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Charles Darwin and the perennial flax— a controversy and its implications

Herbert G. Baker

DURING THE CELEBRATIONS in 1958 and 1959 of the centennial of the theory of evolution by natural selection, much attention was given to the fate of Darwinian ideas from the time of their introduction in the writings of their originator until the present day. In addition, there were a number of attempts to improve our understanding of the circumstances in which Charles Darwin's books, papers, and letters were written. This need not be merely a centennial exercise, however, and there is more to be done. Such was the impact of Darwin's outstandingly important contributions to several areas of biology that, inevitably, they have had to be considered carefully by the succeeding generations of evolutionists who have wished to cultivate any of the fields which Darwin plowed. Equally inevitably, not all of Darwin's successors have found themselves in agreement with his postulates.

Almost all of Darwin's work contained the seeds of controversy, and it may be worthwhile to examine here an incident which is not directly concerned with the usual topic of evolutionary discussion, the origin of species. Instead, it concerns the significance of outcrossing mechanisms in flowering plants, their evolutionary development and their value to the populations of plants which show them. If one needs a "centennial," we had it recently, for 1862 was the year in which Darwin published his first paper on heterostyly, the outcrossing mechanism most directly concerned.

The dramatic centerpiece of the controversy is a letter written by Darwin to Asa Gray in response to a note published by Thomas Meehan, in which the latter cast doubt on the validity of Darwin's belief in the importance of outcrossing. The significance of this incident, however, lies in what it reveals of a much wider rift between workers on the subject of reproductive biology. The documentary record, here, is exceptionally complete, a circumstance which may make it seem surprising that the story has not been pieced together previously. Part of the explanation for this appears to be that some of the crucial letters written by Darwin were incompletely dated when sent and at least one has been mis-dated by those who have collected

them together subsequently. As a consequence, the whole affair has been missed from the excellent recent biography of Asa Gray (Dupree, 1959) and from the many biographies of Darwin, himself.

THOMAS MEEHAN

By way of introduction, it is essential that one of the persons most prominently involved should be fully identified. Biographies of Darwin and Asa Gray need hardly be given here, but another principal, Thomas Meehan (1826-1901), is much less well known. He, like Darwin, was born in England, but the circumstances of his life were as different from Darwin's as could be imagined. Deaf from birth, according to a biographical note (Harshberger, 1899), he was driven by this isolation from the company of potential playmates into being a naturalist (Meehan, 1901, however, denied that he was ever more than slightly hard of hearing!). In any case his opportunities to work with plants stemmed from his father's position as a nurseryman. He published his first botanical article at the age of 13 and produced his first *Fuchsia* hybrid the same year.

In 1845, Meehan entered Kew Gardens but "He fell under suspicion as belonging to the Chartists and thus formed the ill-will of Sir William Hooker, Director of the Gardens, who subjected him to petty annoyances" (Harshberger, 1899 pp. 249-250). Despite any such occurrences, however, he refused to leave until he had received a certificate, whereupon he sailed for the United States of America, in 1848.

Meehan settled in Philadelphia and worked in nurseries before establishing his own business (which suffered a number of vicissitudes before its ultimate success). In 1860 he was elected a member of the Academy of Natural Sciences of Philadelphia, while other appointments and elections followed. He also founded and edited a number of journals.

Harshberger's biographical note on Thomas Meehan may supply another quotation (written, it should be remembered whilst Meehan was still alive): "Professor Meehan, as a scientific man has corresponded with most of the scientists of prominence in both Europe and America. A close correspondence was maintained with Charles Darwin, who relied on Mr. Meehan's observations for many of the facts incorporated in his books. The correspondence continued, until a slight misunderstanding between them was to finally put a stop to their letter writing and pleasant intercourse. Mr. Darwin gives credit to Meehan's acute observations in many places in his epoch-making works." (Harshberger, 1899, pp. 253-254).

Although Harshberger alludes here to the disagreement which is the basis of the present paper, it seems that his reporting is not accurate

otherwise. In all the four volumes of Darwin's correspondence which have been published, there is only one letter of Meehan, dated October 9, 1874, dealing with flower colors (F. Darwin and Seward, 1903 letter no. 265). Similarly, Meehan is mentioned twice by Darwin in his book *The different forms of flowers on plants of the same species* (1877), but not in any other of Darwin's works.

In a letter to Asa Gray,¹ written on June 10, 1862, (1) Darwin did mention that a Mr. Meehan had sent him his paper on parallel differences in trees of North America and Europe and asked "if this can be approximately trusted for the case interests me much as [the] best case I have seen of apparently direct action of conditions of life." Actually, Meehan's whole scientific career was dominated by attempts to demonstrate the importance over any other conditioning factor of the direct action of the environment on plants. Asa Gray's reply (2), written on July 2, 1862, said "Meehan—a good gardener—send(s) me his manuscripts before printing. I tried to find exceptions to this rule, and I thought I had, but he beat me down . . . Meehan is an honest and I suppose very good observer and you may 'approximately' trust him, I should think. He may have got hold of something."

