Occasional Papers from
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Charles Darwin in the British horticultural press
Cover illustration:

Angraecum sesquipedale

(See page 41)

From Curtis’s Botanical Magazine,
vol. 85, pl. 5113 (1859)
Dedication to John MacLeod, RHS Professor of Horticulture

SIMON THORNTON-WOOD

Director of Science & Learning, RHS Garden Wisley

The RHS was founded upon, and remains passionately committed to, a scientific perspective on gardening. John MacLeod, who died in June after many years of service and leadership as RHS Professor of Horticulture, was the most consistent and powerful advocate for horticultural science in recent years. This volume is dedicated in memory of John.

Despite the positive impact of science on people’s daily lives, we live in an age when engaging people with its value, and encouraging a scientific perspective on the everyday problems we face, is increasingly challenging. Indeed, many of those problems might be seen by some as attributable to the unwise application of science. Scientists need both the courage and humility of Charles Darwin, in the modern age, to garner trust and support, and to best serve a sceptical audience. The leadership of science, then, is important.

John served on and chaired the RHS Science & Horticultural Advice Committee for a number of years – the very committee of which Charles Darwin was a founder member. His perspective on horticulture, moreover, was enriched by his own gardening experience. Together with his wife Janet, an accomplished sculptor who died in 2009, he demonstrated that scientific, artistic and practical perspectives on gardening can be brought together with aplomb.

Applied horticultural science is in general decline around the world – at a time when we have the most acute need to secure food supplies and to sustain the natural environment. Over recent years the scientific interests of commercial production and domestic horticulture
have lost much of their past commonality; the RHS benefited greatly
from John MacLeod’s ability to bring such interests back together.
He was Director (and more recently was a trustee) of the National
Institute of Agricultural Botany (NIAB); Chairman of the British Beet
Research Organisation; Vice-President of the International Institute
for Research on Beet, and a Board member and Director of the
National Non-Food Crops Centre.

Today, the RHS redoubles its commitment to science and particularly
to studies of the whole-organism – the applied horticultural science
that is most threatened elsewhere. We are grateful for the life of John
MacLeod and for his counsel and leadership that set us upon this
confident path.
The reception of Charles Darwin in the British horticultural press

BRENT ELLIOTT
Lindley Library, Royal Horticultural Society, London

2009 was the Year of Darwin, but little of the publicity lavished on him concerned his work with plants. This is curious for a man who devoted the last twenty years of his life to botanical research, six of whose 14 books were purely botanical, as were 66 out of the 152 Collected Papers in Paul Barrett’s edition (Darwin, 1977) – or 80 out of 251 in the new edition of Charles Darwin’s Shorter Publications (Darwin, 2009), not counting those on earthworms and vegetable mould. Darwin’s public reputation rests much more firmly on zoology than botany, now as in his lifetime. In 1880, on the occasion of the award to Darwin of a prize from the Turin Academy, a pseudonymous writer in The Garden wrote, “A few years ago we had never heard of him as a botanist at all” (“Justicia”, 1880: 11). This writer must have been inattentive, however, for five years earlier the eighth volume of that very magazine had been dedicated to Darwin, with a full-page portrait. Even those who are aware of his botanical work, however, might be surprised to hear the valedictory pronouncement of D. T. Fish: “No man has done more to raise horticulture than he who has been laid in his right place in the Great Abbey” (Fish, 1882).

This paper will trace the response of the horticultural press to Darwin’s work. Most of the material comes from four journals, the four leading weekly gardening newspapers of the nineteenth century. We do not have circulation figures for these journals, but their primary audience was the country house and its gardening

Because of the variety of editions of several of Darwin’s works, references to them in this paper simply give the chapter numbers, not page references.
Fig. 1. Charles Darwin (1809–1882); carte-de-visite photograph by Ernest Edwards, London, 1866.
staff; larger estates would subscribe to more than one title, and make them available in the bothy for the staff to read. But as the range of correspondents whose letters were published indicates, many amateur gardeners read one or more of them regularly. The *Gardeners’ Chronicle*, under John Lindley’s editorship, was particularly important for its coverage of botanical matters in addition to horticultural.

**The Voyage of the Beagle**
Fitzroy’s account of the *Beagle* voyage was published in four volumes, the final volume of which consisted of Darwin’s natural history observations, later separately published as the *Journal of Researches into the Geology and Natural History of the Various Countries visited by H.M.S. Beagle* (1839). There were no reviews in the horticultural press, which was still in its childhood. Loudon’s *Gardener’s Magazine*, strictly speaking the first gardening magazine in Britain, ran, first as a quarterly and then as a monthly, from 1826 to 1843; neither it nor its other monthly rivals extended their remit into general natural history so far as to review an account of explorations.

