Review

Feature Review

Darwin as a plant scientist: a Southern Hemisphere perspective

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Events around the world this year celebrate the bicentenary of the birth of Charles Darwin (1809–1882) and the sesquicentenary of publication of his most important work, *The Origin of Species* (Darwin 1859). The associated plethora of books and papers now appearing to commemorate Darwin's work continue the traditional emphasis on his zoological and geological contributions. There has been some recent attention directed towards Darwin's relatively unsung but significant accomplishments as a botanist. Here, we bring together a review of Darwin's botanical discoveries and experiments and relevant aspects of his geological investigations, with a focus on the Southern Hemisphere. This is a relatively unexplored aspect of Darwin's contributions that yields some new insights meriting future research.

Darwin as a plant scientist

Although not as celebrated as his geological and zoological contributions, Charles Darwin's (1809–1882; Figure 1) botanical discoveries and experiments were of at least equal importance. He was inspired by Revd John Stevens Henslow and Adam Sedgwick at Cambridge, both of whom gave the young Darwin invaluable encouragement and field experience before the departure of the *Beagle* in 1831. His plant collections in South America were competently acquired and were comprehensive for the Galapagos Islands. However, Darwin's botanical discoveries were never written up systematically. By the time Darwin arrived in Australia and South Africa, homeward bound in 1836, his botanical interests had all but ceased. His geological focus on young lands recently arisen from the sea led to misidentification of some old southern landscapes. As a consequence, he missed significant opportunities and evolutionary insights, especially regarding the south-western Australian and Cape floras. Nevertheless, moving to Down House (Kent, UK) in 1842 and embarking on his major scientific life's work led Darwin back to plants for inspiration and as useful organisms to test many hypotheses. His ability to apply the scientific method consistently and to think through important tests to falsify hypotheses in biology was arguably his greatest strength. Plants figured prominently in his approach to understanding biological variation, geographical isolation, migration, community ecology, evolution, speciation and the development of basic characteristics of living organisms, such as mating systems, carnivory, sensing and tropisms. He used the rich diversity of convergent structures within orchids, carnivorous plants and climbing plants to debunk the prevailing notion of each species being created perfectly through intelligent design. He was surprised to discover that many orchids used fraud and deceit to achieve pollination by insects but was delighted to observe 'endless diversities of structure' that had evolved through natural selection to favour outcrossing. His physiological work pioneered many disciplines and ideas, including his discovery of the first experimental evidence for plant signalling molecules. He speculated uncharacteristically on the 'abominable mystery' of the rapid appearance and diversification of angiosperms in the fossil record [1]. Interestingly, he chose animals rather than plants to explore significant new disciplines, such as evolutionary embryology, anatomy and development. Darwin also did not venture far into plant taxonomy and the details of phytogeography, which were the dominant interests of his friend and confidant, Joseph Hooker, who freely provided Darwin with the evidence needed from these disciplines to advance his ideas and test relevant hypotheses, especially in the years leading up to publication of *The Origin of Species* in 1859. Darwin's rather disparaging early impressions of Australia, formed on the *Beagle* voyage, gradually modified as he realized how singular the biota of the continent was. Despite a concerted effort, he did not achieve a breakthrough in understanding particulate inheritance, and his research followed many false trails. Nevertheless, Darwin stands as a remarkable natural historian and experimental plant scientist, ecologist, morphologist and evolutionary biologist, without peer in his day.

Essential reading for our topic includes Darwin's *Beagle* diary [2] and subsequent writings (see the complete works of Charles Darwin online, http://darwin-online.org.uk/), especially his books dealing with plants [3–10]. As useful background, we also commend reviews from various other botanical perspectives: Darwin's evolutionary phase (to 1862) and physiological phase (to 1882) [11]; physiology and laboratory-based plant science [12]; studies of UK flora at Down House [13]; plant reproductive biology [14,15]; ecology and biogeography [16–18]; origins and rapid radiation of angiosperms [19]; geology [20]; and Darwin's

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Figure 1. Portraits of **(a)** Charles Darwin (1809–1882) in 1840 (watercolour by George Richmond – © English Heritage Photo Library, by kind permission of Darwin Heirlooms Trust) and three botanists who had the greatest influence on his plant science: **(b)** son Dr Francis Darwin (1848–1925 – © English Heritage Photo Library); **(c)** Cambridge teacher Professor John Stevens Henslow (1796–1861 – courtesy Royal Botanic Gardens, Kew); and **(d)** scientific confidant from Kew Sir Joseph Hooker (1817–1911 – courtesy Royal Botanic Gardens, Kew).

hypothesis formulation, testing and revision underpinning his consistent approach to questions as a scientist [21].

We take a broad view of plant science, as Darwin did, encompassing both descriptive and experimental approaches leading to hypothesis formulation and testing in the laboratory, herbarium or field. We do not accept the view (e.g. [12]) that systematics and other field-based botanical disciplines are in some way less rigorous or less scientific than laboratory studies. Darwin arguably made his greatest evolutionary discoveries as a field geologist and biologist in the Southern Hemisphere on the voyage of the *Beagle* (Figure 2) and then, on moving to Down House in Kent, focused on systematics (of barnacles), descriptive morphology and anatomy, experimental plant physiology and ecology. This richness of approach and unfettered willingness to explore evidence and theorize across disciplines, in the field and laboratory, enabled Darwin to hypothesize, experiment and synthesize as no other biologist had done so before. Therein lies his unique contribution and *modus operandi*, generating ideas that literally changed the world.

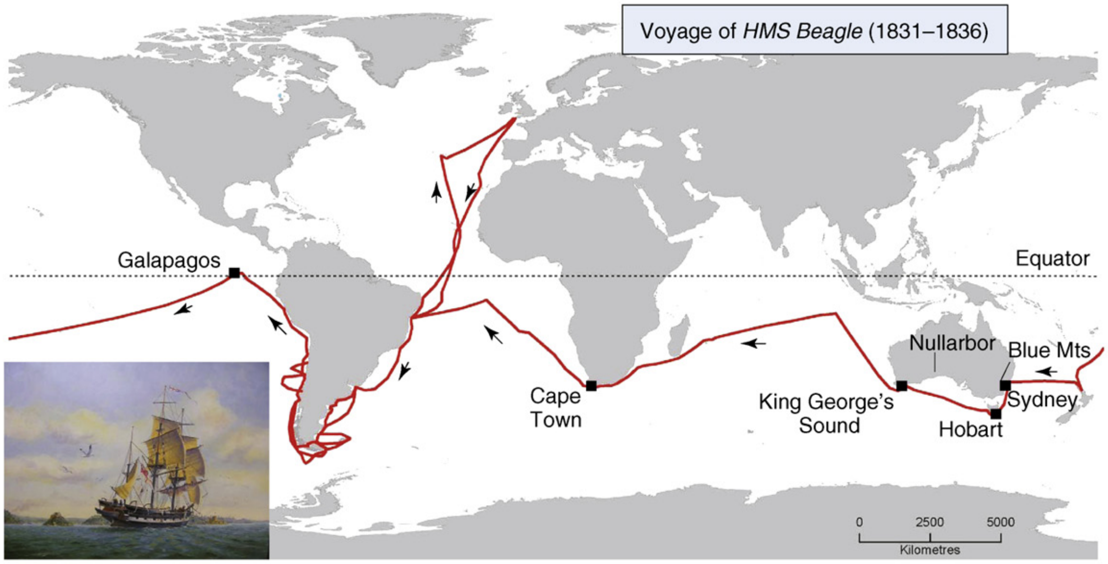
Mentors and inspiration

Mentors were very important to Darwin throughout his life. Keith Stewart Thomson ([22] p. 93) recently advocated that Darwin 'worked well only when he had a mentor, not as a personal tutor but someone to bolster his confidence, someone to believe in him, and also someone safely to draw him out socially'. Although many individuals influenced Darwin in ways he sometimes acknowledged and sometimes did not, a few are of particular importance and pertinence to Darwin's development as a plant scientist.