Nevertheless, it was just this subject of the direct effects of the environment which, 16 years later, produced the obvious symptoms of discord between Meehan and Darwin, as the following report, involving the flax genus, *Linum*, will show.

HETEROSTYLY IN *LINUM PERENNE* L.

In 1864 Darwin published an account of his investigation of heterostyly in the flax genus *Linum*. He showed that, in a number of species, two forms of flowers are to be found borne on separate plants. These are, respectively, long-styled and short-styled (see Figs. 38 and 39). In its most completely developed state, as in *Linum perenne* L., the long-styled flowers bear stamens which are usually only half as long as those in the short-styled flowers and, in fact, the anthers of one form stand at just about the same height as the stigmas in the opposite form. This situation, known as heterostyly, is mechanically very suitable for cross-pollination between the forms (by insect agency). It is significant that Darwin was able to show that only such cross-pollination between the two kinds of flowers (and therefore between the two kinds of plants) is normally effective in producing good seed-setting. The plants are more or less self-sterile (the short-styled plants

¹ Notes pertinent to each of the letters referred to in this paper will be found in the Appendix at the end of this paper (pp. 160-161). Reference to these is by a parenthetical number in the text, *i.e.*, (1).



Fig. 38. Styles and stamens of *Linum perenne*, long-styled form (enlarged).

Photo by J. R. Swanson

being rather more capable of setting some seeds if self-pollinated).

It should be made clear, however, that Darwin also demonstrated that not all *Linum* species are heterostyled, a notable exception to heterostyly being shown by the common cultivated flax, *Linum usitatissimum*. Plants of this species are homostylous, with only one kind of flower in which the styles and stamens are roughly equal in length (cf. Fig. 40). These plants are self-fertile.

Darwin's observations, along with studies of heterostyly in many other



Fig. 39. Styles and stamens of *Linum perenne*, short-styled form (enlarged).

Photo by J. R. Swanson

genera (of 14 plant families), were collected together and published in his book *The different forms of flowers on plants of the same species* in 1877, in London. The first American edition of this work was issued a year later.

It seems to have been the publication of Darwin's results in book form which stimulated Meehan to look again at a wild flax plant (apparently belonging to the species *Linum perenne*) which he had collected on a trip to Colorado and which was now growing in his Philadelphia garden. Meehan was so impressed with the difference between what he saw there

and what Darwin had reported that he wrote a short letter on the subject to the editor of the *Bulletin of the Torrey botanical club*, who subsequently published it (*op. cit.* 6: 189. 1877).

The salient part of Meehan's note is the following:

However, it is well to recognize the fact that plants, and no doubt insects, behave differently in different places. For instance, Mr. Darwin from English experiments utterly denies that *Linum perenne* can fertilize itself by its own pollen. He says we may as well sprinkle over it so much inorganic dust. But a single plant which I brought with me from Colorado in 1873, bears fruit freely in the garden every year. It shows how a plant may behave in one place is no rule as to how it will elsewhere . . .

In itself this would appear to be quite an innocent statement of an observation and what could be considered as one interpretation of it. But Darwin, when he read it, did not accept it as such. Through an unfortunate error, presumably by Francis Darwin, in assembling Charles Darwin's letters for publication (F. Darwin, 1896), the impact of the latter's reaction to Meehan's note and the subsequent developments have been completely obscured. The events are presented here in chronological order. Each letter is referred to in the Appendix, where the reasons for placing them in this order are discussed.

On January 21, 1878, Darwin had written (3) to Asa Gray thanking him for the review of his book, which Gray had just put out in the January issue of the *American journal of science* (Gray, 1878). Later he added an emotion-charged postscript (4) which should be quoted in full:

P.S. I forget to add the following as I wished to do yesterday. Mr. Meehan in a paper lately read before the Philadelphia Society says in a somewhat sneering tone that plants behave differently in one country from another for that a single plant of *Linum perenne* brought from Colorado by him was quite fertile with him, where I state [confirmed he might have added by Hildebrand] that it is absolutely sterile with its own pollen. Now he does not state whether his plant was long-styled or short-styled, and as he speaks of bringing the plant from Colorado, I imagine that it was there endemic. Does *L. perenne* grow there? Dr. Alefeld says *None* of the true American species are heterostyled. Now if Mr. Meehan has mistaken the species it seems to me too bad to throw a slur or doubt on another man's accuracy without taking the slightest pains to be accurate himself. I have been almost tempted to write formally to the Philadelphia Society to enquire how the case really stands. But I have resolved not to do so, as Hildebrand has fully confirmed my statement . . . Mr. Meehan's inaccuracy seems to me injurious in no small degree to Science.