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But Darwin’s *Journal* gradually became an immensely popular travel book, and (since his work on barnacles warranted no coverage in the botanical or horticultural press) provided the foundation on which his reputation stood at the time the *Origin of Species* was published. A delightful tribute to the *Journal* can be found in the notice of dedication to Darwin of the eighth volume of William Robinson’s magazine *The Garden*:

Mr. Darwin’s first work, and still to our mind his best work, is his ‘Journal of His Voyage as Naturalist of the “Beagle”’. This may not inaptly be called the ‘Waverley’ novel of naturalists. We may not have read it quite so often as the ‘Antiquary’ or ‘Rob Roy’; but, as with them, whenever we do re-read it we do so with renewed pleasure. There is a freshness and clearness about it, combined with a power of description that never palls – and there is the same delightful under-current of thought upon every subject that gives such a charm to his other works; he not only sees what is before him and tell one what he sees in vivid language, but turns it over in his mind, and takes one along with him, confidentially as it were, as he does so. To our mind it is one of the most delightful books in the English language (Robinson, 1875).

When the reverence with which Sir Walter Scott was regarded in the later nineteenth century is taken into consideration, this is high praise indeed, though it leaves questions of truth and accuracy curiously to one side. But it is a useful reminder that Darwin’s literary style had a great deal to do with the spread of his reputation, and over and over in the course of this paper we will encounter statements about the accessibility, the simplicity, and the persuasive rhetoric of his writing. Indeed, some of the testimonials he received convey the impression that he was the first writer to make botany lively reading. “He made the dry bones live; he invested plants and animals with an history, a biography, a genealogy, which at once conferred an interest and a dignity on them”, said the *Gardeners’ Chronicle* (Anon., 1875a: 308), while a writer in *The Garden* complained that “Hitherto our botany
has been all words, and very hard and ugly ones”, mostly to do with
taxonomy (“Justicia”, 1880: 11).

“The charm of Mr. Darwin’s work”, wrote a reviewer of The Effects of
Cross- and Self-Fertilisation, seldom remembered today as a lively
read, “is soon felt by the reader, for although as regards the style it is
pitched in a cold matter-of-fact way, the first half dozen sentences fix
our attention, and serve us as a bait to draw us into the trap, and so
we become eager and hungry disciples until the story is told and the
end has come” (Anon., 1877: 51). The figure of speech may testify
to the impact of Insectivorous Plants a couple of years earlier. Indeed,
more than one reviewer used the term “romance” to describe
Darwin’s writing, particularly when reproduction was an issue: from
a reviewer of Cross- and Self-Fertilisation who said that “the facts that
are marshalled before us as results seem to be steeped in the atmo-
sphere of romance” (Anon., 1876b), to Maxwell T. Masters, who
said of the discussion of sexual selection in The Descent of Man that “No romance exceeds in interest this portion of Mr. Darwin’s volumes” ([Masters], 1871).

Masters would eventually remark on the simultaneous publication in 1880 of The Power of Movement in Plants, Disraeli’s Endymion, and Tennyson’s Ballads and Other Poems, asking his readers to “discuss at length the relative value of these productions to the human race, and the probable duration of their influence” ([Masters], 1880). Nor was it only the nineteenth century that responded this way to the power of his writing as writing; the poet Basil Bunting, born in 1900, would later recommend that “Suckling poets should be fed on Darwin until they are filled with the elegance of things seen or heard or touched” (Makin, 1991: 16).

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Table 2. Darwin’s publications in book form