John Stevens Henslow and Adam Sedgwick

Darwin first met Cambridge's Professor of Mineralogy and Botany the Revd John Stevens Henslow (Figure 1) in 1828 at one of the latter's discussions for undergraduates and dons (faculty members). Henslow and the Revd Professor of Geology Adam Sedgwick were leading scientific minds at Cambridge at the time, and both had a profound influence on Darwin. From 1829 to 1831, Darwin attended Henslow's courses, which included interactive field excursions of the most stimulating and social kind. Darwin 'took long walks with him on most days' and became a regular visitor for meals at Henslow's family home. He observed that Henslow's 'strongest taste was to draw conclusions from long-continued minute observations' (*The Autobiography of Charles Darwin*, http://darwinonline.org.uk/), an approach that Darwin himself appreciated and excelled in subsequently. Henslow greatly admired Darwin's penchant for natural history and his questioning young mind.

When Darwin attended his lectures, Henslow, although a creationist, was focusing his research on the nature and limits of species that he investigated by documenting patterns of variation within and between populations [22]. His herbarium sheets typically included specimens



TRENDS in Plant Science

Figure 2. Voyage of *HMS Beagle* 1831–1836, with key Southern Hemisphere locations mentioned in the text. Outbound, the ship left English shores on 27th December 1831, and the Equator was crossed on 17th February 1832. South America and adjacent islands were explored extensively for three and a half years until departure from Lima to the Galapagos on 7th September 1835. Australia was briefly visited over two months from arrival at Sydney (12th January 1836) to departure from King George Sound on 14th March 1836. Cape Town likewise was only a short stop homeward bound (31st May–18th June 1836), as was Brazil (1st–17th August 1836). The Equator was crossed again on the 21st August 1836, and arrival at Greenwich on the Thames was on 28th October 1836, although the perennially seasick and desperately homesick Darwin left the Beagle unannounced at the first English landfall (Falmouth) on 3rd October. Based on endpaper maps in [2]. Inset: view of the *Beagle* entering Sydney Harbour (artist: Ron Scobie, A.S.M.A., http://www.ronscobie-marineartist.com/; reprinted with permission).

from more than one collection to illustrate variation, and each specimen was labelled on the sheet with location, date of collection and collector's name. He was the only British botanist at the time doing this, and he clearly taught Darwin the value of precise and accurate labelling, as well as the importance of rigorously examining variation within and among populations [23]. Henslow was inclined to lump rather than split when defining species, discriminating as varieties what others considered to be full species [24]. The primrose (*Primula vulgaris*) and the cowslip (*P. veris*), for example (Figure 3), were interpreted by Henslow [25] as varieties, following Linnaeus [26] and at odds with J.E. Smith's [27] view that they were species. Henslow in 1826 also meticulously drew the flowers of these taxa, making an original discovery by illustrating styles of different lengths within populations of both taxa (see 'Mating systems' below). He included this material in his lectures and thereby conveyed to students, including Darwin, the need

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Figure 3. Wild primrose (*Primula vulgaris*) (left, and lower inset), a pink primrose cultivar and wild cowslip (*Primula veris*, right and upper inset). Darwin's cross-pollination experiments established both the status as species for the primrose and cowslip and the presence of heterostylous sex forms in both taxa. He also used as an analogy for natural selection the role of artificial selection by horticulturists of colour variants in domesticated plants such as in primroses. Photos by S.D.H. (main) and J.H.D. Hooper (insets).

for careful anatomical description to understand biological variation [23]. Henslow also taught botanical geography, emphasizing endemism ('peculiar species') on oceanic islands, which must have inspired Darwin's interest in seeing such for himself on a voyage of discovery. All of these Henslowian themes loomed large in Darwin's future research.

Darwin's resolve to become a natural scientist, travelling to exotic and poorly known places, perhaps achieving greatness and international renown, was further affirmed by reading works of Alexander von Humboldt (*Personal Narrative*, 1807 [28]) and William Herschel (*Introduction to the Study of Natural Philosophy* [29]), the latter providing penetrating insights into the scientific method. Darwin planned a trip to the Canary Islands in 1831 to explore a volcano that had been visited by von Humboldt in 1799 while in transit to South America, but this was postponed. Henslow encouraged Darwin to hone up on geology before embarking on such a journey. An ideal opportunity emerged in August 1831, when Henslow convinced Adam Sedgwick to take Darwin to North Wales on a summer geological excursion. Sedgwick was renowned as a field geologist and was able to foster Darwin's ability to translate local observations into hypotheses of regional pattern in geological strata. A week in the Vale of Clwyd and nearby sites of Snowdonia involved intense discussions about stratification, as well as visits to fossil sites and glacial valleys (then not understood as such). Darwin was assigned to undertake a solo transect to test Sedgwick's stratification hypotheses, and Darwin reported back with new facts and an accurate interpretation. This task delighted both Sedgwick and Darwin, and student and master worked well together. Collecting for Henslow, Darwin also obtained his earliest herbarium specimen (of *Matthiola sinuata*, Brassicaceae) from Barmouth in North Wales [23]. Darwin's on-the-job scientific training and confidence in his geological field skills were stimulated by this brief trip.

Alexander von Humboldt

By the end of 1831, on Henslow's recommendation, Darwin had been recruited as geologist/natural historian for the *Beagle's* global circumnavigation. Darwin's link to Southern Hemisphere biota was inspired by early readings of Herschel on South Africa and von Humboldt's South American exploration and discoveries. The extraordinary biological novelty revealed by von Humboldt and others in South America remains an irresistible magnet to curious minds right through to the present. South America is the continent with the richest plant diversity known [30] and contains reasonably vast regions that remain formidable to access. The continent is still full of promise of new biological discovery to the intrepid and venturesome. It is little wonder that Darwin as a young biologist leapt at the chance to see for himself some of the natural wonders of South America when the opportunity to travel on the *Beagle* became a possibility.

Sir Charles Lyell

Captain Robert FitzRoy gave Darwin a gift of the first volume of Charles Lyell's *Principles of Geology* (1830) on their departure aboard the *Beagle* from Plymouth. Henslow encouraged Darwin to read it but not to believe it [21]. Sir Charles Lyell espoused James Hutton's principle of uniformitarianism and opposed George Cuvier's catastrophic geology model. That is, geological processes observable today should be interpreted as those that prevailed in the past, rather than invoking global catastrophes such as the biblical great flood. This approach required much more care and rigour in geological observation than had been applied before. Uniformitarianism ensured that logical hypotheses testable through contemporary observation were examined independently by many, building the corpus of geological theory upon a foundation of observable fact. With Darwin's learning and training, this empirical approach to scientific inquiry struck a chord and affirmed a *modus operandi* that prevailed in his work. Of course, Lyell did not discount local catastrophes such as volcanic eruptions and floods as geological phenomena. He was nevertheless intent on establishing a methodology to reveal the more general and global laws of geology, within which local and rapid processes could be interpreted.