It is fortunate that Darwin did not write to the "Philadelphia Society" in view of the fact that Meehan's paper had appeared in the *Bulletin of the*

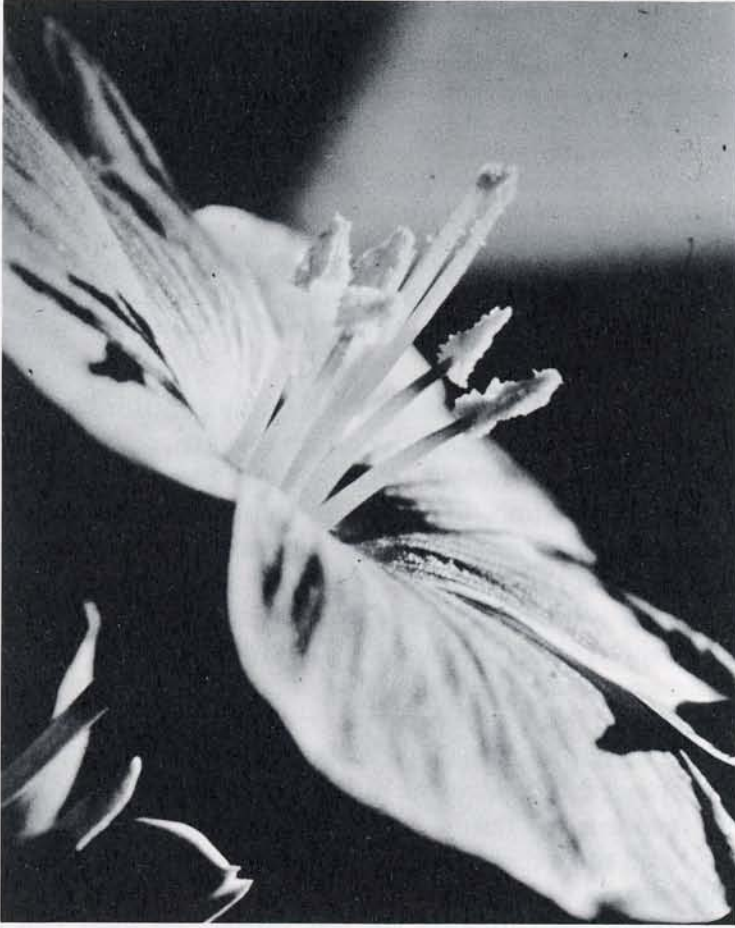


Fig. 40. Styles and stamens of *Linum lewissii* (enlarged). The anthers usually stand slightly below the stigmas, but the physiology of the flower is as if they were equal.

Photo by J. R. Swanson

Torrey botanical club, published in New York. Darwin's sensitivity to criticism and his willingness to unburden himself to his close friends are well known, but the intensity of his feeling here demands further explanation, as is attempted later.

Asa Gray lived up to his championship of Darwin. He had already reviewed Darwin's book in the January issue of the *American journal of science*, but he added a supplementary note in the March issue (Gray, 1878). This reveals, in its wording, the direct influence of Darwin's letter quoted above, proving that letter to have been written in 1878. After quoting from Meehan's note, Gray wrote,

This extremely remarkable induction of a general rule,—that plants and insects cannot be depended upon for behaviour,—is inferred from two instances, one of which has been sufficiently examined; and now a few words may dispose of the other. Mr. Meehan must have noticed (in *Forms of Flowers*, p. 92) that Darwin's result has been completely confirmed by Hildebrand; and he might have read on p. 100 the statement taken from Alefeld, that no American species is heterostyled; and on p. 100 that the Colorado plant, *Linum Lewisii*, of Pursh, the American representative of *L. perenne*, is suspected to be a distinct species, of a sort fully capable of self-fertilizing. This is what Mr. Meehan's observation goes to prove; and so, instead of showing that the behavior of species cannot be relied on, he has unwittingly brought evidence of the correctness of Mr. Darwin's surmise.

It will be observed that, in the latter half of the penultimate sentence of the passage quoted, Gray added the all-important piece of information which reconciles the observations of Darwin and Meehan. Then, however, Gray concluded by writing, in rather lordly fashion, "We looked upon Mr. Meehan's little article as a piece of pleasantry, and should not have referred to it if it had not been noticed abroad as something serious."

In addition, on February 8, 1878, Gray replied (5) to Darwin's January letter, presumably reassuring him and pointing out the true situation regarding *Linum perenne* and *L. lewisii*. However, Darwin, who received this letter and replied to it (6) on February 17, expressing his gratitude, had not merely sought assistance from Gray. As he makes clear in this latest letter, he had also invoked the aid of his other botanical confidant, Sir Joseph Hooker. He recounts the results of the investigation which Hooker made on his behalf and this report to Gray contains a very gentle retraction of his previous view. Darwin wrote that Hooker had looked at his own specimens collected in Colorado (in 1877, during his joint trip through North America with Gray) and found that "the American form is less strongly heterostyled than the European" and that, although there is some variability, "the stamens and styles are even equal in some specimens." In this letter it is notable that Darwin still referred to these specimens as *Linum perenne*—as some botanists do even at the present day (e.g., Hultén, 1941-1950; Munz, 1959).

