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HALDANE AT 125

J. B. S. Haldane: the John Innes years

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Introduction

J. B. S. Haldane worked part-time at the John Innes Horticultural Institution (JIHI) in Merton in Surrey, a London suburb, from 1927 to 1937. His appointment has been discussed in several biographical accounts (in most detail in Clark 1968; Harman 2004). Although the main outlines of this history are well known, this decade in Haldane's life is worth closer scrutiny. This was a transitional time for JBS. His position at the John Innes was on terms that prevented him feeling settled in his personal life and career. Intellectually, his time there straddles the divide between his Cambridge years (1923–1932), when he did his most important scientific work on population genetics and enzyme kinetics, and his time at University College London (UCL) (1932–1950s) when he concentrated on human genetics. Scientifically, his introduction to JIHI's long running studies of the ornamental plant *Primula sinensis* provided him with the material for his most important contribution to linkage theory (Pirie 1966; Dronamraju 1985, p. 49), and his contact with the Institution's cytologists inspiration for the first demonstration of the cytological basis of genetic interference (Haldane 1931). This group also inspired him to begin his search for possible partial sex linkage in humans (Haldane 1936a; Wright 1968, p. 9). The flower pigment research he introduced at JIHI 'did most, at least in England, to convince geneticists of the importance of the biochemical approach to genetics' (Caspari 1968; Dronamraju 1968; Fincham 1969, p. 454). Personally, friends said his acrimonious break with JIHI (a crisis he had to cope with soon after the death of his father) confirmed him in his anti-authority viewpoint and helped propel him into the Communist Party (Clark 1968, p. 101). Moreover, it is perhaps his idealized vision of what Bateson's Institution could have been that later provided JBS with the model for his planned research in India (Dronamraju 1985, p. 48).

Haldane's appointment

The John Innes Horticultural Institution was founded in 1910 following the bequest of a London property developer. William Bateson was the founding Director, beginning the work with just six scientists, supported by a garden staff of around 16, together with a 'pomologist' (a specialist in the genetics of fruit) and his assistants. Bateson's policy had been to appoint talented and promising young scientists on 'Studentships' rather than have higher paid permanent staff. In addition, numbers were increased by a floating population of temporary 'volunteer workers' who did (unpaid) scientific work and used the facilities. Bateson's sudden death in February 1926 'left English genetics looking very empty indeed' (Darlington 1966). The John Innes staff feared that the effect on their Institution would be worse than just emptiness. He had made JIHI 'into a nursery for the growth of the new subject' but had not been able to retain his ablest (male) staff, who with few job prospects at home, had emigrated to work in the botanic gardens and plant breeding stations of the Empire (Darlington 1965, 1966; Clark 1968). The core genetics group he left behind comprised of five (mainly women) researchers who had mostly been with him since the institute opened. There was no obvious home-grown successor to replace Bateson and to take over his group. The John Innes Council spent February looking at 'an exhaustive

list of the scientific workers' in Britain whose qualifications and experience were equal to filling Bateson's shoes. At the Linnean Society on 23rd March they concluded 'that one name—that of Sir R. H. Biffen, FRS, stands in a class apart from the other names before them' (Minutes of Council 1, pp. 152–153). For a while it looked as if Biffen, Director of the Plant Breeding Institute at the University of Cambridge, would accept their offer, and negotiations continued with him through to June. Finally though Biffen wrote to withdraw his candidacy.

Their immediate solution was to offer the post to Sir Alfred Daniel Hall, FRS, a member of the John Innes governing body, someone they knew well and could trust as caretaker of the institute. Hall had been a Director of Rothamsted Research Station, was architect of the agricultural and horticultural research policy inaugurated by Lloyd George's government in 1910, still an active advisor to the Ministry of Agriculture, and from 1930 also a member of J. Ramsay MacDonald's new Economic Advisory Council. Hall offered to work initially as 'Honorary Director' and 'have a look round each day' until he was ready to take up his post the following year (Minutes of Council 1, pp. 159–160). Meanwhile, he and his wife moved into the Manor House at Merton in August 1926. The appointment of Daniel Hall, one of Bateson's own generation, at least provided JIHI with some breathing space, though he lacked any specialist knowledge of genetics.

One of Hall's first acts as Director was to ask Council for an 'Assistant Director' post. 'Sir Daniel considered it essential that the Institution should obtain the services of a man of high quality in the study of genetics at a salary of £1000 or £1200 per annum' (Minutes of Council 1, p. 161). Council agreed and authorized him to look out for a man of proven ability, someone who could be expected to succeed to the Directorship of the Institution. Four months later in March 1927, on the advice of Julian Huxley, Hall recommended that Haldane should be

> engaged for Genetical work at £400 per annum and £200 expenses, the arrangement for the present to be: Mr Haldane to visit the Institution fortnightly for a day and a night during the Cambridge terms, to put in two months also at Easter and long vacations in two continuous blocks and to be free in the Christmas vacation (Minutes of Council 1, pp. 166).