Southern Hemisphere travels and Darwin's botanical opportunities

Darwin's now legendary accomplishments on this voyage have been ably summarized elsewhere [16,21,22,31]. His experiences were important in forging links with other biologists back in England who similarly had ventured on long voyages under sail to southern waters and experienced fascinating biota unknown to Western science [32].

Darwin's ambition to visit the Canary Islands was soon realized on the *Beagle* voyage. His geological training was drawn upon as he encountered new places – observing, theorizing, and experimenting. On the Cape Verde Islands he struggled with a rapid and total conversion to Lyell's uniformitarian ideas [33]. However, increasing evidence, such as marine terraces and fossils well above present sea levels, convinced him that land had risen slowly from the sea on volcanic Atlantic and Pacific islands, on the Patagonian coast and on Andean slopes. His coral reef theory derived from a similar principle of slow geological change in that atolls and barrier reefs were hypothesized to grow upwards where the sea floor was subsiding [21]. Thus, the notion of geological change, subsidence and uplift slowly infused his thinking about the mutability of species and, ultimately, underpinned the theory of evolution by natural selection [21,22].

Despite the great botanical opportunities presented to Darwin by the *Beagle*'s circumnavigation, his journal and subsequent monographs make it clear that he saw his primary role in geological observation and discovery. South America entranced him from the outset. Moreover, he maintained an undiminished zeal and enthusiasm for geological fieldwork: 'Darwin never lost his ability to combine a sense of wonder with scientific detachment and keen observation as he experienced new landscapes across South America' [22] (p. 150).

Biological collections also were made competently by Darwin, with a clear focus on zoological specimens. He collected some 1400 plant specimens [34,35], making a special effort in the relatively poorly sampled temperate

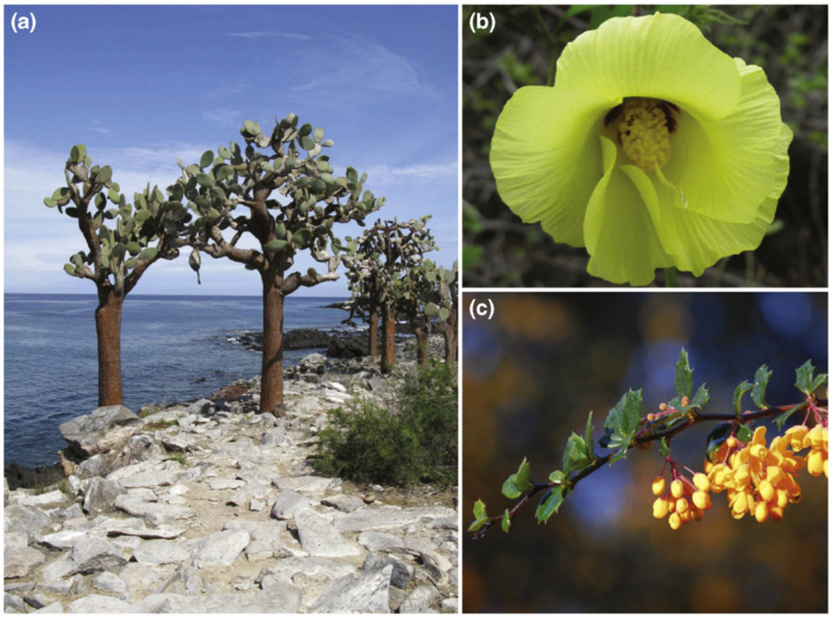


Figure 4. South American plants exemplifying Darwin's discoveries and skills as a botanical collector on the *Beagle*. **(a)** *Opuntia echios* (Cactaceae) forming typical Galapagos vegetation seen by Darwin in September–October 1835. Photo by P. Cribb. **(b)** The Galapagos endemic *Gossypium darwinii* Watt (= *G. purpurascens* Poir., Malvaceae) collected by Darwin and named after him in 1907. Photo by P. Cribb. **(c)** *Berberis darwinii* Hook. (Berberidaceae) collected by Darwin at Chiloe Island, Chile in June 1834, and named after him by the foundation director of Kew Sir William Hooker in 1844. Photo by S.D.H.

regions of southern South America and on the Galapagos Islands, the latter especially done for Henslow, given the interest of Darwin's teacher in oceanic island floras and plant endemism (Figure 4). However, Darwin collected little from places he regarded as already explored by European botanists, and these included Brazil, Pacific islands visited by Joseph Banks and others, New Zealand, Australia and the Cape of South Africa. Indeed, by the time the *Beagle* landed briefly in each of the last three territories on this final long leg of the circumnavigation, Darwin was suffering self-proclaimed home sickness and travel weariness. Nevertheless, he maintained a credible pace of collecting, observing and thinking in geology and zoology [36]. His botanical contributions were minor and herbarium collections were few. Darwin freely acknowledged inequalities in his efforts across the disciplines of natural history. On the return haul of the *Beagle* across the North Atlantic back to England, he famously penned a belated admission that botanical studies on long voyages might, in fact, be most productive for the natural historian: '..a traveller should be a botanist, for in all views plants form the chief embellishment' (Darwin in [2], p. 443).

Of all Darwin's natural history collections made on the *Beagle* voyage, it is significant that the botanical material was neither compiled nor published as a monographic record. Darwin's attempts to secure the services of the Revd John Stevens Henslow and Robert Brown [37] in identifying the collections and publishing a botanical monograph came to naught. Only when Henslow approached Joseph Hooker (Figure 1), son of Sir William, Director of the Royal Botanic Gardens Kew, did Darwin succeed in finding an enthusiast willing to work through botanical collections from the *Beagle* voyage (especially Darwin's reasonably thorough material from the Galapagos [38]). This collaboration was the start of Darwin's closest scientific friendship, an 'enspiriting companionship' [11], as Hooker became his trusted confidant and botanical advisor during and after the momentous years leading up to publication of the *Origin* in 1859.

Darwin's challenge in understanding the geology and plant evolution on old southern lands

Darwin in Australia

Australia presents a significant challenge to geological exploration and interpretation [39,40]. Classically, Australia is divided into three geomorphic zones, the Western Plateau, the Eastern Highlands and the Central Lowlands. However, Gale [41] proposed that a more useful classification might be made between the inland areas of low relief, low denudation rates and ancient land surfaces and the marginal zones of higher relief, higher denudation rates and more recent landscapes. Some very old landscapes are found on the western shield, inland of the subdued drainage divide known as the Meckering Line, as well as in scattered places elsewhere on the continent, such as parts of the Blue Mountains (reviewed by [41–43].

With his focus on Lyellian geology, reinforced by observations on volcanic islands, coral reefs and the young uplifting Andean landscapes of southern South America, Darwin's encounter with the old stable landscapes of Australia [41–43] in the Blue Mountains (New South Wales) and at King George Sound (Western Australia) was an experience for which he was unprepared, and he failed to appreciate their great age. Darwin [44] proposed, for example, that the sheer cliffs of the Blue Mountains were caused by marine erosion and subsequent uplift, rather than the correct interpretation of fluvial erosion of an old stable landscape [39,40]. Darwin was much more comfortable in the glacial landscapes of Tasmania, geologically so reminiscent of North Wales and Scotland [45]. The Tasmanian geological pattern seemed accountable in terms of by then well-formulated hypotheses drawn from observations in Darwin's notebooks made in other young landscapes. The unfamiliarly quiescent and ancient landscapes on parts of the Australian mainland scarcely raised novel comment from Darwin, who uncharacteristically failed to see the evidence before him with fresh eyes and from a rigorous perspective. It would seem that, by the end of the five-year journey of the *Beagle*, Darwin was so preoccupied with the merits of geological hypotheses concerning land emerging from oceans that he had abandoned his normally prudent and uniformitarian methodology in theorizing about landscape evolution. Indeed, one reviewer of the history of Australian geological science suggested that 'Darwin on Australian geology is no shining original' [45] (p. 28).