Meehan seems to have taken his treatment remarkably well and referred only obliquely to the controversy in subsequent publications. In the *Gardener's monthly and horticulturalist* for April, 1878, his editorial notes contain this statement, "The pretty blue flax of the Rocky Mountains has hitherto been thought to be the same with the Old World *Linum perenne*. Some of our earlier botanists named it *Linum Lewisii*. In a recent number of Silliman's Journal [*The American journal of science*] Dr. Asa Gray remarks that it may possibly yet prove to be a distinct species, and to bear this name" (Meehan,

1878). In the same year, Meehan treated the Perennial Flax in his *The native flowers and ferns of the United States*" (Meehan, 1878) and, although he called it *Linum perenne* and never mentioned the epithet *lewisii*, he did admit that "Asa Gray thinks the American Perennial Flax may not be heterostyled as the Asiatic form is, and may, therefore, be a distinct species." He repeated his own observations with the Coloradan plant, however, and did not back down in his disagreement with Darwin.

The fact that neither Meehan nor Darwin realized at first that Meehan's plant was *Linum lewisii* is both surprising and explicable. As early as 1849, Planchon had pointed out that, in *Linum lewisii*, separate flowers on the same plant might produce styles which were longer, shorter, or equal in length to the stamens. Although, in his 1864 paper, Darwin was inclined to believe that the flowers with stigmas and anthers at the same height would be self-fertile, he thought that those with these organs at unequal heights would require reciprocal fertilization. He did not experiment with this species, although he had discussed the desirability of doing so in correspondence with Asa Gray in 1863 (7) and with John Scott (8) in the same year. By the time his book was published in 1877 he knew more about the biological significance of heterostyly and self-sterility in flowers and realized that it was unlikely that these flowers borne on the same plant would differ in their reactions. Consequently, on p. 101, he remarked, ". . . I am now inclined to believe that it [the case] is merely one of great variability."

In 1864, Darwin had been aware of the close relationship of *Linum lewisii* to *L. perenne*, for he wrote of it thus, ". . . *Linum Lewisii* which is ranked by Planchon as a variety of *L. perenne*, but which, now that we know the meaning of reciprocal dimorphism, surely deserves specific honours . . ." (Darwin, 1864, p. 82). Despite this, in 1878, Darwin failed to recognize that he already knew the answer to the question which he addressed to Asa Gray, simply because he was not a botanical taxonomist. Neither was Meehan; a nurseryman, he was like Darwin, more concerned with the behavior of plants than with painstaking systematic and nomenclatural studies. As Harshberger (1899, p. 254) remarks in his biographical note about Meehan, "Many of his observations lack the force which a perusal of the literature of the subject would give them."

It was left to William Trelease (1888, p. 9) to put the matter in an evolutionary context, which he did in the following manner: "It appears therefore that forms of a single species, originally distributed over the northern portion of both continents [not in eastern America however], have in the course of time differentiated so far as to acquire heterogony [heterostyly] in the Old World, or lose it in the New—the latter appearing more proba-

ble." The significance of derived heterostyly in relation to establishment after long-distance dispersal has been discussed relatively recently (Baker, 1955).

Despite his lapse of memory, Darwin's scientific acumen shines through. Part of his genius lay in his ability to distinguish the time and place to make an observation or perform an experiment and we should do him an injustice if another quotation were not made from his letter of February 17, 1878 (6): "If I were forced to wager I would bet that the American form would prove at least functionally a distinct species. If you could get and send me seed of the Colorado form, I would grow both forms and see if they could be crossed artificially and I would try whether the homostyled individuals were self-fertile."

Even in the middle of the twentieth century, writers of floras dealing with portions of North America have continued to be divided into two camps—those who consider *Linum lewisii* to be a separate species and those who treat it as a subspecies or variety of *L. perenne*. The crucial test is just what Darwin proposed, that the two forms be brought together and attempts be made to hybridize them.

For this purpose, materials of both taxa have been assembled at the University of California Botanical Garden in recent years, and all appropriate crosses have been made between them. It is pleasant to report that Darwin's prediction was completely borne out; not only is *Linum lewisii* thoroughly self-fertile, but strong barriers to crossing exist between it and *L. perenne*. A detailed presentation and discussion of these results will be made elsewhere, but there is no question that these morphologically rather similar taxa are correctly regarded as separate species.

CONFLICT OVER THE IMPORTANCE OF CROSS-POLLINATION

It does not seem reasonable that Darwin would have reacted as strongly as he did in January, 1878, if Meehan's note had represented an isolated discordance in the interpretation of natural events. The key to this situation may, possibly, be found not in Meehan or his work but in the writings of the man with whom Meehan threw in his scientific lot. This was the Reverend George Henslow, chief opponent of the Darwinian interpretation of the function of pollination systems and a prolific author. To appreciate Henslow's opposition, we must understand what it was that he opposed; how his opposition evolved from original support of Darwin's view that cross-fertilization brought real benefits to plants and animals, and the extent of his documentation of his views. Then it may become

clear why, in 1878, Darwin might well have been irked by the loss of another potential supporter.