Haldane continued this arrangement after he became part-time professor of genetics at University College, London in 1933, and was at JIHI for 10 years. The John Innes was now 'the most completely equipped organization in the country for the study of plant genetics, without reference to economic problems' (Hall 1929, p. 195), a caveat that nodded to the parallel existence of the Plant Breeding Institute at Cambridge. There is no doubt that Haldane's presence there in the 1930s helped establish the John Innes as 'the liveliest place for research in genetics in Britain', rivalled only by Francis Crew's Institute of Animal Genetics at Edinburgh (Beale 1997, p. 4). His reputation among students was boosted by his excellent lectures at UCL (where the more impenetrable R. A. Fisher was also lecturing at the opposite side of the quadrangle). And beginning in 1928 he also lectured on the biannual John Innes Summer Courses. These were designed to showcase the institute's research and methods in the 'New Genetics' to University students from all over the country. Though minute in effect to begin with, over the decade these courses helped make John Innes a recognized route for advanced training.

Though there were many promising aspects of his new post, from the start Haldane had to work within some serious constraints. To begin with he was never more than a transient resident at Merton and so was not able to personally supervise much of the day-to-day work of the institute. Then he had limited scope for hiring new staff. Already in 1929 JIHI's increasing salary costs (swelled by the introduction of a superannuation scheme), and the heavy cost of maintaining the experimental glasshouses and gardens, meant that money was tight. Salaries remained below average for the Ministry of Agriculture's research institutes, and this plus job insecurity meant (as in Bateson's day) it was difficult to retain staff. Even before the economic crisis of the early 1930s produced a fall in value in the investments that provided the Institution's income, vacancies were being left unfilled until the books could be balanced. The income available to the Director was further curtailed by the Council's decision to set aside some of the annual income for building up an emergency reserve fund (Minutes of Council 1, pp. 229–230). Overall in 1931–1932, Hall had to contemplate a £3,500 (17%) fall in annual expenditure: the garden budget was reduced, posts were cut and the remaining staff had to take pay cuts of from 3 to 7.5% (JBS had a 5% pay cut). But Haldane's most serious difficulty was that his authority over the scientific work and staff was divided with Hall (a situation that rankled and finally became intolerable, see below).

Some of Haldane's frustration with the administration of JIHI stemmed from structural problems inherited from Bateson's day. There were no formal 'departments', no written contracts or fixed retirement ages—a situation that came to dog the next Director. On the upside for staff, they had 'long years of peaceful and interesting work, without in any way being compelled to rush into print' (Cayley 1938, p. 301). Just after Haldane joined, the staff numbers were up to 15 scientific researchers (figure 1), boosted by around five 'voluntary workers' and seven 'visiting workers', with a garden staff of 38. The institute's annual income, (originating from the late John Innes's property portfolio) was around £20,500 (c. 1.23 M today), with 12 acres of plot land, and 2.5 acres of buildings: biology and chemistry labs, a recently added 'insectarium', a library and lecture room, nine greenhouses erected since 1910, and other buildings for plant growth, hardy and tender.

Figure 1. John Innes Staff at Merton, 1929 with A. D. Hall, Director (centre) and Haldane's chief coworkers Alice Gairdner and Dorothea de Winton (front row, second and third from left, respectively). John Innes Historical Collections.

Haldane, Bateson and genetics

Before looking in more detail at Haldane's career at John Innes it is worth recalling his early interest in genetics and his contact with Bateson, for this formed part of his credentials for a post in the field of genetics. His introduction to the subject as a boy in Oxford has been well documented (Clark 1968; Crew 1968; Mitchison 1968; Endersby 2007, pp. 231–239). His correspondence with Bateson is usually thought to have begun in March 1915 with a now famous letter on reduplication in mice written on active duty with the 1st Black Watch in France (Harman 2004, p. 55). However, there is a letter that is in likelihood even earlier (Bateson Letter H1A04; it is undated but c. 18th December 1913, addressed from Oxford). Haldane begins 'pardon me for writing', but he wanted to throw light on a point in Bateson's *Problems of genetics* (1913). It seems that early on JBS had fallen under Bateson's spell, and perhaps his attraction to JIHI was connected to the aura Bateson's Directorship had cast over it. On his return from the war JBS went on to publish six genetics papers while a Fellow of New College, Oxford (Pirie 1966), and he was one of the 26 interested people who gathered to found the new 'Genetical Society' in the summer of 1919, giving one of the first presentations (Genetical Society Minute Book). This was probably the first-time Haldane met Bateson in person (although the John Innes Visitor's Book (1910–1949) records a 'J. Haldane' as visiting the Institution on 27th March 1919), and JBS knew Bateson until his death (Haldane 1926). 'He could be described as an angry and obstinate old man', Haldane recalled, but he found him still an inspiring thinker. Bateson combined a 'characteristic

anger with my ignorance with great generosity in helping me … to me at least he showed no signs whatever of a senile failure of original thought' (Haldane 1957, p. 16). A man 'never for half-measures or compromise' (Morgan 1926, p. 532), Bateson was a personality Haldane clearly appreciated.