Darwin did, however, correctly dispel George Vancouver's [46] idea of a coralline origin for limestone rhizocasts at Bald Head on King George Sound in south-western Australia. Nevertheless, Darwin echoed erroneous earlier ideas on the age of landscapes in the Southwest Australian Floristic Region (*sensu* Hopper and Gioia [47]) when he proposed that the granite headland of Flinders Peninsula terminated by Bald Head had arisen recently from the sea [48]. Darwin was simply repeating published ideas of Australia as a young continent, especially the west, evidenced by the sandy nature of the soil, salty groundwater and low coastal vegetation. Indeed, the coastlines and associated continental features seen by most early visitors are often as young as any landscapes on Earth, having formed only after sea level reached its present elevation perhaps 6000 years ago. This might provide a partial explanation, at least, for the failure of pioneering maritime explorers to see anything novel in the relief.

Among early dissenters, Hooker [49], on the basis of plant geographical data that he had assembled, challenged the view that south-western Australia was geologically young inland from its coastline. Hooker noted the anomaly of such a supposedly young land in south-western Australia having an extraordinarily rich native flora full of endemics. Elsewhere such endemics were concentrated on old landscapes. Subsequent inland exploration revealed that marine fossils were conspicuous by their absence on most of the southwest, as were marine sedimentary rocks [50], refuting the hypothesis of recent marine inundation. Most southwest landscapes, except for coastal features, some wetlands and slopes, are indeed old, and this observation has profound implications for understanding the origins of biodiversity [47,51]. Of course, some ongoing Neogene landform evolution is evident even on such broadly old landscapes [52], but much of the region is older than previously believed. Here, Darwin was misled by a singular focus on the idea that many lands are recently emergent from the sea, an issue that caused him difficulties elsewhere as well (e.g. Glen Roy in Scotland [53]). Darwin's preoccupation with emergent young landscapes hampered his ability to understand and investigate some truly remarkable evolutionary phenomena in old southern lands, aspects of which he only came to appreciate many years after his return to England, and some of which remained enigmatic and unresolved to him.

Geomorphologists and biologists continue to marvel at and explore this theme of extraordinarily old, weathered landscapes in Western Australia, stable within the centre of the Australian continental plate, with little recent mountain building or uplift. New theory is being developed for the understanding of the evolution, ecology and conservation of biota on such old, climatically buffered, infertile landscapes [51,54–57].

The Cape flora and Darwin

Darwin's *Beagle* journal was full of dismissive comments regarding the Cape region of South Africa. He saw 'nothing worth seeing' at Simons Town on False Bay soon after making landfall on 31st May 1836 (Darwin in [2], p. 423) and was similarly critical of the road north to Cape Town, noting that '..with the exception of the pleasure which the sight of an entirely new vegetation never fails to communicate, there was very little of interest' (p. 423). He was enchanted by the 'uncommon beauty' of the houses and plantations 'backed by a grand wall of mountains [i.e. Table Mountain]' near Wynberg. On June 4th he 'set out on a short excursion to see the neighbouring country, but I saw so very little worth seeing.' (p. 425). Journeying east towards Paarl, he commented on 'very pretty oxalis's and mesembryanthemums, and on the sandy spots, fine tufts of heath', as well as 'several very pretty little birds'. He ascended the granite inselberg above Paarl, enjoying the view but not finding anything biological worthy of comment. He ascended and descended the adjacent Cape Fold Mountains, which were incredibly rich in fynbos vegetation [58], yet he wrote 'There was not even a tree to break the monotonous uniformity of the sandstone hills. I never saw a much less interesting country.' (p. 426). He enjoyed meeting Sir John Herschel and Sir Thomas McClear (the Astronomer Royal) in Cape Town and joined Dr A. Smith on 'some long geological rambles' until the Beagle departed on June 18th.

Darwin, homesick and utterly tired of seasickness after five years' voyaging, could be forgiven for such a lack of enthusiasm, except that he was in the midst of the richest temperate flora on Earth [59–62]. Extraordinary evolutionary stories abound in the Greater Cape region (e.g. [61,63–68]). As with south-western Australia, it was not until Darwin started working up data for his books and journal publications in England that he belatedly recognized the importance of the Cape for various matters of keen interest. For example, in 1863 Darwin wrote to Roland Trimen, a civil servant in Cape Town, regarding work on orchids in the genera *Disa* and *Herschelea* (Darwin Correspondence Project, Letter 4179, 23rd May 1863). Darwin also corresponded with Hooker regarding floristic affinities of the Cape with south-western Australia during an emerging new appreciation of the island continent's biological interest.

Plants and the 'species theory'

Despite not having a systematic botanical treatment of his collection from the *Beagle* voyage, observations on plants permeated Darwin's subsequent writings. Patterns of

Figure 5. Thrift (*Armeria maritima*, Plumbaginaceae) exemplifies a European plant that Darwin found disjunct in southern South America at coastal sites (enclosed by red lines). Such observations provoked early thinking about whether disjunctions were due to multiple creation events or a single origin followed by long-distance dispersal. Photos by S.D.H.

plant distributions, for example, were crucial to Darwin's thinking as it evolved on the *Beagle* and afterwards. Darwin's observations of European plants also being present in southern South America, but not in between (Figure 5), sparked his thinking about whether this pattern was caused by multiple events of special creation or by a single common ancestor and subsequent long-distance dispersal. He retained a life-long interest in long-distance dispersal thereafter, as evidenced by his famous experiments with seeds in saline water to test their viability for trans-oceanic dispersal [69]. He consistently rejected the hypothesis of land bridges as the vehicle for dispersal – a hypothesis favoured by Hooker, among others – as this was not the simplest hypothesis. Evidence for such bridges was not available; plate tectonics theory and continental drift hypotheses did not become widely accepted until the 1960s. Also, with the advent of phylogeographic analysis over the past two decades, Darwin's views on the capability of many plant groups to disperse across oceans have been vindicated [18,70].

Spatial isolation and speciation

In making the first comprehensive collection of Galapagos plants (Figure 4), Darwin noticed that endemic species were concentrated on some islands and not others, irrespective of geographical proximity within the Archipelago [71]. This, he reasoned, was due to strong isolation, and he discovered that deep water and strong prevailing currents isolated plants dependent for dispersal by floating across water, even when they occurred on closely adjacent islands. Hence the fundamental idea of spatial isolation and barriers to reproductive communication being pivotal to speciation (allopatric or geographical speciation in today's terminology) was stimulated as much by Darwin's observations of Galapagos plants as by the more celebrated finches [16,21,72].

Darwin's encounter with Australian plants reinforced his conviction that spatial isolation was important to understanding the origin of different species and varieties on different land masses. After reading the exploration journal of Edward Eyre [73], the first European to cross the arid southern Australian coast between Adelaide and King George Sound, Darwin wrote to Hooker (Darwin Correspondence Project, Letter 1719, 18th July 1855) that the presence of the arid Nullarbor Plain between south-western and south-eastern Australia might well have isolated these two floras and thereby help to explain the anomalous richness and high endemism characteristic of the southwest (Figure 6). This is perhaps the best Australian example of how Darwin looked for evidence of geographical barriers to plant dispersal to explain local endemism and the origin of species and varieties.

