FEATURE

What Henslow taught Darwin

How a herbarium helped to lay the foundations of evolutionary thinking.

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The kindly Professor John S. Henslow of Cambridge, well known for arranging Charles Darwin's berth on HMS *Beagle*, was also a rigorous researcher who recorded patterns of variation within and between plant populations and was motivated to understand the nature of species: the big question of natural history as he saw it. The focus of Henslow's research is evident in his herbarium at Cambridge, which holds 3,654 sheets of British plants that he began assembling in 1821. These sheets represent 89% of the species that Henslow recognized in his 1829 *A Catalogue of British Plants*. We have analysed all 10,172 plants on these sheets and infer that he intentionally organized his dried-plant collection to serve as the tool for an inquiry into species and their limits.

Henslow's research on this fundamental question was at its peak during the three consecutive years Darwin attended his lectures (1829–31). Darwin's exposure to his mentor's thinking was part of the exciting intellectual framework that he took with him on the *Beagle*. Indeed, his scientific manuscripts show that direct contact with Henslow provided the context not only for Darwin's botanical studies but also for his comprehension and very acceptance of evolution.

Henslow was a creationist, but with a major difference: he set out to explore the nature of created species as stable entities. Elected professor of botany in 1825, he had already held the chair of mineralogy since 1823. As early as 1821, however, Henslow began establishing a herbarium of British flora. This grew so quickly that by 1829, Darwin's first year as a botany student, Henslow had published the *Catalogue* illustrating his understanding of species.

The herbarium was the product of Henslow's own collecting in Cambridgeshire and Kent, with major contributions from his family, his friends, and most particularly from the Lancashire solicitor William Wilson. His network included the leading botanists W. J. Hooker of Glasgow and J. H. Balfour of Edinburgh, about 60 collectors strategically deployed to capture floral diversity, and eventually about 30 of his own Cambridge students. One such student was Darwin. On his geological excursion to North Wales with Professor Adam Sedgwick in the summer of 1831 — just before he received the invitation to join the *Beagle* voyage — Darwin collected *Matthiola sinuata* for Henslow. This is the oldest known herbarium specimen collected by Darwin (Fig. 1).

Figure 1 | *Matthiola sinuata*. Herbarium sheet collated by J. S. Henslow from three plants collected by Charles Darwin in 1831 at Barmouth, North Wales, and a single plant collected by Miss Blake at Braunton, Devon. This is the earliest-known herbarium specimen collected by Darwin.

The distinctive feature of Henslow's herbarium was his practice of comparing specimens, which he called 'collation'[1]. A collated Henslow sheet carries several plants of a single species from one or more locations, each typically numbered directly on the sheet, with a label recording location, date of collection and collector's name. Collated sheets usually carry two or three plants, but there may be as many as 32. Two-thirds of the sheets are collated and 90% of these show variation in height, leaf shape, branching pattern or flower colour. Collated sheets that show height variation have several distinctive display patterns, such as bell curves and ascending/ descending series (Fig. 2, overleaf). They can depict continuous variation within a single population, or may include plants from across Britain.

Organized approach

Thus Henslow was not just identifying plants: he was organizing his herbarium to emphasize variation within species. Remarkably, he seems to have been the only British botanist at the time doing this. We have surveyed the herbaria of C. C. Babington, J. H. Balfour, William Borrer, W. A. Bromfield, John Downes, R. K. Greville, W. J. Hooker, Leonard Jenyns, W. A. Leighton, N. J. Winch and William Wilson. Henslow's fellow botanists seldom placed more than one plant on a sheet and none practised 'collation'. In Henslow's hands, however, plants received from these same people were collated in a comparative display that illustrated natural variation. This rigorous attention to variation throughout the 1820s was unique to Henslow.

The aim of collation was to analyse the limits of variation within 'created' species. Indeed he was conforming to the orthodox species concept, which included the idea that species only have the capacity to vary within limits[2,3]. But Henslow recognized that the inherent tension between the stability and variability of species posed a major problem[4]: "Our knowledge…has not been hitherto sufficiently advanced, to furnish us with any precise rule for distinguishing the exact limits between which any given species of plant may vary." What distinguished Henslow's practice from that of his contemporaries was his intention systematically to turn the creationist species concept into a precise instrument of scientific analysis. This difference of approach may have arisen because Henslow had originally been a physical scientist — a professor of mineralogy who applied the rigour of contemporary crystallography to the species problem[5]:

> *…[botany] is pretty much in the position which mineralogy occupied before the discovery of the laws of crystallography; mineralogists were frequently in the dark as to what crystals were to be included under one species, and they knew almost nothing of the numerous forms in which any given species might occur…But now, a single crystal at once puts the mineralogist in possession of the primitive form of the species, and he can calculate 'a priori' the possible forms under which it may occur.*