Early on Haldane made his mark in the Genetical Society. At the fourth meeting in April 1920 he gave a communication on 'Sex ratio and unisexual sterility in hybrids' after which Bateson (who JBS credits as the first person to believe the generalization) congratulated him from the Chair for his detection of 'a new and remarkable principle' which others at the meeting began to refer to as 'Haldane's rule' (Genetical Society Minute Book). Bateson closely mentored him as he prepared his sex ratio paper for publication, counselling him on the difficulty of getting accurate documentation, and instructing him in which sources to trust (Bateson Letters, G2H01-G2H05). Haldane visited the John Innes with the Genetical Society at their meeting there on February 14th 1920, an opportunity to see at first-hand the work Bateson and his staff were doing on primulas, plums and mosses. In these early years Haldane attended Society meetings regularly, his contributions including presentations on the genetics of poultry and rabbits (1923), but he had stopped going a year or two into his appointment as Reader in Biochemistry at Cambridge until drawn back to the fold by Bateson's death. It was only after his appointment at John Innes that he joined the leadership of the Genetical Society, as a committee member in 1930, as one of three Vice-Presidents in 1931, and finally as their elected President in 1932–1935 (figure 2).

Haldane and his John Innes colleagues

Haldane had already been introduced to his colleagues, in imagination at least, by 'the boss' (William Bateson) one morning in 1925. Bateson had heard about Haldane's (temporary) dismissal from his Readership at Cambridge for sexual misconduct and wanted to share his opinion that a man should not run 'about the streets like a dog' (Darlington 1966). Whatever interest Bateson had shown in the youthful Haldane, he found the adult unsettling; Haldane had even haunted his deathbed delirium: 'Haldane … Haldane, a most disagreeable ingredient in an afternoon's entertainment' (Bateson 1974, p. 19).

When news of Haldane's appointment as the new head of genetical experiments filtered through to the Institution it was his reputation as a biological chemist that preceded him. His qualification to lead the genetics research was not so obvious to the younger staff who thought it 'quaint' to put a chemist in charge of geneticists (Chittenden 1927). Looking back from the 1970s Darlington recalled Haldane's appointment as a gamble: 'They knew that he was interested in the mathematics of genetics and evolution, but he had no connection with horticulture and never proved to have any understanding of it' (Darlington 1979). At the time though his younger colleague regarded him as a 'saviour', the institute would not now disintegrate 'sheltered by his powerful figure', and the feeling was of 'intense relief' (Darlington 1966).

Darlington became his closest colleague; more than that, Darlington regarded Haldane as his 'infallible mentor' (Harman 2004, p. 121). Haldane sat in the desk next to him in the cytology lab:

> I was drawing chromosomes. He was doing sums. Thousands of sheets he covered. No plants, no microscopes for him. No calculating machine, no slide rule, no logarithms even. All long division sums. (Darlington 1966)

In the 'care-free' summers of 1930 and 1931 they went off to holiday in the Tyrol, travelling first-class in England so that JBS could write. Walking 12 h and climbing a thousand feet per hour Darlington recalled JBS's unsurpassed powers of walking—'It nearly killed me' (Darlington 1966).

JBS's exchanges with other colleagues showed his playful side, among them joke experimental reports, shared poetry and even a spoof examination paper (Haldane 1935), a selection of the questions is given here:

> Genetics (Special)
>
> 2. Discuss the genetics of local races, illustrating your answers from the University boat race. Account for the dominance of light blue over dark blue.
> 5. What evidence would be required to convince Professor McBxxxe of the non-transmission of acquired characteristics?
> 7. What methods do you suggest for the biological control of the Drosophila pest in genetical labs?

