

## The extent of Charles Darwin's knowledge of Mendel

Gregor Mendel read his cornerstone paper, "Versuche ueber Pflanzen-Hybriden," to the Brünn Natural History Society in 1865 (Mendel 1866; for a translation of the paper, Stern and Sherwood 1966), but only in the twentieth century has the scientific community recognized its importance. Indeed, Mendelian genetics as a science may be said to date from the dawn of the twentieth century, nearly two decades after Mendel's death in 1884. Its problematic beginnings can be traced in the edition that gathers Mendel's seminal papers together with his letters to Carl Nägeli (Stern and Sherwood 1966). The edition also includes papers by W O Focke, H de Vries, C Correns, R A Fisher and Sewall Wright, all of which added substance to the foundations of the new science. Although in the twentieth century Mendel's 1865 paper came to be regarded as "one of the triumphs of the human mind" (Stern 1966), its value lay unrecognized for decades. This paper seeks to correct claims that Darwin knew about Mendel's work, and to dispel speculations that Mendel's results held meaning in Darwin's thought.

Three and a half decades elapsed between the reading of Mendel's paper and its 'rediscovery' in 1900, when Correns and De Vries independently published supporting evidence (Stern and Sherwood 1966). Their work provided the essential context in which to understand Mendel's pioneering studies and to recognize them as fundamental to the understanding of inheritance in the twentieth century. Nevertheless, the time lapse leaves us with an enigma: Why were Mendel's results of so little consequence for so long? The comprehensive account of Mendel's life by Orel (1996) shows that Mendel's paper was not widely circulated, that Mendel largely gave up experimental work after becoming an abbot in 1868, and that he was not helped by his scientific confidant Nägeli, who failed to appreciate the significance of his results.

The enigma of non-discovery seems to have led some to search for new evidence of Mendel's impact on science before the 1900 'rediscovery'. Thus, in Philip Kitcher's (1982) *Abusing science* (p. 9), Michael Rose's (1998) *Darwin's spectre* (p. 33), and Robin Marantz Henig's (2000) *Monk in the garden* (pp 143–144), it is alleged that unread copies of Mendel's paper were found among Charles Darwin's effects. However, none of these authors gives a source for the information. A further dimension to Darwin's alleged knowledge of Mendel is given in Gabriel Dover's (2000) *Dear Mr Darwin* (p. 11), which refers to the 'mystery' of Darwin supplying Mendel's name for inclusion in the hybridism entry for *Encyclopaedia Britannica*.

Fortunately, Darwin's own library is conserved at Down House, in the care of English Heritage, and at Cambridge University Library, in the care of the Manuscripts Department. A listing of the entire extant collection of his books has been published in the first volume of *Charles Darwin's marginalia* (Di Gregorio and Gill 1990), the editors of which are currently compiling a second volume based on their listing of the extant copies of Darwin's extensive collection of journals and offprints of published papers. Mendel's name does not appear as an author in either listing. Furthermore, Nino Strachey, former curator of Down House, has noted the absence of any evidence that Darwin ever subscribed to the proceedings of the Brünn Natural History Society, in which the paper appeared (personal communication). This is not surprising, as the proceedings were not very widely circulated, as shown by the circulation list appearing in the front matter of each volume.

The question remains as to whether Darwin could have found out about Mendel by means of a secondary source. The references to Mendel published before Darwin's death in 1882 may be identified in the wider survey made by Orel (1996, pp 276–278; see also Olby and Gautrey 1968 and Keynes 2004). Among these sources Darwin may have had access to the Royal Society's Catalogue of scientific papers (1864–1873), being himself a fellow of the society. However, the catalogue gave no indication of the content of Mendel's paper and was published in 1879, only three years before Darwin's death.

It is possible that Darwin could have come across information on Mendel in his own library. Indeed, two publications in his library contain reference to Mendel; both are now kept at Cambridge University Library.

The first of these, *Untersuchungen zur Bestimmung des Werthes von Species und Varietät* by H Hoffmann (1869), was annotated by Darwin and cited by him in *The effects of cross and self fertilization* (1876). However, Darwin did not refer to Mendel in that work, nor did he annotate the references to Mendel in his copy of Hoffmann (1869). Furthermore, Hoffmann himself did not recognize anything exceptional in Mendel's results and was thus not capable of introducing his readership to their significance.

The second work, *Die Pflanzen-mischlinge*, by W O Focke (1881) was acquired by Darwin in November 1880, less than 18 months before his death. While Focke's commentary mentions Mendel's claim that 'constant numerical relationships' existed among the different phenotypes in what we now call the F2 generation, Focke took no special note of the "theoretical potential" of Mendel's work, which he ranked together with that of a host of other plant hybridisers. Furthermore, Focke considered Mendel's work with *Phaseolus* and *Hieracium* in greater detail than his work on that genus which underpinned the subsequent formulation of Mendel's laws: *Pisum*.

The solution to Gabriel Dover's 'mystery' of why Darwin "provided Mendel's name for inclusion in an article on plant hybridization for the *Encyclopaedia Britannica*" is provided by Darwin's copy of Focke (1881). On 13 November 1880, shortly after acquiring his copy, Darwin was asked by George Romanes to read through a draft entry on hybridism for the ninth edition of the encyclopedia and to suggest references (Burkhardt *et al* 1994, calendar No. 12814). Darwin, however, did not list the most influential works on hybridism as requested, but simply sent his copy of Focke's book to Romanes to "aid you much better than I can" (Burkhardt *et al* 1994, calendar No. 12814). Thus, Mendel was not afforded privileged status in this exchange. Even more significant is the fact that pages 108–110, in which reference is briefly made to Mendel's pea experiments, remain uncut in Darwin's copy of Focke (1881).

It is apparent that Darwin, like so many others at the time, was unaware of the significance of the segregation ratios that Mendel recorded from his pea experiments. Darwin habitually added marginal notes to passages that interested him, yet he made none in the section on peas and *Geum* in Hoffmann (1869), although he did in Hoffmann's brief and rather inexact section on hybridization in *Phaseolus*, a genus that did not show clear segregation ratios. Furthermore, Hoffmann's account of Mendel's work with *Phaseolus* was very brief and rather inaccurate.

In conclusion, we should remember that to know of Mendel's work in the second half of the nineteenth century was not tantamount to understanding it as the basis of modern genetics. The scientific community was extremely slow in realizing the significance of Mendel's work, probably because he himself was not capable of fully explaining the difference between his clear-cut findings with peas and his less easily interpreted results from crosses in other genera. Hence, even if Darwin had studied the results of Mendel's work, he may well have failed to appreciate their significance. The fact remains that Mendel's name does not appear in Darwin's published work, or in his correspondence. Indeed, as has recently been argued, it is quite likely that Darwin would have had difficulty accepting Mendel's work, which appeared to ascribe variation to the results of hybridization rather than natural selection (Gayon 1998, p. 288).

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