Darwin had been greatly influenced by a statement made in 1799 by T. A. Knight. Knight carried out experiments on the cross- and self-pollination of pea plants and proposed that, "In no plant does self-fertilization occur for an unlimited number of generations." Darwin found his own observations to be in agreement with this and, in 1859, in chapter IV of the *Origin of species*, he elaborated this idea. As a result, the aphorism "Nature abhors perpetual self-fertilization" has been attributed to Darwin and the principle referred to as the "Knight-Darwin Law." (cf. Müller, 1883)

The early observations on the effects of cross- and self-pollination on plants by Knight, Herbert, von Gärtner, and Darwin were greatly strengthened by numerous experiments which Darwin carried out subsequently. The results from these formed the basis of another of his books, *The effects of cross and self-fertilization in the vegetable kingdom* (Darwin, 1876). In this work Darwin demonstrated that, compared with self-pollination, cross-pollination produces better seed-setting and more vigorous (at any rate taller) plants in the next generation. By this means he set the stage for our present appreciation of heterosis and such practical benefits of scientific plant breeding as hybrid corn. Of course, we now know (as Darwin could not have known) that another great virtue of cross-pollination is its promotion of genetical recombination. By the continual production of new combinations of characters upon which natural selection can act, the chances of the ultimate production of more closely adapted types are increased.

Thus, it was in the promotion of cross-pollination, with its attendant advantages, that Darwin saw the value of the various means of attracting and utilizing insect visitors which are employed by flowers. It was clear to him that these attractive devices would be favored by natural selection and, also, that if any mechanical features of such a flower system could be reinforced by a physiological system such as self-sterility, so much the better.

In 1867, George Henslow (1835-1925) published the first two of his many treatments of pollination systems in flowering plants. In that year, and again in 1869, he may be said to have taken a typically Darwinian position (and he includes, in one of the 1867 papers, data which he received in personal communications from Darwin).

However by 1876, when his next paper on the subject was published, Henslow's point of view had changed. The turning point seems to have been in 1869 when he watched a large bumblebee hanging on the dependent stamens of *Epilobium angustifolium* L. Then it occurred to him "that the way

the stamens hung down might perhaps have become an hereditary effect from the repeatedly applied weight of the bees" (Henslow, 1876, p. 543). This observation, coupled with his own long-standing difficulty in accepting natural selection as an agent in the *origin* of species (although he would accept it as an agent of extinction), led him to re-examine the structures of flowers in a new anti-Darwinian light.

Henslow continued to profess to appreciate the general soundness of Darwin's experiments on the value of cross-pollination. However, he was now concerned to give them an exactly opposite interpretation. Thus, he commented at length upon Darwin's experiments with continual self-pollination of plants through several generations (Henslow, 1879). Here in a paper read to the Linnean Society of London on November 1, 1877, he pointed out instead of repeated self-pollination producing a continuous deterioration in vigor, after a while a steady state was generally reached if the experiments were carried on long enough. In two cases (*Ipomoea* and *Mimulus*), thoroughly self-fertile and quite vigorous forms made their appearance. In this paper, it is notable that Henslow gave thanks (and prominence) to Thomas Meehan (Henslow, 1879, pp. 320 and 396).

Henslow seized upon another weakness in Darwin's crossing program by pointing out that Darwin nearly always worked with plants which, in nature, are usually cross-pollinated. He claimed that Darwin had nowhere demonstrated any value in cross-pollination for those plants which are normally self-pollinated in the wild. Henslow pointed out that the weeds and similar plants with usually rather inconspicuous flowers which have encompassed the world are generally self-fertilizing (Henslow, 1879, pp. 390-396).

As his subsequent writings showed, Henslow believed implicitly in the inheritance of acquired characters (cf. Henslow 1888, 1891, 1895, 1908, etc.). Instead of accepting the idea that forms of flowers adapted to insect visits are selected for their positive value to the plants which bear them, he thought that it was the insects themselves which distorted the flowers into forms advantageous only to their own pollen- and nectar-gathering.

Whatever an insect does to them, they must yield to it, and grow in adaptation to it; but while they are thus being stimulated to become what we may choose to call finer flowers, and handsomer plants . . . all this is secured at a sacrifice of fertility. They neither set seed in anything like the proportion that the "weedy" plants produce nor can they hold their own so well when they find themselves transported to distant countries (Henslow, 1891, pp. 147-148).

The year of Henslow's conversion was also the year in which the Swede,

Severin Axell (1869) published a counterattack on the rather over-enthusiastic Darwinism of Friedrich Hildebrand (1835-1915) and Federico Delpino (1833-1905). At this time they were attempting to declare the Knight-Darwin Law absolute by indicating that self-fertilization either cannot occur or, if it does, is inevitably injurious. Darwin had never gone this far. Axell, however, was something of an extremist in the opposite direction, lauding self-fertilization as the most economical method of seed-production and, therefore, the most highly evolved system.