Revival of Darwinian views

Darwin's concept of species, long misunderstood due to its type-casting as taxonomic essentialism by Mayr [74] and followers, continues to inform and guide recent thinking on speciation [75]. Darwin's approach was exemplified by his work on the specific or varietal rank of the primrose (*Primula vulgaris*) and cowslip (*P. veris*), a topic of interest from when he attended Henslow's lectures in Cambridge (see above) (Figure 3). After extensive experimental pollinations and careful morphological and field studies, Darwin [76] (pp. 448–449) resolved: '...as the Cowslip and Primrose differ in the various characters before specified, as they are in a high degree sterile when intercrossed, as there is no trustworthy evidence that either plant, when uncrossed, has given birth to the other plant or to any intermediate form, and as the intermediate forms which are often found in a state of nature have been shown to be more or less sterile hybrids of the first or second gener-

Figure 6. The Nullarbor Plain with its impressive sea cliffs **(a)** at the head of the Great Australian Bight figured prominently in Darwin's early and later thinking about Australian geology and plants. The Nullarbor's aridity, documented first by explorer Edward John Eyre, led Darwin to propose to Hooker that therein lies an isolating barrier explaining floristic differences between the southwest and southeast of Australia. Examples of endemic southwest genera which to Hooker were 'the most extraordinary thing in the world' include: **(b)** *Ecdeiocolea* (Ecdeiocoleaceae); **(c)** *Nuytsia* (Loranthaceae); **(d)** *Dasypogon* (Dasypogonaceae); **(e)** *Anarthria* (Anarthriaceae); **(f)** *Anigozanthos* (Haemodoraceae); and **(g)** *Cephalotus* (Cephalotaceae). Photos by S.D.H. except (e) – W.R. Barker, with permission – and (g) – A.P. Brown, with permission.

ation, we must for the future look at the Cowslip and Primrose as good and true species.'

Mallet [75,77] argued that there has been a revolutionary return to Darwinian views of species and their origins in recent decades after 60 years of 'blind alley' research down the lines of an essentialist hypothesis that biological species are somehow fundamentally different from other categories in the classificatory hierarchy. To explain the mechanism of speciation, Darwin [3] proposed a principle of divergence:

> . . .the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so been abled to increase in numbers.
>
> Thus, for plants:
>
> It has been experimentally proved, that if a plot of ground be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can thus be raised. The same has been found to hold good when first one variety and then several mixed varieties of wheat have been sown on equal spaces of ground. . . . The truth of the principle, that the greatest amount of life can be supported by great diversification of structure, is seen under many natural circumstances. . . . For instance, I found that a piece of turf, three feet by four in size, which had been exposed for many years to exactly the same conditions, supported twenty species of plants, and these belonged to eighteen genera and to eight orders, which shows how much these plants differed from each other.

Although the above statements relate to Darwin's interest in the assembly of communities and the relationship between productivity and diversity, there are clear implications concerning his concept of the origin of species. In essence, he hypothesized that competitive selection is more important than environmental selection in driving community ecology and speciation.

The elusive origin of species

Paterson [78] (p. 75) proposed that Darwin made this conceptual shift focusing on competition in the mid 1850s and that 'emphasizing competition led Darwin away from an understanding of species, laid the foundations of competition in ecology, and determined the course of evolution theory thereafter'. Essentially, Darwin's competitive view, especially in regard to sexual selection, blinded him to 'viewing reproductive behaviour in a more biological way'. Paterson [78,79] argued that to elucidate the origin of species in biparental organisms as incidental by-products of adaptive divergence, we need to understand how new reproductive signals are entrained by natural selection and become co-adapted with an appropriate receiver in the opposite sex. Ultimately, through focusing so much on competition, which he saw everywhere in the plant world at Down House and beyond, Darwin [3] missed this fundamental insight on speciation. Thus, his plant studies both helped and hindered resolution of the key question embraced in the title of Darwin's most famous book – the origin of species.

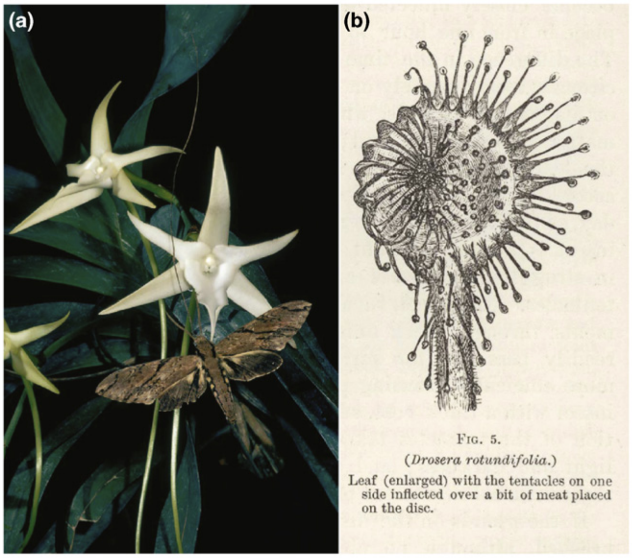
Debunking intelligent design

It has been argued that Darwin's greatest discovery was that life on Earth is governed by laws accessible to scientific investigation, rather than being the product of divine creation [80]. Plants had a key role in the evidence marshalled by Darwin to argue his case. Carnivorous plants, for example, provided Darwin with two avenues of research pertaining to adaptation and natural selection. First, he explored the nutritional benefits for carnivorous plants from nutrient-impoverished habitats and thereby pioneered studies of the specialized ecophysiology involved. Second, through meticulous observation, description and experiment, he established that carnivory was assembled through evolution in different ways in different lineages – descent with modification, not perfect adaptation or 'intelligent design', as creationists would have it. He showed that natural selection builds on existing frameworks in different groups, resulting in the same outcome. Darwin became so fascinated by these studies that he wrote to Lyell: 'I care more about *Drosera* than the origin of all the species in the world.'

Darwin's observations on *Drosera rotundifolia* (Figure 7) established that the glandular hairs are highly sensitive to pressure as well as to fluids released from the prey. These physical and chemical cues trigger the hair to move. He also observed that nitrogenous compounds were digested and subsequently absorbed by the plant [6]. This work has fundamental implications still under active research today. Carnivorous plants are relatively common in nutrient-impoverished habitats. It is becoming increasingly clear that in the most severely nutrient-impoverished environments, a range of other adaptations occur that allow roots to access scarcely available nutrients. In the most ancient and nutrient-impoverished regions on Earth, such as south-western Australia and the Greater Cape of South Africa, these adaptations include the formation of 'proteoid' or 'dauciform' root clusters, especially, but not exclusively, in plants that lack the capacity to engage with mycorrhizal fungi [81,82]. These highly specialized roots mobilize phosphate that is sorbed onto soil particles and not readily available for plants that lack these adaptations [56]. Moreover, many plants in these environments operate at low leaf phosphorus concentrations and have a tremendous capacity to remobilize phosphorus from senescing leaves and roots [83].