Henslow is referring here to the revolution in crystallography articulated by Haüy[6], who showed in 1801 that complex crystals could be understood as transformations of 'primitive' crystal forms. So when Henslow moved from mineralogy to botany in 1825 he sought a similarly rigorous means to define the natural lines of cleavage within and between plant species. Consequently, in an age of 'splitters' who proliferated new species on the basis of slight differences, Henslow tried to make a precise science out of 'lumping'. He saw varieties where others distinguished species and it was his own collated herbarium that gave him this view. The summary of Henslow's collations was *A Catalogue of British Plants* and the results are most clearly recognized in the 1835 revision, in which he demoted 100 species to the rank of variety. He was thus able to challenge the authority of the great taxonomists of the day: J. E. Smith, A. P. de Candolle, W. J. Hooker and John Lindley.

What Darwin learned from Henslow

What part did Henslow's research play in shaping Darwin's concept of species and his eventual shift to evolution? Darwin learned to read rock formations during his geological tour with Sedgwick in the summer of 1831. Did he also learn to 'read' species from Henslow over the previous three years? We can be sure that Darwin was exposed to Henslow's mode of thinking about species, with its emphasis on discriminating varieties, because this perspective appears in *Principles of Descriptive and Physiological Botany* (1835), the textbook Henslow based on his lecture course. More importantly, Henslow wove his own research into his teaching. His 1829 *Catalogue* became a set book for his course. In this work, all Cambridgeshire plants were marked for the students in Henslow's classes, who dissected fresh flowers collected on field trips. The *Catalogue* was published in October and so was in preparation when Darwin took Henslow's botany lectures for the first time.

A further attempt to determine the natural lines of cleavage in species came in 1830 — Darwin's second year of botany. Henslow showed that, by manipulating moisture, manuring and shade in garden-grown primulas, he could experimentally reproduce morphological variants observed in the field[4]. Again, the stability of created species is the assumption underlying this work. Henslow supported the linnaean analysis of *Primula veris* with its three varieties: α *officinalis* (cowslip), β *elatior* (oxlip) and γ *acaulis* (primrose) in opposition to J. E. Smith's more modern 'splitting' view. Smith distinguished two separate species: *P. vulgaris* (primrose) and *P. veris* (cowslip) and inclined to the opinion that the oxlip was a hybrid, which he called *P. elatior*, that "originated from a Primrose impregnated by a Cowslip"[7,8].

Darwin's absorption of Henslow's research activities is seen in his awareness of an immensely important observation that Henslow made during his *Primula* studies — but that he never published. In April 1826, Henslow collected local cowslips and oxlips. He drew whole flowers of each and, more significantly, details of their stamens and ovary (pistil) in half-flower sections. He depicted styles of different lengths in different flowers and also showed the associated differences in anther insertion height. These are what we now refer to as the 'pin' and 'thrum' forms (Fig. 3). Remarkably, he also depicted a form of oxlip flower with short styles and low anthers — the rare short-homostyle form. These drawings, recently discovered in Cambridge, were original observations not known to British botanists.

Stirring memory

Darwin repeated Henslow's *Primula* experiments during the 1850s in the run-up to *On the Origin of Species*, and then, in May 1860, he rediscovered the two flower forms in cowslips[9]. Vaguely remembering that Henslow had seen the same thing three decades before, he wrote to J. D. Hooker[10]: "I have this morning been looking at my experimental Cowslips & I find some plants have all flowers with long stamens & short pistils…others with short stamens & long pistils…This I have somewhere seen noticed, I think by Henslow." But Henslow never published on the lengths of *Primula* pistils, although he did literally notice the different forms. Nowhere in the scores of *Primula* specific-identity articles published between 1830 and 1860 were these different flower forms noticed. Darwin could only have been remembering the cowslip and oxlip drawings that Henslow had shown him when he was a student. Darwin ultimately interpreted the forms of *Primula* flowers as a complex outbreeding mechanism (heterostyly)[11,12]. But, more importantly, the way he remembered Henslow at the moment he 'discovered' heterostyly demonstrates a hitherto unsuspected familiarity with the heart of Henslow's research.

Much of what Henslow taught would eventually be reflected in Darwin's six botanical books, published between 1862 and 1880. But we see Henslow's core ideas in Darwin's most crucial *Beagle* notes. On the very first Galapagos island he visited, in 1835, while surveying the plants and birds, he asked himself[13]: "I certainly recognize S America in Ornithology, would a botanist?"