Although Henslow's lengthy paper attacking the Darwinian view of cross-pollination was not published until 1879, it was read to the Linnean Society more than two months before Darwin's letter was written to Meehan in January, 1878, giving Darwin enough time to be exasperated by it. In addition, Henslow had published articles with a similar theme in 1876 and 1877, while an abstract of the big paper appeared in more than one journal in the same year (1877) in which it was given verbally. Also in 1877, Henslow reviewed Darwin's book *The effects of cross- and self-fertilization . . .* at such length in the *Gardeners' chronicle* that the resulting article had to be distributed through seven issues of the journal. Thus, Henslow's opposition to his views must have been fresh in Darwin's mind at the time he saw Meehan's note on *Linum*.

Meehan's note may well have had an extra disturbing influence because it was published at a time when Darwin himself seems to have been giving increased weight to the direct action of the environment in the production of variation. He had never succeeded in banishing the inheritance of acquired characters from his own evolutionary postulates and, many years later, Henslow (1915) was able to describe such inheritance as Darwin's "alternative explanation of evolution."

In 1859, Darwin, although by no means rejecting "direct action," had been inclined away from it as a cause of variability. When dealing with the constancy of some varieties in the *Origin of species* he wrote, "Such considerations incline me to lay less weight on the direct action of the surrounding conditions than on a tendency to vary, due to causes of which we are quite ignorant." (Darwin, 1859, p. 107). By 1868, however, Darwin had been swung over sufficiently to make direct action by the environment (producing inheritable modifications) the central plank of his theory of pangenesis (Darwin, 1868, vol. 2, p. 428). Similarly, direct effects of the environment take their place in the statement which forms the core of his book *The effects of cross- and self-fertilization . . .* published in 1876 (p. 27)—"the mere act of crossing by itself does no good. The good depends on the individuals which are crossed differing slightly in constitution, owing to

their progenitors having been subjected during several generations to slightly different conditions, or to what we call in our ignorance spontaneous variation."

If further evidence be needed of this growing suspicion in Darwin's mind that organisms might be acted upon by different environments in such a way that they could "behave differently in different places" (to use Meehan's words), this can be found in a letter (9) written in 1876 by Darwin to Moritz Wagner, "When I wrote the 'Origin' and for some time afterwards, I could find little good evidence of the direct action of the environment; now there is a large body of evidence . . ."

After Darwin's death in 1882, Herbert Spencer, in particular, drew attention to the manner in which Darwin had increasingly accepted the inheritance of acquired characters. Much more recently, Eiseley (1958) has shown that Darwin's retreat from reliance upon natural selection followed from his inability to answer the mathematically based criticisms of Fleeming Jenkin in 1867.

Any man who is worrying over the validity of his views may be expected to prefer to work out his own decisions rather than to have them thrust on him, particularly in public. Darwin is hardly likely to have been different from the rest of us in this respect and this may explain his outburst against Meehan. In January, 1878, plenty of attempts were being made to induce him to retreat from previously held positions. To some extent he was doing this for himself (witness his improved regard for his grandfather, Erasmus Darwin), but at the same time Samuel Butler (1878) was building up his case for Lamarckism, against Natural Selection and even against Darwin himself.² An off-and-on friend, Thomas Carlyle, appears to have been involved in another upsetting episode, for the same letter (5) to Asa Gray which bore the postscript about *Linum* refers to an anti-Darwinian letter attributed to Carlyle (but called by him a forgery or, at any rate, "all infernal lies"). Now, an erstwhile ally, George Henslow, had launched his onslaught on Darwin's cherished view that cross-fertilization was almost always valuable and its promotion the basis for the evolution of most of the morphological and behavioral features of entomophilous flowers.

It is ironic that Darwin was the discoverer of the functional significance of cleistogamy and observed numerous other means of promoting self-fertilization in flowering plants. Had he been allowed to evolve gradually, and for himself, the idea that pollination systems are adaptable, like any

² Although dated 1878, Butler's book *Life and habit* was published on December 4, 1877—at a critical moment for our story (cf. Hoppé, 1925, p. 25).

other character (and that heterosis may or may not be manifested in nature according to the circumstances), the history of this controversy might have taken a different course.

In fact, for completeness of the record, it should be noted that Darwin later found reason for a return to his old enthusiasm for natural selection rather than direct action. Less than a year before his death he wrote (10) to Professor Karl Semper (1832-1893) of Wurzburg, indicating how the careful cultivation studies on wild plants carried out by H. K. Hoffmann, in Germany in 1865, had diminished the apparent evolutionary power of direct action and indicating that this vindicated his own earlier thoughts (see item 10 in Appendix). Hoffmann, incidentally, was many years ahead of his time in making these studies (Hoffmann, 1865) which anticipated those of Turesson (1922) and his successors in genecology by over half a century.

RELATIONS BETWEEN DARWIN AND GEORGE HENSLOW

Darwin's strong reaction to Meehan's note (which he interpreted, wrongly perhaps, as a deliberate slur on his own experiments) contrasts strongly with the reserve which he maintained in the face of George Henslow's publications. Although Darwin read Henslow's epic review of *The effects of cross and self-fertilization . . . in The Gardeners' chronicle*, he was roused only to write (11) to the editor (on February 19, 1877) to point out that an unfortunate typographical error in the book had misled the reviewer in one place, and also to clarify a statement made in another. In view of the magnitude and obvious plausibility of much of Henslow's attack upon Darwin's reasoning and conclusions, the concluding words of the latter's letter (11) are almost incredibly restrained (and inadequate)—

I have long been convinced that controversy is a mere waste of time; I will, therefore, not make any other remarks on Mr. Henslow's criticisms, though I think that I could answer them satisfactorily. I hope that any reader who is interested in the subject will not take Mr. Henslow's interpretation of my statements without consulting my book.