Insect pollination, outbreeding and orchids

Orchids afforded Darwin excellent material to demonstrate some of the best plant examples of adaptive diversification from a basic ground plan (Figure 7). On his orchid studies he wrote to Hooker: 'Why I care about it is that it shows that visits of insects are so important, that these visits have led to changed structure.' (Darwin Correspondence Project, Letter 2770, 27th April 1860). In writing about orchid pollination, Darwin aimed to demonstrate how significant was cross-fertilization by insects, thus favouring the evolution of such complicated flowers that fostered outbreeding. With self-fertilization, variation in populations would be limited, so that natural selection had little basis for its operation. Darwin made an additional discovery in his careful work on insect pollination of orchids: many orchid species are pollinated through intricate mechanisms involving deceit, for both food and sex [84,85]. This pioneering insight made clear to Darwin that nature is neither inherently moral nor benign. Natural selection works without purpose, assembling structures that deliver reproductive fitness to individuals irrespective of the mechanisms involved. If deceit improves the ability for plants to contribute more offspring to the next generation than their competitors, structures favouring deceit will be favoured by natural selection.



TRENDS in Plant Science

Figure 7. Three plant groups provided Darwin with ample evidence for adaptation under natural selection and to counter notions of perfect 'intelligent design' promulgated by creationists – *Drosera*, orchids and climbing plants. **(a)** The Madagascan lithophytic orchid *Angraecum sesquipedale*, which has extraordinarily long nectar tubes, and its hawkmoth pollinator *Xanthopan morganii praedicta*, which was predicted by Darwin to have a matching elongate proboscis. Courtesy of Marcel Lecoufle. **(b)** A drawing from Darwin's *Insectivorous Plants* [6] illustrating the response of sensitive leaf hairs of the common British sundew *Drosera rotundifolia* to experimentally placed animal tissue. Courtesy of University of Cambridge.

Darwin commenced his orchid pollination studies in 1838 on British terrestrials and started his book with descriptions of the pollination mechanism for *Orchis mascula*. On moving to Down House in 1842, the nearby Orchis Bank (Rough Pell, now in Downe Bank Nature Reserve) provided ample material for study of orchid genera, such as *Dactylorhiza*, *Anacamptis*, *Orchis*, *Cephalanthera* and *Epipactis*, growing adjacent to the beech forest [86]. In 1860 *Orchis pyramidalis* had caught his attention, and in 1861 he finally committed to write the orchid book he had thought about for so long. Darwin enthused to his readers:

'The contrivances by which orchids are fertilized are as varied and almost as perfect as the most beautiful adaptations in the animal kingdom.'

In exploring orchid pollination by insects, Darwin [4] benefited from the orchid collections, many from tropical South America, assembled at Kew and held by the renowned orchidologist John Lindley. He also drew upon studies of terrestrial species from temperate South America, Australia and South Africa. For example, he included in his book beautiful illustrations of the flower and half-flower of the Australian greenhood *Pterostylis longifolia*, showing its entrapment mechanism with a motile labellum triggered by visiting insects. Once trapped, the pollinators are obliged to exit past the stigma and pollinia through a narrow gap created by the two column wings. Darwin studied the foot-long nectar tube of Madagascar's *Angraecum sesquipedale*, suggesting that only a large hawkmoth would have a proboscis sufficiently long to reach the basal nectar. An appropriately equipped hawkmoth, *Xanthopan morganii praedicta*, was discovered subsequently (Figure 7) [87]. Darwin also theorized from this case on the coevolutionary race between long-spurred plants and long-tongued pollinators. His ideas have been put to empirical tests only very recently in studies on North American columbines (*Aquilegia*) [88] and on the interactions between the remarkable long-tongued flies of the Greater Cape Region in South Africa and the suite of tubular-flowered plants that they pollinate [65]. In columbines, pollinator shifts, rather than coevolutionary races, underpin a directional trend in the evolution of nectar-spur length. In the South African flies and flowers, Darwin's hypothesis of a coevolutionary race was affirmed because 'additional species become attached to the network of interacting mutualists by convergence' [65] (p. 268). Orchids yielded 'endless diversities of structure' to Darwin's meticulous observations and experiments, affirming the importance of insect-mediated outcrossing under natural selection. Right through to the present, studies of Southern Hemisphere orchids (e.g. [89,90]) continue to illuminate the principles first discovered by Darwin. The innovation of this, Darwin's first venture into books on botanical subjects, was grasped immediately by his closest friends. A most significant tribute to the novelty and quality of Darwin's work on orchid pollination came from the pen of Joseph Hooker, who in 1862 wrote to Brian Hodgson in India:

> Darwin…startles us by the surprising discoveries he now makes in Botany: his work on the fertilization of orchids is quite unique – there is nothing in the whole range of Botanical Literature to compare with it. (cited in [16], p. 209)

Movement and discovering evidence for the existence of plant signalling molecules

In what some claim to be his best botanical research [12], Darwin [10], ably assisted by his son Francis (Figure 1), who was trained in laboratory physiology, published his last book on plants two years short of his death. Darwin [10] made elaborate observations on two forms of plant movement: tropic movements, which depend on growth, and nastic movements, which require a specialized organ, a pulvinus [91]. His detailed observations on phototropic movements of cotyledons led him to the conclusion that the stimulus (light) is perceived in the upper part of the cotyledons, leading to the transmission of that stimulus to the lower part. Darwin used the term 'heliotropism' for this movement. Unfortunately, that highly appropriate term is now used for a nastic, solar-tracking movement involving a pulvinus [92]. Transmission of the signal from the illuminated to the darkened side of the leaf was further investigated half a century later by Frits Went and his colleagues at Utrecht University, who discovered auxin, the first plant hormone [93]. The involvement of auxin in phototropic movements remains a topic of active research up to this day [94]. Darwin [10] was also well aware of the fact that plant organs can re-orientate themselves with respect to gravity; he used the term 'geotropism', now commonly replaced by 'gravitropism'. By removing the tips of roots of *Vicia faba*, he firmly established that the root tip is involved in sensing gravity, leading to the bending of adjoining parts. Decapitated roots would respond to gravity only after a tip had regenerated. If the tip was allowed to transmit a signal to a basal part of the root before being decapitated, the root acted as if the root tip was still attached. The discovery of the nature of that signal had to wait until further work on geotropism was done by Frits Went and Nicolai Cholodny, leading to the Cholodny–Went theory. That work established the involvement of auxin in gravitropism [95]. Gravisensing involves cells (statocytes) that contain movable amyloplasts of which their potential energy activates calcium channels by exerting tension on the actin network and/or pressure on the cytoskeleton elements lining the plasma membrane [96]. Darwin's discoveries were not restricted to phototropic and gravitropic movements; he also studied nastic movements. In addition, he pioneered research on thigmotropic (contact-sensing) movements, which he observed in roots [10], the glandular hairs of *Drosera* [6] (Figure 7) and the tendrils of Bignoniaceae [7]. The tendrils of *Bignonia unguis* (i.e. *Dolichandra unguis-cati*) are highly sensitive to contact, especially on their under surfaces. When a shoot grows among branches, the tendrils are brought into contact with them by the revolving (circumnutating) movement of the internodes, causing them to bend and attach themselves to the twigs. Thigmotropism tends to depend upon transmission of a signal from the cell wall through the plasmalemma into the cytoplasm, possibly involving cytoskeletal structures as transduction components. This might require some modification of the calcium/calmodulin signal-transduction system, but details of transduction systems remain poorly understood [97].

Mating systems

Darwin derived his greatest pleasure from experiments on *Primula* (Figure 3) and other heterostylous plants in relation to their mating systems: 'I do not think anything in my scientific life has given me so much satisfaction as making out the meaning of the structure of these plants.' [98] (p. 91). He meticulously pursued experimental crossing and selfing programmes, revealing the fundamental basis and mechanism of heterostyly [14,15], and came close to identifying ratios of simple allelic Mendelian inheritance. However, Darwin missed seeing the significance of the latter because of false leads he pursued concerning the nature of inheritance (see below).