Our picture of Haldane's research at the John Innes is coloured by Darlington's memoirs, but it is possible to give a more rounded account from fragments in the John Innes Centre Archives. These confirm that he had little in common with his colleagues' working methods. Haldane with his pencil and sheets of mathematical calculations; the plant geneticists with their plots, scores and crossing experiments; the cytologists with their microscopes, chemicals and microtomes, fixing and staining the chromosomes. Colleagues remembered him as very definitely not an experimental scientist. Even in biochemistry (the field he was still employed in at Cambridge) the biochemist he appointed, Rose Scott-Moncrieff, remembered him as 'at no time contributing any practical work' (Scott-Moncrieff 1981). As a supervisor in the plots he was not any more involved. Geoffrey Beale remembered his encounters with Haldane as brief and uncomfortable: when he would point out individual plants in his plot, JBS would 'make some

Figure 2. Genetical Society Meeting, 1936. John Innes Horticultural Institution, Merton. Haldane is the third person seated on the left of the person who is standing. John Innes Historical Collections.

critical remark, or no remark at all, and then stump off without a word' leaving Beale bewildered (Beale 1997). Another colleague described him as 'an onlooker in the field of practical genetics' (Lawrence 1980, p. 32). Only in the 'Ladies Lab' did he seem to give any direction, with instructions on which plants to cross.

Here his closest collaborator was Dorothea de Winton. The 37-year-old Dorothea had joined the Institution in 1920 with no training as a geneticist but had experience working as a professional gardener, wishing to learn about the 'research side'. Bateson put her to work on *Primula sinensis*, a plant introduced into England in 1819 and 1826, with no known parent species in the wild state but a great range of variation in the cultivated forms that had arisen since its introduction. Her work on tetraploid forms built on the research of Reginald P. Gregory between 1910 and 1918, one of Bateson's original 'volunteer workers'. She began her linkage studies as a technical assistant to Bateson. The year JBS joined, Dorothea presented her work at the International Genetical Congress in Berlin. By now she was an acknowledged expert on the plant and on her way to being recognized finally as a 'Geneticist' at JIHI in 1929. Haldane, like many other new students, would have appreciated Dorothea's years of breeding work with *P. sinensis* and (by the end of her research) her knowledge of the 40 mutants, half of which she had discovered herself (figures 3 & 4). Her expertise and meticulously kept records were the basis of Haldane's linkage studies with this plant (De Winton and Haldane 1931, 1933, 1935). Over time he formed the opinion that she was an 'Excellent technician, not capable of very original work, but a most valuable subordinate'.

Haldane's other main coworker in plant genetics was Alice Gairdner, nearly 20 years his senior. She joined JI as a 'Student' in 1919; little is known about her background, but she was one of the small group of 'Mendelian' followers Bateson had cultivated at Cambridge, where she had worked on leaf variegation in *Tropaeolum* (Nasturtium) in the early 1910s. Collaborating first with Bateson and later with JBS, Alice worked on the inheritance of male sterility in *Linum* (flax). She was one of the first to introduce cytological determinations into genetics at JIHI and by 1929 had progressed from 'technical assistant' to 'Cytologist to JIHI'. In *Cheiranthus* (wallflowers) Alice studied the inheritance of doubleness, leaf and flower colour and height. The pigment problem proved complex and by 1933 Alice was collaborating with Haldane and Rose Scott-Moncrieff, which led to a joint publication in 1936. In

Figure 3. *Primula sinensis* glasshouse, c. 1930s. John Innes Historical Collections.

Figure 4. (a&b) *Primula sinensis* record cards. Two examples from Haldane and De Winton's meticulously kept collection, John Innes Historical Collections.

Antirrhinum (snapdragons) she studied the inheritance of leaf colours, albinism and height; the *Antirrhinum* work culminated in two papers with Haldane on balanced lethal factors (Gairdner and Haldane 1929, 1933). Haldane's private verdict on her abilities was 'Very good for her age, but has very little initiative'.

Apart from these two coworkers Haldane struggled to make his mark on plant genetics at John Innes. This was in large measure down to the ethos carried over from Bateson's days, as Darlington put it '[The research workers] work chiefly on their individual initiative rather than by group collaboration' (Darlington 1932a). Haldane submitted a bitter memorandum summing up his problems to a committee of the John Innes Governing Council in the summer of 1936. There is some humour too in the entry he gives himself in the document: 'J. B. S. Haldane. Nominally head of genetical work. Actually controls genetical work of Miss de Winton and Mr. Beale. Otherwise gives advice'. For some of the staff even advice was not readily taken: the botanist E. J. Collins 'refuses to co-operate with

me in any way'; geneticist Irma Andersson-Kotto 'Very good and original, but difficult', 'Does not need or desire assistance' (Minutes of Working Sub-Committee 1936); Caroline Pellew, working on the genetics of *Pisum* also remained resolutely independent. Nevertheless, Haldane's arrival had changed the Institution, where 'many of the genetical and cytological problems have been subjected to closer mathematical treatment under the direction of Professor JBS Haldane' (Darlington 1932a). Haldane in turn used JIHI to gather a new repertoire of plant examples for his genetics theorising. His lectures on the *Causes of evolution* (Haldane 1932a) show his debt to his colleagues' unpublished work and his discussions with them.