Darwin made no reply at all to Henslow's Linnean Society paper when that was published. Once again it was left to Asa Gray to take up the cudgels, which he did with some vigor in the *American journal of science* (Gray, 1879), although this time without extraneous remarks.

It is not surprising that Darwin should have eschewed public argument over the significance of pollination-systems. It was never his nature to indulge in it and he had sufficient public reputation at this stage for Henslow to be at a very considerable disadvantage in getting a favorable reception for his ideas. Nevertheless, on the surface, it is surprising that

mention of these attacks from Henslow, and his own reactions to them, is completely missing even from Darwin's letters to confidants. It would take more than doubts of the complete correctness of his own position to induce such restraint.

Perhaps the omission of discussion is explicable on the basis that George Henslow was the son of John Stevens Henslow (1796-1861), the great biologist who had inspired Darwin whilst he was an undergraduate at Cambridge. This same man had suggested Darwin as Naturalist for H.M.S. *Beagle*, and had been the recipient of his specimens from the voyage (as well as Darwin's admiration all the rest of his life). Darwin's eulogy contributed to Jenyns' biography of the elder Henslow (Jenyns, 1862), must convince any reader that he could not have brought himself to argue publicly with the son of such a great man, nor even to criticize him privately.

Sir Joseph Hooker (1817-1911), Darwin's champion on a number of other occasions, also took no action. This, too, is not surprising, for Hooker had married and was devoted to George Henslow's sister. Although she had died in 1874, it is understandable that Hooker, too, would have felt inhibited (and respect for his feelings would also have helped to hold Darwin back). T. H. Huxley (1825-1895) would not have been involved to the usual extent because this was a botanical matter, and anyway, he would have been subject to the same restrictions of Victorian decency amongst friends. Only Gray could, and did, put up a fight. As a result, it is probably true that the scientific world at large has scarcely been aware of the controversy, whereas it could hardly have been overlooked if there had been a series of confrontations.

DARWIN AND HERMANN MÜLLER

Of significance to any historical treatment of the subject of pollination systems and their effects is the existence of Hermann Müller's magnificent book, *Die befruchtung der Blumen durch Insekten*. Originally published in Germany, in 1873, this work had served Darwin well as a source-book of information on the relationships between insects and the flowers of many European species of plants. Nevertheless, in it, Müller's wise judgment on the "Knight-Darwin Law" had been given—that the "law" should be set aside as an overstatement. Müller (1829-1883) presented a more moderate view, that cross-fertilization results in offspring which vanquish the offspring of self-fertilization in the struggle for existence but that many species which are regularly self-fertilized, and in which the struggle for existence between the offspring of self-fertilization and cross-fertilization never takes place, reproduce by self-fertilization for an unlimited number of generations.

On this basis, the many adaptations for self-pollination seen by Darwin and by others (including Henslow and Meehan) fall into place. Darwin had recognized, years before, that it was not the mere act of crossing which was valuable. Unfortunately, he does not appear to have realized with the same clarity that the converse was equally likely; there is nothing in the act of self-fertilization itself which is injurious. As we know now, it is the genetical constitutions of the plants and the environmental circumstances in which they find themselves which determine the value of crossing or selfing at any time.

Just before Darwin's death in 1882, an English translation of Müller's book was in preparation. D'Arcy W. Thompson (1829-1892), the translator and editor, obtained for this edition a prefatory note from Darwin—which, actually, was the last item which he ever wrote for publication. It was dispatched on February 6, 1882 (*cf.* Müller, 1883). The fact that Darwin could write this prefatory note, full of appreciation for Müller's book, adds substance to the belief that Müller's conclusions regarding the merits of cross- and self-fertilization could, ultimately, have been Darwin's too, had he been given time to reach them. However, Darwin's opponents were spared to promote their views longer than Darwin lived to maintain or modify his. Meehan lived until 1901, and Henslow at the age of 90, died in 1925. Nevertheless, they were never able to influence more than a minority of their readers. With the reaction of the twentieth-century biologists against Lamarckism, "direct action" by the environment became discredited and Henslow's and Meehan's reputations suffered for their outspoken advocacy of it. By contrast, it was forgotten by many that Darwin sometimes subscribed to "direct action" as well.

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APPENDIX

THE LETTERS FROM AND TO CHARLES DARWIN CITED IN THE TEXT

(1) Charles Darwin to Asa Gray, June 10, 1862. Reproduced in part in F. Darwin (1896), vol. 2, p. 446. The portion quoted here (p. 143), however, is not given there but is taken directly from the letter, now in the Gray collection at Harvard University. Dr. A. Hunter Dupree kindly furnished the material.