<table>
<thead>
<tr>
<th>Year</th>
<th>Title</th>
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<tbody>
<tr>
<td>1839</td>
<td>Journal of Researches … during the Voyage of HMS Beagle</td>
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<tr>
<td>1840–1843</td>
<td>The Zoology of the Voyage of HMS Beagle</td>
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<td>1842</td>
<td>The Structure and Distribution of Coral Reefs</td>
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<td>1851–1854</td>
<td>A Monograph of the Sub-class Cimipedia</td>
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<tr>
<td>1859</td>
<td>On the Origin of Species by Means of Natural Selection</td>
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<tr>
<td>1862</td>
<td>The Various Contrivances by which Orchids are Fertilised by Insects</td>
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<tr>
<td>1865</td>
<td>The Movements and Habits of Climbing Plants (2nd ed., in book form, 1875)</td>
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<tr>
<td>1868</td>
<td>The Variation of Plants and Animals under Domestication</td>
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<tr>
<td>1871</td>
<td>The Descent of Man</td>
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<td>1872</td>
<td>The Expression of the Emotions in Man and Animals</td>
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<td>1875</td>
<td>Insectivorous Plants</td>
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<td>1876</td>
<td>The Effects of Cross- and Self-Fertilisation in the Vegetable Kingdom</td>
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<td>1877</td>
<td>The Different Forms of Flowers on Plants of the Same Species</td>
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<td>1880</td>
<td>The Power of Movement in Plants</td>
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<tr>
<td>1881</td>
<td>The Formation of Vegetable Mould, through the Action of Worms</td>
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But there is more to be said about the comparison with the Waverley novels. A year before Robinson’s dedication, Robert Louis Stevenson had published an article in the *Cornhill Magazine* which examined “the difference between Fielding and Scott. In the work of the latter, true to his character of a modern and a romantic, we become suddenly conscious of the background.” By this he meant that while Fielding’s characters are presented as self-sufficient individuals, whose interests are rational or at least largely conscious, Scott’s characters are presented as products of particular environments, the influence of which is as determining as rational decision-making. “He can show his readers, behind and around the personages that for the moment occupy the foreground of his story, the continual suggestion of the landscape … the fatality of distant events, the stream of national tendency, the salient framework of causation” (Stevenson, 1874: 181). If we take this as a mode of thinking about Scott that was in the air in the 1870s, Robinson’s comparison might therefore suggest that, in Darwin’s writing, there is a greater consciousness of the environment as a whole than in the work of his predecessors.

To test this, compare Darwin’s narrative of the *Beagle* voyage with the travel writing of a botanist of the previous generation, as each examines a problem involving grassland. First, take Darwin, on contrasting vegetation patterns:

I was very much struck with the marked change in the aspect of the country after having crossed the Salado. From a coarse herbage we passed on to a carpet of fine green verdure. I at first attributed this to some change in the nature of the soil, but the inhabitants assured me that here, as well as in Banda Oriental, where is as great a difference between the country around Monte Video and the thinly-inhabited savannahs of Colonia, the whole was to be attributed to the manuring and grazing of the cattle. Exactly the same fact has been observed in the prairies of North America, where coarse grass, between five and six feet high, when grazed by cattle, changes into common pasture land. I am not botanist enough to say whether the
change here is owing to the introduction of new species, to the altered growth of the same, or to a difference in their proportional numbers. Azara has also observed with astonishment this change: he is likewise much perplexed by the immediate appearance of plants not occurring in the neighbourhood, on the borders of any track that leads to a newly-constructed hovel. In another part he says, “ces chevaux (Sauvages) ont la manie de préférer les chemins, et le bord des routes pour déposer leurs excréments, dont on trouve des monceaux dans ces endroits.” Does this not partly explain the circumstance? We thus have lines of richly-manured land serving as channels of communication across wide districts (*Beagle*, chapter 6).

Compare this with William Jackson Hooker’s *Journal of a Tour in Iceland* (1811; cited here from the 2nd edition, 1813). Hooker had been told that the feeding habits of sheep had altered in the wake of a volcanic eruption:

It was still farther remarked in different parts of Iceland, during the summer of 1783, that the sheep, in direct opposition to the experience of the inhabitants, and to the supposed natural propensity of the animals themselves, avoided the dry elevated places, and even the heaths and commons, which most abounded in rich grass; and, as soon as they were driven up to the heights, snuffed at the earth and searched among the grass, but without tasting it: then immediately turning round, ran to the morasses and wet places... the grass and herbage on heaths and commons, where sheep principally delight to go, is small and short. Consequently, as often as a heavy rain fell upon the ashes and sulphureous dust here collected, these were converted into a kind of paste which could not penetrate the soil; so that all vegetation was covered with it: whereas, in the morasses, this paste was gradually dissolved in the watery soil, and, as the grass in such situations generally rises to a considerable height, the mixture of ashes only affected the lower part of it (Hooker, 1813: vol. 2, 231–232).
Hooker was intent, possibly beyond the limits of strict accuracy,¹ on recording the species of mosses and lichens he encountered, but felt no curiosity about the differing growth patterns of the grasses; his description forms part of an account of the effects of volcanic ash, an attempt to explain an unusual phenomenon, rather than an inquisitive account of the operations of the normal environment. Whatever the interest of Hooker’s account, it is Darwin’s that invokes “the salient framework of causation”.

Stevenson suggested that “art precedes philosophy and even science ... art is the pioneer of knowledge” (Stevenson, 1874: 182), and it is intriguing to speculate on Scott’s possible influence on Darwin; we know of the “awe and reverence” with which the young Darwin regarded Scott (Darwin, 1958: 52). Such questions, however, go beyond the limits of this paper.