Haldane had also introduced a vibrant biochemistry section to JIHI's work (Rose Scott-Moncrieff and an assistant). In this Haldane made a pioneering contribution—by his own later assessment perhaps his 'most important contribution to biochemistry' overall (Haldane 1937, p. 4). Not only was it his inspired idea to bring together Scott-Moncrieff with Professor Sir Robert and Lady Gertrude Robinson at Oxford to study the methods of isolating and qualitatively testing the anthocyanin plant pigments (developing the essential tool kit for biochemical testing at Merton), but he introduced her to JIHI's geneticists and the extensive genetical material there—combining two distinct disciplines. 'Pigment genetics' was not new but Haldane was original in appreciating the potential of this (at the time novel) approach, and he actively encouraged and contributed ideas throughout the course of their research. Haldane lectured and published extensively and built theories on their findings, and 'kept closely in touch with our work' (Scott-Moncrieff 1981). These beginnings in the biochemical study of gene action have recently been reviewed by Cathie Martin, who reminds us that Scott-Moncrieff's 1931 article, 'clearly established the concept of genes determining enzyme activity and was supported by considerable additional research on the biochemical/genetic determinants of flower colour, well before Beadle and Tatum's seminal 1941 publication' (Martin 2016). For many English biochemical geneticists, their work became essential reading (Fincham 1969). Haldane summed up much of the JIHI work in a chapter in his book *New paths in genetics* (1941).

Haldane's domain did not extend over the pomology or cytology sections of JIHI, although he maintained a friendly interest, particularly in the young Darlington, and encouraged and supported where he could (Harman 2004). One feels that Darlington's biographical memoirs overplay Haldane's isolation from his coworkers. Differences in style of working aside, his was not an intellectual isolation: looking at his publications, e.g. we find Haldane making connections between his genetical observations on *P. sinensis* and his colleagues' cytological work on the behaviour of chromosomes (De Winton and Haldane 1931); using Crane and Lawrence's work on *Prunus* and *Rubus* as examples in a discussion of time in the action of genes (Haldane 1932b); and invoking Darlington's *Recent advances in cytology* (1932b) in a discussion of recurrent mutation in evolution (Haldane 1933). Darlington, in turn, was drawing on Haldane's work, especially between 1931 and 1932 when Haldane freely gave Darlington ideas and access to his articles in press. Darlington also received Haldane's help with his *Oenothera* paper (a key publication for Darlington)–Haldane contributing a mathematical appendix on the number of possible pairing types in the genus and a mathematical theory of ring formation in general (Darlington 1931; Harman 2004).

However, JBS did begin to move on after his appointment as part-time Professor of Genetics at UCL in 1933; his publications mark his growing involvement in human genetics, and in commentary on eugenics (Pirie 1966). The last plant papers he worked on at JIHI saw him uncharacteristically involved in botanical fieldwork (as if to answer his younger colleagues' criticisms). In these he focussed on heterostyly in natural populations (Haldane 1936b, 1938), a subject that had interested Darwin, and more recently E. M. East and R. A. Fisher. Haldane studied five natural populations of the trimorphic *Lythrum salicaria* in August 1935, counting three populations of plants found within a length of about 500 metres in the Lake District, and two populations in accessible spots over about 8 km of river valley in Wiltshire and Dorset, 3770 plants in all. He followed up with natural populations of *Primula acaulis*, counting 2302 pin and thrum plants at 17 mostly roadside locations in Wales and southern England.

Daniel Hall and Haldane's departure

Haldane's departure from John Innes was the culmination of his difficult relationship with the Director Daniel Hall. Initially it seemed that Hall was working hard on Haldane's behalf. In June 1929 Hall began negotiations with the University of London to try to create a full-time post for Haldane. The Institution was already regularly visited by the London schools of botany and these student opportunities were supplemented by occasional scholarships to provide training in plant breeding. Hall wanted to see a more regular flow of postgraduate students and a closer relationship with the University. To secure the appointment of JBS as a 'Professor of Plant Genetics', alongside Readers or Lecturers in Plant Cytology and Taxonomy, he suggested that the University part-fund the posts in partnership with JIHI. Two years later he courted the Rockefeller Foundation to see if they might secure funding for the posts.

An undated draft [c. 1932] from JBS in response to Hall's scheme reveals something of his discomfort (Haldane 1932c):

> I should like to discuss it with you some time, but that would be a long job. I do not care for the scheme as it stands, and do not think it is

> workable. The Professor of Genetics must be able to control the conditions under which his plants are kept, and (at least to some extent) the research personnel. This would not be possible unless the Professor were also Director.