Darwin's crossing experiments established the importance of outcrossing in many genera. He wrote:

> It is an astonishing fact that self-fertilization should not have been an habitual occurrence. It apparently demonstrates to us that there must be something injurious in the process. Nature thus tells us, in the most emphatic manner, that she abhors perpetual self-fertilization. [4] (p. 359)

He was fundamentally interested in the evolution of sex, which on face value reduces the reproductive fitness of individuals. He used plants to explore and test empirically whether this was, in fact, the case. Darwin became entranced by the subtleties and sensitivities exhibited by plants to selfing and crossing:

> There is hardly anything more wonderful in nature than the sensitiveness of the sexual elements to external influences, and the delicacy of their affinities. We see how sensitive the sexual elements of those plants must be, which are completely sterile with their own pollen, but are fertile with that of any other individual of the same species. [9]

He was hampered in understanding the detailed mechanisms involved because of the lack of theory concerning particulate genetic inheritance and the need for biochemical and micromorphological experimentation [15]. Significant advances in these fields are relatively recent.

The abominable mystery – angiosperm origins

Darwin's famous quote in an 1879 letter to Hooker about the abominable mystery surrounding the sudden appearance and rapid diversification of angiosperms in the fossil record has provided fertile material for countless authors (e.g. [1,99]). Darwin's fossil plant collections from the *Beagle* voyage were few: 20 from Argentina and Chile, two from New South Wales and six from Tasmania [100]. They were mostly of coniferous wood or *Nothofagus* leaves and contributed little to a better understanding of the abominable mystery. Darwin's interest in the topic nevertheless was concerned primarily not about angiosperm evolution *per se* but about the most striking exception to his view that *natura non facit saltum* (nature does not make a leap). He recognized that saltational rather than gradual evolution would play into the hands of creationists, and he was particularly focused, therefore, on securing evidence for gradual evolutionary change. The angiosperm fossil record as known in his time provided the most significant exception to gradualism. To account for this mystery, and contrary to his otherwise rigorous application of Occam's Razor in explaining the origin and dispersal of taxa, Darwin posited a 'long, gradual and undiscovered pre-Cretaceous history of flowering plants on a lost island or continent', possibly in the Southern Hemisphere [1]. He also favoured Gaston de Saporta's [101] view that coevolutionary interdependence of flower-visiting insects and angiosperms was responsible for rapid diversification in the mid-Cretaceous, seeing enhanced outcrossing by insect pollinators as the primary evolutionary stimulus to this seemingly explosive radiation of flowering plants. Although he added little, therefore, by way of original data or insight to the question of angiosperm origins, Darwin stimulated future research, which has generated a deeper and more profound understanding of the origins and radiation of angiosperms (e.g. [102,103]).

In one important respect, Darwin's lead has proven insightful – his emphasis on an intrinsic mating system phenomenon (outcrossing) as a primary explanation for rapid radiation. Angiosperms do indeed exhibit attributes of the genetic and mating systems that are exceptional among vascular plants and favour consistently high speciation and low extinction rates. Such attributes include the annual habit, homeotic gene effects, accentuated hybrid polyploidy and asexual reproduction [103]. Annuals, for example, display a higher propensity than other life forms for chromosomal and novel phenotype fixation when reproductively isolated.

Plant disciplines unexplored – evolutionary anatomy, embryology, taxonomy, phytogeography and genetics

Darwin chose animals rather than plants to explore significant new disciplines such as evolutionary embryology, anatomy and development. He also did not venture far into plant taxonomy and the details of phytogeography, the dominant interests of Joseph Hooker, who freely provided Darwin with the evidence needed from these disciplines to advance his ideas and test relevant hypotheses, especially in the years leading up to publication of *The Origin of Species*. It is probably his relatively limited experience in these specific disciplines of botany that caused Darwin to claim that he was no botanist. He made several attempts and followed several false leads in trying to ascertain the mechanism of inheritance. Blending through the transmission of minute cellular particles (gemmules) from one generation to the next was the central idea he explored, fruitlessly. Echoing Lyellian uniformitarianism in geology, Darwin's preoccupation was with barely perceptible inherited changes favoured uniformly by natural selection over long periods of time. In short, 'the finest possible grain of quantitative variation' [104] (p. 15.5). Such a focus blinded Darwin to inheritance of unit factors of qualitative effect, even though he derived classic Mendelian ratios in the progeny of crosses undertaken when investigating the sex forms of *Primula*. Like any scientist, Darwin was not immune to oversight and errors of judgement. He did not always ask the right questions, nor appreciate significant data when they lay before him. Despite these pitfalls, Darwin might well have been on to something with his ideas of blending inheritance. His pangenesis theory, largely ignored after early experiments by Francis Galton and the advent of Mendelian genetics, involved the hypothesized movement of gemmules from somatic cells to gametes and subsequent transmission to the next generation. Until recently, little evidence for this mode of inheritance existed. However, epigenetic inheritance is an active research field, yielding fresh evidence for the existence of gemmules as circulating nucleic acids and prions in plant sap and animal blood [105]. Darwin might have been correct, at least in part, for such forms of potential inheritance.

Australian botany reassessed and Hooker's conundrum

One of Darwin's enduring attributes was an ability to modify or dispense with hypotheses in the light of new evidence. His science was not faultless, as he was the first to admit. His strength, nonetheless, remained a consistent commitment to hypothesis testing and synthetic thinking. With the exception of collaboration with his sons late in life, Darwin worked largely alone at Down House, communicating with scientific colleagues mostly by mail. When testing ideas he was his own harshest critic, and he would experiment again and again to be sure of his results before refining hypotheses. His rather disparaging early impressions of Australia, formed on the *Beagle* voyage, gradually modified as he realized how singular the biota of the continent was. By the time the artist Marianne North visited the aged Darwin at Down House in 1879, he urged her to ensure that she included Australia on her itinerary to paint the world's most distinctive plants in the wild [106]. This reassessment by Darwin was prompted in part by Joseph Hooker's increasing enthusiasm for the Australian flora as he analysed data for his pioneering biogeographical assessment of the continent [49]. Hooker wrote to Darwin in March 1855 (Darwin Correspondence Project, Letter 1638) about a significant biogeographical conundrum (Figure 6):

> . . .it is really the most extraordinary thing in the world. – The flora of Swan River i.e. of extratrop[ical] S.W. Australia will I believe turn out to be the most peculiar on the Globe and specifically quite distinct from that of N.S. Wales.