Figure 2 | Pattern of display on collated herbarium sheet of *Phleum arenarium*. Eight numbered individuals are arranged in order of increasing height from right to left. Plants 1–5 were collected 3 June 1829 at Mildenhall, Suffolk by J. S. Henslow. Plants 6–8 were collected in June 1822 at Liverpool by W. Wilson.

Darwin went on to collect plants, carefully labelled by island and by date. A decade later, J. D. Hooker used this material to demonstrate what Darwin had already suspected[14–16]: the high rates of 'endemism' (geographically restricted range) in the Galapagos flora. As Sulloway has shown, Darwin could never make the same case stick for his finches, because he had not labelled them by island[17]. Indeed, when he first landed in the Galapagos, Darwin obviously thought the plants were more interesting than the birds, so he took due care with labelling. As a faithful Henslow student, he identified his botanical specimens by date and by place.

Moreover, he was collecting plants with a purpose in the Galapagos. This collection was to be a prize for Henslow, who had taught him that oceanic islands tend to be rich in peculiar species, by which he meant endemics. 'Botanical geography' was the last topic in Henslow's course of lectures and in his textbook. Henslow listed several oceanic floras among the 45 botanical regions that he considered to be at least 'partially examined'[18,19]; the Galapagos flora is absent from this list. Darwin knew it was important to establish the endemism of his plants. Remarkably, although he still held a creationist view of species, the question of botanical endemism motivated Darwin's collecting in the Galapagos.

As his exploration of the archipelago proceeded, Darwin recognized an unexpected form of endemism in four of his ornithological specimens. We see a striking development of his thinking in two notes, the first written soon after the *Beagle* sailed from the Galapagos in October 1835 (ref. 20):

> *This bird which is so closely allied to the Thenca of Chili (Callandra of B. Ayres) is singular for existing as varieties or distinct species in the different Is[ds]. I have four specimens from as many Is[ds]. These will be found to be 2 or 3 varieties.*

Darwin called the thencas "singular" here because they are different on different islands. But are they different varieties or different species? At this point he settled for the orthodox view — they were "2 or 3 varieties" of the same species. He thus lumped them together, applying the creationist species concept that Henslow had taught him.

Eight months later, in June 1836, while arranging his birds as if they were a Henslow collation, Darwin rewrote these notes on the last leg of the voyage. His opinion had changed[21]:

> *In each Is[d] each kind is* exclusively *found: habits of all are indistinguishable…When I see these islands in sight of each other, …tenanted by these birds, but slightly differing in structure and filling the same place in Nature, I must suspect they are only varieties…If there is the slightest foundation for these remarks the zoology of Archipelagoes will be well worth examining: for such facts [would] undermine the stability of Species.*

Figure 3 | J. S. Henslow's drawings of variation in style length and stigma insertion height in *Primula*. a, Oxlip (8 April 1826, Westhoe) **b,** cowslip (18 April 1826).

This is the most famous passage that Darwin penned on the entire *Beagle* voyage. Frank Sulloway at the Massachusetts Institute of Technology has established the date of this note and recognizes that Darwin was operating within a creationist species concept on the *Beagle*[22]. We offer a new interpretation of the passage in the context of what Darwin had learned from Henslow. Darwin now "suspects" they are "only varieties". He could mean he is now *suspicious* of the idea that they are merely varieties. Thus they may be species, which would indeed "undermine the stability of Species". Or he could be going one step further. He could also mean that they are "only varieties" and that is what "would undermine the stability of species" — in which case we are witnessing the birth of Darwin's most fundamental view, namely that varieties are incipient species.

Either way, here we glimpse Darwin struggling with a radical shift in his henslovian species concept, just as he crosses the threshold between creation and evolution. Henslow would have preserved species stability, which Darwin no longer attempts to do. But without an appreciation of the depth of his botanical foundation, it has been unclear just how far Darwin was breaking with his past in this passage. We now see that the conceptual framework he received from Henslow was disintegrating and — because of Darwin's complete facility with the tight logic of that framework — a new way to see species was inevitably crystallizing.

Not surprisingly, Henslow is not acknowledged here by name. We do not cite our teachers for the fundamental ideas they transmit. Rather, they are part of our mental architecture. It seems this was the case with Darwin and Henslow. But in Darwin's case, the henslovian framework he had been given at Cambridge switched into a new configuration. The matter could only be settled by an expert ornithologist, and Darwin no doubt hoped that his carefully labelled Galapagos plants would also provide rich material with which to test the possibility of transmutation.

Henslow had launched Darwin's voyage when he helped to secure a berth for him on the *Beagle*. But, more significantly, during Darwin's undergraduate career Henslow had also launched his mind on an intellectual voyage that led from species stability to *On the Origin of Species*. ■

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