Haldane attempted to be more diplomatic in his finished letter where he wrote: 'If it is proposed that a professor of genetics should be other than the director, it is essential that the relations of the two should be defined'. But he still could not conceal his irritation:

> As things stand the professor would have no control over the conditions under which his plants were kept, and very little over the research personnel under him. Such a situation is all very well for a couple of years, but could not work permanently. (Haldane 1932d)

Haldane did not want the extra PhD students—he had experience of this at Cambridge and found it 'exhausting' dealing with 'scattered researchers', far easier to give a course of lectures and demonstrations than the close supervision, that in his view, junior colleagues might be better suited to manage. Nor did he want a full-time Professorship 'I could only give about 2/3 of my time'. However, JBS did want the Directorship, and all this time he had expected to succeed Hall. Because of definite promises that Hall would resign in 1934 he had refused several posts that had been offered to him. The Council Minutes reveal that in 1936 a 'relation of Professor Haldane' had even made a personal appeal to Council to raise the matter of his invidious position (Minutes of Council 2, p. 263).

Hall, however, stayed on in the Manor House, and in the background, Lady Hall was apparently determined that Haldane's wife would not take possession of the Manor if she could prevent it. Darlington revealed that the first meeting of the couples, one weekend in 1927, had been disastrous, 'the scene was a very terrible one' (Darlington 1979); the wives had disliked each other ever since. But JBS's promotion must also have been blocked by the John Innes Governing Council. Time and again Hall's appointment was renewed with their unanimous support, while discussion of Haldane's succession was repeatedly deferred. Haldane's negotiations with Council did not go well. In November 1935 he had been invited (as presumed next director) to give his views on the future use of the Manor House and another JIHI property, Merton Cottage. JBS proposed taking over the ground floor of the Manor House and having the upper floor converted into bedrooms and a common room for 'junior male workers'. It is a sign of the times that he envisaged that both floors would be allocated a servant to cook their breakfasts and suppers, clean rooms and do the laundry (very like a Cambridge college). 'Merton Cottage [a smaller, darker property] would not, I think, be a suitable residence for the Director'. But the Council ignored Haldane's wishes: moving in to the Manor House was not an option for him, he would be offered Merton Cottage only, a decision that must have rankled.

Council had also asked JBS to prepare a document setting out how he saw the future development of JIHI. In response Haldane submitted a memo on 23rd July 1936 taking stock of the staff on the payroll and giving his frank assessment of each in turn (Minutes of Working Sub-Committee 1936). He then itemized eight areas where he felt the organisation was falling short—his lack of control over the genetics work, already discussed, being his principal complaint. The solution he offered was a reorganization of staff so that intensive work on a smaller number of plants, with each staff member working on a different aspect of each, was undertaken. Some new appointments would be required. However, he added 'It seems to me entirely futile to attempt any serious reconstruction so long as the present Director remains'. Hall, JBS protested, did not keep his promises, and the scheme of dual control was not working. Without sparing any blushes Haldane delivered Council his verdict on the Institution's overall performance: 'I do not hesitate to class most of the genetical work done at the Institution as second-rate. It conforms to no plan, and is not in general inspired by modern ideas'. Burning his bridges, he concluded by telling them that he had written to the Agricultural Research Council asking them to set up a new place with land for 'serious genetical research in the neighbourhood of London' since JI was incapable of reform under Hall (whose reappointment for another three years had just been confirmed [in May 1936]).

Haldane's official report on the genetics work for 1936 was only 12 lines long (Annual Report 1936), and news of the contents soon got back to the staff. The Institution's secretary Brenhilda Schafer summed up its damning commentary in verse (Schafer 1937):

> Professor H …'s report to the Council (verses 2–4) by Brenhilda Schafer 1937
>
> I have no wish to shirk
> An admission quite plain,
> The genetical work
> *Is cauld kale het again**
> In ideas we are sadly deficient,
> Which the same I am free to maintain.
>
> The work may be sound,
> But I haste to report
> No results have been found
> Of outstanding import;
> Which state of affairs will continue
> While it's nobody's job to take thought.
>
> But I have you on toast
> For I shall not retire
> Till I'm offered a post
> At the same pay or higher:
> And a person of my reputation

> You haven't the courage to fire
>
> (*Literally cold cabbage reheated, a colloquial expression for nothing new or original)

The 'Special Committee' appointed by Council to consider Haldane's and other staff grievances reported on 26th November 1936. They showed that they understood the structural problem of his part-time appointment:

> This arrangement, though at the time it promised to be satisfactory, was in fact unfortunate. It left the oversight of the most important work of the Institution to a part-time officer who did not share in the actual work of plant breeding as Bateson had done, and whose supervision took the form of such suggestions and criticisms as were possible during occasional visits.