Intriguingly, Hooker considered that such high local endemism in the southwest was in some way caused by infertile soils and harsh climate inhibiting seed production and thereby allowing many species to coexist in a small area (Darwin Correspondence Project, Letter 2358, 12th November 1858). In reply, Darwin was unconvinced, urging Hooker to instead 'consider the lapse of time' (Darwin Correspondence Project, Letter 2361, 14th November 1858). Presumably, Darwin was alluding then to the geological timescales over which new species could evolve and accumulate in the southwest. Hooker responded affirmatively (Darwin Correspondence Project, Letter 2367, 20th November 1858), saying he would now focus on the great age attained by individual plants and low levels of competition ('vegetable strife') as possible explanations for high species richness, local endemism and taxonomic distinctiveness at the generic and specific levels. A few days later, when Darwin received an advanced copy of Hooker's introductory essay to the flora of Tasmania [49], which dealt comprehensively with Australian plant biogeography, Darwin was effusive in praise, saying it was 'admirably good' (Darwin Correspondence Project, Letter 2371, 24th November 1858). However, he chided Hooker for exaggerating the floristic differences between the southwest and southeast of Australia. Indeed, to some extent Darwin was right. For example, Hooker [49] estimated floristic endemism at species-level of 90% for the southwest. It is now known that it is 49% [47], although this is still extraordinarily high for a temperate continental region [107]. Repeating an idea earlier published by Lyell [108], Darwin had proposed to Hooker that perhaps the southwest and southeast of Australia had been islands at some time in the past and that such isolation might explain their divergent floras. Darwin also was keen to look at similarities rather than differences in biogeographical relationships and receive from Hooker affirmation that the floras of southwest Australia and the South Africa's Cape were related. Darwin was advocating that intervening Antarctic islands in preglacial times provided a connecting corridor for plant migration. Such affirmation on geographical relationships was not forthcoming, as in fact few species and genera are shared between the two floras either side of the southern Indian Ocean [70]. Moreover, nor did Hooker [49] retract from his views on the singularity of the southwest Australian flora with respect to that of southeast Australia or the rest of the globe. Today, on balance, Hooker seems to have been closer overall to the correct interpretation [51].

Darwin was still seeing the southwest flora through European eyes, stating: 'it is odd their [southwest v/s southeast Australia] productions have not become more mingled: but it accords with, I think, a very general rule in the spreading of organic beings' (Darwin Correspondence Project, Letter 2386, 27th November 1858). The oddness was because plant dispersal appeared to have been unusually impeded between the southwest and southeast. Darwin was still thinking in terms of glacial (Quaternary) timescales. In Europe, plants had rapidly migrated distances equivalent to that separating southwest from southeast Australia across postglacial landscapes, and this interested Darwin. Astoundingly, the isolation and local endemism of the southwest flora is now known to be at least Eocene in age [47]. Severe impediments to plant dispersal have existed over periods unimaginable to a European plant biogeographer. Theory explaining this extraordinary phenomenon, first quantified by Hooker, is emerging only just now [51]. Darwin annotated his copy of Hooker [49] adjacent to sections dealing with southwestern Australia with the words: 'Was not SW Corner an archipelago with representative species like Galapagos' [48] (p. 64). With considerable prescience, Darwin was proposing that allopatric replacement series of local endemics might underlie the floristic species richness of the southwest. Darwin was only wrong in the proposed mechanism of isolation, suggesting marine inundation and formation of continental archipelagos, a phenomenon now known to be confined to elevated peninsulas and hilltops along the south coast. Most of the old plateau of the southwest has been spared inundation for many hundreds of million years. Isolation instead has occurred through fine-scale terrestrial mosaics of soils, hydrological conditions, slight topographical change and moderate climatic fluctuations [47]. Twenty years later, Darwin and Hooker had cause to revisit the issue of the peculiarity of the southwest Australian flora when Alfred Wallace [109] published in *Island Life* a section on the floras of south-eastern and south-western Australia. Wallace foresaw the modern evidence that the southwest remained an island when

Cretaceous seas covered large areas of central and eastern Australia. He speculated that this south-western island supported a flora rich in endemics from which today's species-rich endemic plants were derived. Wallace's interpretation took Hooker's [49] hypothesis on the age of the southwest landscapes and their flora a step further back in time. Hooker conveyed to Darwin that he differed with Wallace on attributing such a great age to the southwest flora, and he instead ascribed its peculiarities to isolation from the rest of Australia by an inland sea (Darwin Correspondence Project, Letter 12838, 22nd November 1880). Darwin's response the next day made no further reference to the southwest flora.

Darwin's interest in the Australian flora extended to pollination mechanisms in the Goodeniaceae and for such striking plants as Sturt's desert pea (*Swainsona canescens*; [110]). He corresponded on Goodeniaceae with the Swan River Colony's resident botanist James Drummond in 1860, receiving information that backed up Hooker's assertion about the extremely poor seed set evident in many southwest Australian plants. Again, only relatively recently has this phenomenon become better elucidated [111,112]. Rather than solely being caused by low-nutrient soils, as Hooker first thought, seed sterility is often caused by genetic system responses to overcome the effects of inbreeding in small isolated populations that might persist for millions of years in some cases [51,113]. Darwin did not comment further on such matters to Hooker, Drummond or others, presumably deciding that resolution of such problematic phenomena was best left to those better placed geographically to work on the Australian flora. Darwin corresponded with many contacts in eastern Australia, including his collector on the *Beagle*, Syms Covington, who sent barnacles from the New South Wales coast back to his old master in England. Comments in Darwin's correspondence regarding eastern Australian plants were brief and less engaging than those with Hooker regarding the south-western flora. The enigma of old Southern Hemisphere floras and their evolution continues to be overlooked, ignored or regarded as a minor exception by some in global models and theory [114–116]. Hooker's conundrum regarding the richness and 'peculiarity' (high endemism) of the south-western Australian flora continues to surprise and intrigue those who choose to look.

An updatable global list of plant names

A relatively unknown and final contribution Darwin made to botany was in the form of a bequest to pay for the compilation of an index to the names and authorities of all known flowering plants and their countries of occurrence. Hooker had raised the need for such a work in 1880, and Darwin, seeing the value of an ongoing global taxonomic inventory, committed in January 1882 to donate £250 p.a. for four or five years. He was thus the patron of what became *Index Kewensis*, the forerunner of the *International Plant Name Index* now online (http://www.ipni.org/) and an essential prerequisite for global plant conservation and the sustainable use of plants. This generous donation was made just a few months before Darwin's death.

Botanical science legacy and conclusions

Darwin stands as a remarkable natural historian, as well as an experimental plant scientist, ecologist, morphologist and evolutionary biologist, without peer in his day. He devoted most of his professional career, in what his son called his physiological phase [11], to work using plants as the objects for study and experiment. Although he used the simplest of equipment, his approach led to ideas that have changed the world. Darwin was the first to explore the rich fields of enquiry that the theory of evolution by natural selection heralded. As others have emphasized, Darwin was a complex, meticulous, self-critical, synthetic, fallible and sometimes brilliant scientist [12,21]. Thomson [22] (p. 243) described Darwin's attributes as a scientist as well as any reviewers have done:

> In following the progress of Darwin's ideas, as expressed in his scientific notebooks, we see a very human Darwin who sometimes found it hard to give up a favourite notion. We see a certain ruthlessness when it came to the ownership of ideas. We also see the sheer brilliance with which he was able to seize upon a crucial element and make an intellectual breakthrough in the association of facts and theories.

Darwin's greatness 'lay in analytical thinking, rather than intuition, scientific rather than artistic judgement, and painstaking observation rather than fiery debate.' (p. 83). Above all, Darwin was extraordinarily hardworking, despite perpetual seasickness abroad and personal health issues at Down House: '…the one word that one never associates with Darwin is lazy' (p. 92). Darwin cut his teeth on a long voyage in the Southern Hemisphere, discovering and collecting remarkable items and developing and testing hypotheses primarily in geology and zoology. To this day, landmasses of the Southern Hemisphere remain richly productive for biological exploration, and the isolation of its continents and islands, many with extremely infertile soils, are still largely unexplored in any depth beyond formal taxonomic description. Extraordinary discoveries still unfold, even in temperate areas regarded by Darwin on the *Beagle* expedition as already sufficiently known then to Western science [51]. New techniques are being applied to questions intractable in Darwin's time (e.g. the molecular clock and speciation). We have much still to learn in plant science, but all who study in this field will follow in the footsteps, to some extent, of ground already trodden by biology's most celebrated naturalist.

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