be disputed. It is hardly necessary to advance evidence on this head; we can perceive the difference between individual plants of the same species which have grown in somewhat more shady or sunny, dry or damp places. Plants, which have been propagated for some generations under different climates or at different seasons of the year, transmit different constitutions to their seedlings. Under such circumstances, the chemical constitution of their fluids and the nature of their tissues are often modified. Many other such facts could be adduced. In short, every alteration in the function of a part is probably connected with some corresponding, though often quite imperceptible change in structure or composition.

Whatever affects an organism in any way likewise tends to act on its sexual elements. We see this in the inheritance of newly acquired modifications, such as those from the increased use or disuse of a part, and even from mutilations if followed by disease. We have abundant evidence how susceptible the reproductive system is to changed conditions, in the many instances of animals rendered sterile by confinement; so that they will not unite, or if they unite do not produce offspring, though the confinement may be far from close; and of plants rendered sterile by cultivation. But hardly any cases afford more striking evidence how powerfully a change in the conditions of life acts on the sexual elements, than those already given, of plants which are completely self-sterile in one country, and when brought to another, yield, even in the first generation, a fair supply of self-fertilised seeds" (Darwin [1876] [23]: 446–447).

What is missing in all of this, obviously, is any reason why exactly it should be that organisms need shaking up. What is the point behind this? Why should organisms not simply keep going on in a straight line as it were, as obviously Darwin knew some asexual organisms do very happily for generation after generation? Those of us who know of the ideas of Herbert Spencer might think that something along the lines that he suggested might have appealed to Darwin, namely that it is all a matter of

equilibrium lost and having to regain this equilibrium but at a higher level after disruption. However, although Darwin may have been tempted, as always with Spencer he rather distrusted the metaphysics simulating real science.

"The fertilisation of one of the higher plants depends, in the first place, on the mutual action of the pollen-grains and the stigmatic secretion or tissues, and afterwards on the mutual action of the contents of the pollen-grains and ovules. Both actions, judging from the increased fertility of the parent-plants and from the increased powers of growth in the offspring, are favoured by some degree of differentiation in the elements which interact and unite so as to form a new being. Here we have some analogy with chemical affinity or attraction, which comes into play only between atoms or molecules of a different nature. As Professor Miller remarks: "Generally speaking, the greater the difference in the properties of two bodies, the more intense is their tendency to mutual chemical action... But between bodies of a similar character the tendency to unite is feeble". This latter proposition accords well with the feeble effects of a plant's own pollen on the fertility of the mother-plant and on the growth of the offspring; and the former proposition accords well with the powerful influence in both ways of pollen from an individual which has been differentiated by exposure to changed conditions, or by so-called spontaneous variation. But the analogy fails when we turn to the negative or weak effects of pollen from one species on a distinct species; for although some substances which are extremely dissimilar, for instance, carbon and chlorine, have a very feeble affinity for each other, yet it cannot be said that the weakness of the affinity depends in such cases on the extent to which the substances differ. It is not known why a certain amount of differentiation is necessary or favourable for the chemical affinity or union of two substances, any more than for the fertilisation or union of two organisms.

Mr Herbert Spencer has discussed this whole subject at great length, and after stating that all the forces throughout nature tend towards an equilibrium, remarks, "that the need of this union of sperm-cell and germ-cell is the need for overthrowing this equilibrium and re-establishing active molecular change in the detached germ—a result which is probably effected by mixing the slightly-different physiological units of slightly-different individuals". But we must not allow this highly generalised view, or the analogy of chemical affinity, to conceal from us our ignorance. We do not know what is the nature or degree of the differentiation in the sexual elements, which is favourable for union, and what is injurious for union, as in the case of distinct species. We cannot say why the individuals of certain species profit greatly, and others very little by being crossed. There are some few species, which have been self-fertilised for a vast number of generations, and yet are vigorous enough to compete successfully with a host of surrounding plants. We can form no conception why the advantage from a cross is sometimes directed exclusively to the vegetative system, and sometimes to the reproductive system, but commonly to both. It is equally inconceivable why some individuals of the same species should be sterile, whilst others are fully fertile with their own pollen; why a change of climate should either lessen or increase the sterility of self-sterile species; and why the individuals of some species should be even more fertile with pollen from a distinct species than with their own pollen. And so it is with many other facts, which are so obscure that we stand in awe before the mystery of life" (Darwin [1876] [23]: 456–458).

That basically is it. In the end Darwin has to profess ignorance. Let us say charitably that in the total ignorance of a theory of heredity, it was hardly a case of failure that he could not puzzle out sexuality. Many feel that we have failed to do so even to this day. But we can say that here was an area where Darwin only managed to give part of the solution. He could show that cross-fertilization was important, but he could not show why.

4. Epilogue

In these days of social constructivism, some readers will have remembered that Darwin married a first cousin and wonder if his work on cross-fertilization was at all connected to this. Without being definitive, I rather doubt it, if only because Darwin was worrying about sexuality before he proposed to and married Emma Wedgwood. However, Darwin does raise the issue in this book under discussion, if obliquely.