This difficulty was compounded by Hall's frequent absences from the Institution on other work which meant that their meetings were very few. The Committee concluded that although the immediate cause of Haldane's protest was his disappointment at not succeeding to the Directorship in 1936, the foundation of this crisis was laid earlier—for a long time Haldane and Hall had not been communicating. 'As a result of recent incidents' the Committee judged 'it would be impossible for Mr. Haldane to remain a member of the permanent staff' under Hall. 'Fortunately, circumstances have arisen which, quite apart from the relations now existing between him and the Director, should lead to his early resignation. A Chair [the Weldon Chair of Biometry] is about to be created by University College, London, which we were informed he will certainly be selected to fill'. The Committee advised that they should bide their time (Report of Special Committee). Although the part-time appointment was now considered 'unsatisfactory' on both sides, Council decided not to sack Haldane. As well as hoping he would soon leave on his own accord they wanted to retain 'amiable relations' with Haldane after he'd taken up his new duties. With one of the (unspecified) chief projects on which JIHI had worked, Haldane's advice had been 'freely sought, freely given and very highly appreciated'. They had no evidence that his relationship with staff members was anything otherwise than friendly. It was in the interests of both JIHI and UCL that friendly relations continued. Antagonism would only hinder the progress of British genetics.

Haldane had already attended an interview with the Committee at which he was not left in any doubt that they intended to hire someone else to be the full-time geneticist at John Innes. They even asked him to suggest possible candidates, a request he refused to help with, 'he was emphatic … no first-rate Geneticist was available' (with one possible exception, 'an entirely unsuitable suggestion' (Report of Special Committee, p. 5). How JBS dealt with this misfortune is glimpsed through Darlington's memoirs. His 'proud, resolute and lonely character never allowed him to reveal distress'. But nevertheless, over the years as Hall became more deeply dug in at JIHI 'the more aggressive Haldane became' (Darlington 1966). JBS came as frequently as ever but was more and more impatient about his lack of promotion and about the administration. During his last two years he 'made no secret of his discontent' among the staff (Schafer 1938). He felt himself to be the injured party, telling Beatrice Bateson that he was being 'forced to leave this place' by Hall's behaviour; her circle was equally sure that JBS's conduct had played a large part in the debacle (Beatrice Bateson Letters 1937). Finally, he resigned on 1st October 1937, and withdrew from the Institution in 'high dudgeon, literally shook the dust off his feet' (Darlington 1979, p. 21). By this time other factors were also at work. The world outside was beginning to darken and Fascism was on the march: '[JBS] was, in his unexpressive way, deeply sensitive to that' (Darlington 1966).

He had one last arrow to fire at John Innes. He submitted a memo to the Chairman of the University of London's Visitation Committee, Dame Helen Gwynne-Vaughan, laying his grievances out again in detail (Haldane 1936c). Firstly, his lack of control over experimental material, from losing valuable pedigree plants through the carelessness of the horticultural staff, to having no say over the proliferation of new projects, sometimes on plants that 'appear to me to be very unsuitable for genetical work'. Secondly, it was impossible for him to plan for at least three years ahead. His plans for the numbers of plants to be grown had been suspended by the Director, another crop grown in place of his experimental plants, all without consulting him. Thirdly, he complained of 'having no control over research workers' or their record keeping ('I cannot even get them to keep notes in a form intelligible to themselves, let alone to their successors ...'). Finally, he had no control over appointments and the turnover of junior research workers was 'impossibly rapid'. For example, on the plant *Lathyrus* (sweet pea), in seven or eight years the work had been under six different researchers, none of whom had time to become proficient with it: 'in consequence irreplaceable material has been lost'. His overall verdict: 'At present the Institution is in a state of hopeless indiscipline', his example the behaviour of junior colleagues who he'd found playing ping-pong in the laboratories among the valuable microscopes. Haldane's parting shot was that 'if genetical research is carried on at Merton under the auspices of London University the standard of research set in the university will definitely be lowered'. With that he was off to Spain 'for the same reason which led me to join the British army in August 1914. I wish to defend a foreign nation against German aggression, and to prevent the conquest of Europe by a power hostile to my own country ... I may not return'.