(2) Asa Gray to Charles Darwin, July 2, 1862. Quoted from Jane L. Gray (1893), vol. 2, p. 485.

(3) Charles Darwin to Asa Gray, January 21, 1878. See (4).

(4) In the collection of Darwin's letters to Asa Gray, at the Gray Herbarium, Harvard University, there is one letter dated "Jan. 21, 78." Two others are dated, respectively, "Jan. 20" and "Jan. 21" (the latter commencing "P.S...."). When these were collated by Francis Darwin for the production of the *Life and letters*, the first of them was numbered 123. The second and third were placed together and numbered 127 (with the date "1880" added in pencil). They are combined this way in both the *Life and letters* (F. Darwin, 1896) and in the later publication by Holbrook (1939). There can be no doubt, however, that the first and third letters are the ones which should have been combined as letter and postscript respectively. This is shown positively by Asa Gray's publication, in March 1878, of his supplementary review of Meehan's note, based on Darwin's postscript, proving the latter to have been written earlier in the same year.

Darwin's postscript, itself, contains evidence of dating, because it ends with an addendum "I have just spent a delightful two hours at Kew, and heard prodigies of your strength and activity—that you run up a mountain like a cat!" At Kew, Darwin would have met Joseph Hooker who had recently returned (in October, 1877) from travelling through the United States with Asa Gray.

Contributing to the mistake in collation of these letters must have been Darwin's opening words in the postscript "I forgot to add the following as I wished to do yesterday . . .". Despite this, it is clear that the letter and the postscript to it were both given the same date, "Jan. 21."

There is no question that the remaining letter (no. 127 *sensu stricto*) was truly written in 1880, despite the fact that Charles Darwin, himself, did not indicate the year. This is because, in this letter, Darwin refers to an illustration on page 21 of Gray's "text book" showing the seedling of *Megarrhiza californica*. It was not until the sixth edition of this book³ that this illustration makes its appearance on page 21, and this edition was published late in 1879.

(5) Asa Gray to Charles Darwin, February 8, 1878. This letter is referred to by Darwin in his reply dated February 17, 1878. See (6).

³ *Structural botany; or organography on the basis of morphology* Part 1. New York, Ivison, Blakeman, Taylor and Co., 1879.

(6) Charles Darwin to Asa Gray, February 17, 1878. This letter (no. 129 in the Gray collection at Harvard) was not dated as to year. Its contents reveal that the year was 1878. In particular, it could not have been earlier because of the reference to Hooker's Colorado specimens, which were collected in 1877.

(7) Charles Darwin to Asa Gray, January 19, 1863. Quoted from Holbrook (1939), p. 49.

(8) Charles Darwin to John Scott, June 6, 1863. Quoted from F. Darwin and A. C. Seward (1903), vol. 2, p. 323.

(9) Charles Darwin to Moritz Wagner, October 13, 1876. Quoted from F. Darwin (1896), vol. 2, p. 338.

(10) Charles Darwin to Karl Semper (1832-1893), July 19, 1881. Quoted from F. Darwin (1896), vol. 2, pp. 516-7. This letter appears to be so important for an appreciation of Darwin's vacillation (and yet to be so neglected) that it is quoted here *in extenso*.

Down, July 19, 1881

My Dear Professor Semper,—

I have been much pleased to receive your letter, but I did not expect you to answer my former one . . . I cannot remember what I wrote to you, but I am sure that it must have expressed the interest which I felt in reading your book.⁴ I thought that you attributed too much weight to the *direct* action of the environment; but whether I said so I know not, for without being asked I should have thought it presumptuous to have criticised your book, nor should I now say so had I not during the last few days been struck with Professor Hoffmann's review of his own work in the 'Botanische Zeitung,' on the variability of plants; and it is really surprising how little effect he produced by cultivating certain plants under unnatural conditions, as the presence of salt, lime, zinc, etc., etc., during *several* generations. Plants moreover, were selected which were the most likely to vary under such conditions, judging from the existence of closely-allied forms adapted for these conditions. No doubt I originally attributed too little weight to the direct action of conditions, but Hoffmann's paper has staggered me. Perhaps hundreds of generations of exposure are necessary. It is a most perplexing subject. I wish I was not so old, and had more strength, for I see lines of research to follow. Hoffmann even doubts whether plants vary more under cultivation than in their native home and under their natural conditions. If so, the astonishing variations of almost all cultivated plants must be due to selection and breeding from the varying individuals. The idea crossed my mind many years ago, but I was afraid to publish it, as I thought people would say 'how he does exaggerate the importance of selection.'

I still *must* believe that changed conditions give the impulse to variability, but that they act *in most cases* in a very indirect manner."

(11) Charles Darwin to the editor of *The Gardeners' chronicle*, headed "Fertilisation of Plants," dated "February 19." In, *Gard. Chron.* ser. 2. 7: 246. (24 Feb.) 1887.

⁴ Published in the "International Scientific Series," in 1881, under the title, "*The natural conditions of existence as they affect animal life.*"