"With respect to mankind, my son George has endeavoured to discover by a statistical investigation whether the marriages of first cousins are at all injurious, although this is a degree of relationship which would not be objected to in our domestic animals; and he has come to the conclusion from his own researches and those of Dr Mitchell that the evidence as to any evil thus caused is conflicting, but on the whole points to its being very small. From the facts given in this volume, we may infer that with mankind, the marriages of nearly related persons, some of whose parents and ancestors had lived under very different conditions, would be much less injurious than that of persons who had always lived in the same place and followed the same habits of life. Nor can I see reason to doubt that the widely different habits of life of men and women in civilised nations, especially amongst the upper classes, would tend to counterbalance any evil from marriages between healthy and somewhat closely related persons" (Darwin [1876] [23]: 460–461).

One hears the voice of the upper-class Charles Darwin who had spent his youth clambering over the rocks of South America while Emma stayed at home in rural Staffordshire playing the piano and visiting the deserving poor.

References

[1] C.R. Darwin, On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life, John Murray, London, 1859.
[2] J.-B. de Lamarck, Philosophie Zoologique, Dentu, Paris, 1809.
[3] C. Darwin, The Descent of Man, and Selection in Relation to Sex, John Murray, London, 1871.
[4] A.R. Wallace, Contributions to the Theory of Natural Selection: a Series of Essays, Macmillan, London, 1870.
[5] M. Ruse, Philosophy after Darwin: Classic and Contemporary Readings, Princeton University Press, Princeton, 2009.
[6] C.R. Darwin, Journal of Researches into the Geology and Natural History of the Various Countries Visited by H.M.S. Beagle, Henry Colburn, London, 1839.

[7] C.R. Darwin, Journal of Researches into the Natural History and Geology of the Countries Visited During the Voyage of H.M.S. Beagle Round the World, 2nd ed., John Murray, London, 1845.
[8] C.R. Darwin, The Structure and Distribution of Coral Reefs. Being the First Part of the Geology of the Voyage of the Beagle, under the Command of Capt. Fitzroy, R.N. During the Years 1832 to 1836, Smith Elder, London, 1842.
[9] C.R. Darwin, Geological Observations on the Volcanic Islands Visited During the Voyage of H.M.S. Beagle, Together with some Brief Notices of the Geology of Australia and the Cape of Good Hope. Being the Second Part of the Geology of the Voyage of the Beagle, under the Command of Capt. Fitzroy, R.N. During the Years 1832 to 1836, Smith Elder, London, 1844.
[10] C.R. Darwin, Geological Observations on South America. Being the Third Part of the Geology of the Voyage of the Beagle, under the Command of Capt. Fitzroy, R. N. During the Years 1832 to 1836, Smith Elder, London, 1846.
[11] C.R. Darwin, A Monograph of the Sub-Class Cirripedia, with Figures of all the Species. The Lepadidae; or Pedunculated Cirripedes, Ray Society, London, 1851.
[12] C.R. Darwin, A Monograph of the Fossil Lepadidae; or, Pedunculated Cirripedes of Great Britain, Palaeontographical Society, London, 1851.
[13] C.R. Darwin, A Monograph of the Sub-Class Cirripedia, with Figures of All the Species. The Balanidge (or Sessile Cirripedes); the Verrucidae, and C, Ray Society, London, 1854.
[14] C.R. Darwin, A Monograph of the Fossil Balanidae and Verrucidae of Great Britain, Palaeontographical Society, London, 1854.
[15] W.A. Newman, Darwin and cirripedology, in: F. Truesdale (Ed.), History of Carcinology, Balkema, Rotterdam, 1993, pp. 349–434.
[16] C.R. Darwin, The Variation of Animals and Plants under Domestication, John Murray, London, 1868.
[17] C.R. Darwin, The Expression of the Emotions in Man and Animals, John Murray, London, 1872.
[18] C.R. Darwin, On the Various Contrivances by which British and Foreign Orchids are Fertilized by Insects, and on the Good Effects of Intercrossing, John Murray, London, 1862.
[19] C.R. Darwin, The Movements and Habits of Climbing Plants, John Murray, London, 1875.
[20] C.R. Darwin, Insectivorous Plants, John Murray, London, 1875.
[21] C.R. Darwin, The Power of Movement in Plants, John Murray, London, 1880.
[22] C.R. Darwin, C. Darwin, The Formation of Vegetable Mould, Through the Action of Worms, with Observations on their Habits, John Murray, London, 1881.
[23] C.R. Darwin, Cross- and Self-Fertilization of Plants, John Murray, London, 1876.
[24] C.R. Darwin, The Autobiography of Charles Darwin 1809–1882. With the Original Omissions Restored. Edited and with Appendix and Notes by his Grand-Daughter Nora Barlow, Collins, London, 1958 .
[25] F. Darwin, The Life and Letters of Charles Darwin, Including an Autobiographical Chapter, John Murray, London, 1887.
[26] E. Darwin, Zoonomia; or, the Laws of Organic Life, J. Johnson, London, 1794–1796.