Conclusion

Haldane and the John Innes years: a reassessment

Haldane's 'John Innes' period is often viewed through Darlington's lens, and as such is cast as a relative failure or a missed opportunity. I've attempted instead to show where Haldane focussed his energy and where he successfully made connections with the cytology, genetics and biochemical work going on around him. The biochemical work he introduced at JIHI was of crucial importance, providing a window for his more speculative views on the nature of the gene and gene expression. Haldane may have had little feel for horticulture, as Darlington claimed, but his colleague underestimated Haldane's practical understanding of genetics, honed originally not with plants but with generations of guinea pigs and mice. He understood the importance of genetic stocks, the length of time it took to really 'get your eye in' with any new plant or organism, before it was possible to spot slight variations and mutations. Two of his repeated complaints were that mismanagement at John Innes had on more than one occasion endangered the survival of precious genetic stocks, and that too many lines of work were started without his permission, on too many plants. Both comments stemmed from his respect for the plant geneticists' skill, and his understanding that a thorough knowledge of even one plant species took 'at least 3 years' to attain. His own knowledge he admitted extended only to two or three plant species.

Certainly, there were aspects of Haldane's character and working methods that made him a difficult 'fit' for his nonmathematical colleagues. It is interesting that he did not try to found a mathematical or population genetics group at John Innes (as the younger Kenneth Mather did when he was appointed Head of Genetics to succeed Haldane). His output over these years encompassed an astonishing variety of subjects, ranging from rodents, gastropods, Eland-ox hybrids, and humans, as well as plants. One wonders what the John Innes Council made of his inclusion of his work on human blood groups in the *Annual Reports* of their 'Horticultural Institution'. Overall, Haldane had over 56 publications as single author and 15 as coauthor in the list of John Innes staff publications between 1927 and 1935; only one other employee, C. D. Darlington, was as prolific. At home and abroad he was collecting accolades, including his election to FRS in 1932, his citation acknowledging contributions to no less than five branches of biology. Haldane's own 'obituary' for the *Daily Worker* (1964): 'Please don't think I have done nothing but mathematical theory, I have done some animal breeding, some plant breeding, and at least worked out a few human pedigrees of various abnormalities' suggests he was proud to include the plant work at John Innes as part of his scientific legacy.

Additional material

Transcript of Haldane's letter to William Bateson, December 18th [1913?]

[Written on Oxford Union Society notepaper]
December 18th

Dear Professor Bateson

I trust you will pardon me for writing, but I thought that I might conceivably be able to throw some sort of light on the question which you raise in "Problems of Genetics" p. 45, as to "how it is that neither of a pair of twins has transposition of viscera".

Though cells and other organisms are themselves often symmetrical, yet the proteid and carbohydrate molecules of which they are largely built up, are all, or almost all asymmetrical, and rotate the plane of polarized light. Even so apparently symmetrical an organism as a mould may show its fundamental asymmetry by the fact that it can only break up one of a pair of sugars, the molecule of each of which is the "mirror image" of that of the other. Hence, even if to outwards appearance one of a pair of twins were the complete "mirror image" of the other, it could not be so throughout, since if the ferments molecules in it were the "mirror-images" of those of the other, it would be incapable of digesting its food. This would undoubtedly have been the fate of Mr. Plattner, who, in H. G. Wells's story, was blown out of space into the 4^{th} dimension by an explosion, and returned as the "mirror image" of his former self.

Hence I suggest that perhaps at least one source of the asymmetry of organisms is to be found in the asymmetry of their constituent molecules. On this view the symmetry of cell or nuclear divisions is not something [fundamental?], but either due to the unimportance, when dealing with masses of molecules, of the asymmetry of the individuals, or else adaptive.

As we do sometimes get inversion of viscera in these cases, it looks as if the asymmetry were here partly due to the visible structures, partly only to the invisible molecules.

I fear I have explained myself very badly; of course, mere asymmetry of the molecules is not sufficient; we must have one of an enantiomorphous pair present alone or in great excess, & this we do.

I offer this suggestion, in all humility, for it certainly does not take us far, and you probably know facts which render it quite worthless. So please don't trouble to answer this note. I hope to have 2 papers for the Journal of Genetics in summer, one on guinea pigs, where I have got 2 fresh factors, and one on mice, where I am working at a case of reduplication (partial repulsion).

Yrs v. sincerely
J. B. S. Haldane

Haldane's FRS election citation

'He has contributed to our knowledge of acid–base equilibrium in man and of the causes and effects of alterations therein. The work has led to the therapeutic use of ammonium chloride in tetany, lead-poisoning, etc. He is the author of other papers on biochemical subjects and of a valuable monograph on enzymes. He has worked both experimentally and theoretically on plant and animal genetics. His discoveries in this latter field include the first case of autosomal linkage in vertebrates and a general law regarding the sex of hybrid animals. In a series of papers on the mathematical theory of natural selection he has developed some

of the consequences following logically from Darwin's hypothesis'.

Election proposed by: A. D. Hall; R. C. Punnett; R. H. Biffen; G. Udny Yule; R. A. Fisher; A. V. Hill; C. S. Sherrington; E. A. Milne.

Elected FRS: 5/05/1932; Darwin Medallist 1952; Croonian Lecturer 1946.

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