**Darwin as a contributor to the *Gardeners’ Chronicle***

Darwin’s first letter to the *Gardeners’ Chronicle* was published in the issue of 9 September 1843; the subject was double flowers (Darwin, 1843). This was a subject which John Lindley, the editor of the journal, had dealt with on more than one occasion; in 1826 he had published an article in the *Transactions of the Horticultural Society* in which he attributed doubling to the conversion of the flower’s male organs into female (Lindley, 1826), and he briefly restated this in his *Theory of Horticulture* (Lindley, 1840: 57). Darwin’s letter addresses Lindley directly: “You state in your ‘Theory of Horticulture’ that the origin of double flowers is not well understood” – though this statement does not appear in the *Theory*; Darwin had evidently chased up Lindley’s earlier article, which was much more tentative in its rhetoric. Darwin offered an alternative hypothesis, that double

¹ “The plants gathered by Hooker himself were all destroyed when the ship by which they were sent from Iceland to England caught fire. Some of the species Hooker has entered in his list from memory, and in such cases it has not always been possible to corroborate the finds” (Gröntved 1942: 8–9).
Fig. 3. John Lindley (1799–1865), Assistant Secretary of the Horticultural Society, and editor of the *Gardeners’ Chronicle*. Undated carte-de-visite photograph by Sawyer’s Italian Studios, Norwich.
flowers arose because the plants had been rendered sterile through some environmental change, and converted their “organizable matter” into petals. Lindley replied that “this is at least as reasonable an hypothesis as any that we have seen”.

And thus began Darwin’s long career as a contributor to the *Gardeners’ Chronicle*, which became his principal (though not sole) medium for canvassing the horticultural community for information. Lindley learned from this first letter to treat him with respect, and Darwin owed a debt to Lindley’s works, using his *Vegetable System* as his guide to taxonomy, and even adopting some of Lindley’s curiosities of nomenclature.¹ Lindley tried at various periods to reform English as well as Latin plant nomenclature (Elliott, 1992: 475–477), proposing the use of abbreviated versions of Latin names as English terms; some of his coinages, like “conifer” and “orchid”, have stood the test of time, but others, like “odontoglot” for odontoglossum, “oncid” for oncidium, “ceanothe” for ceanothus, have not. Darwin can be seen using Lindley’s terminology in an 1857 letter on “hybrid

¹ And possibly even his orthography. Readers may note the inconsistency in the spelling of “fertilisation / fertilization” and related words in the various quotations in this article. Honoured authorities from Samuel Johnson to the *Oxford English Dictionary* gave preference to “-ization”, but there was a strong undercurrent in favour of the French “s” spelling, which became mainstream practice in 20th-century England. (A scholar of the old Oxbridge sort once explained to me: it is easy to determine which words should be spelled with “s” and which with “z”. If the word entered English from French, use “s”; if it came directly from Greek, use “z”. So no difficulties there.) Darwin used the “s” spelling, but his usage was generally ignored by his reviewers; even in citing his titles, the magazines tended to say “Fertilization”. Even Darwin’s publisher, John Murray, could not ensure consistency: in every edition of *Cross- and Self-Fertilisation* the lettering on the spine title rendered the word as *Fertilization*. Now John Lindley consistently used the “s” spelling, as did the *Gardeners’ Chronicle*, under his editorship. Darwin’s “s” usage may have resulted from adapting to the conventions of the *Chronicle*. 

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B. ELLIOTT

Ideas of plant evolution before 1859
Before we look at the response to the *Origin of Species* in the horticultural press, let me establish a context by summarising quickly the notions of evolutionary development that would have been familiar to the botanical and horticultural communities by 1859.

First of all, a caveat about the use of the word “evolution”. Nowhere in the 1859 edition of the *Origin of Species* did Darwin use the word “evolution”. This may well be because the word bore with it implications of progressive development that Darwin wanted to avoid: an inherent progression in Nature from primitive to complex, inferior to superior, moving towards increasing perfection, and culminating in man. It was particularly associated with Herbert Spencer, who had been trumpeting “the Theory of Evolution” since his essay on “The Development Hypothesis” in 1852. It is worth remembering Morse Peckham’s handy formulation: “Spencer uttered a law of evolution; Darwin proposed a theory of the origin of species from pre-existing species” (Peckham, 1959: 26). In the fifth edition (1869), Darwin finally allowed the word into his text – though not into the index. I suspect that he probably thought that it was no longer worth struggling against common usage, in much the same way that the leading newspapers in the 1980s abandoned the struggle to keep the word “media” as a plural. In what follows, I shall follow contemporary practice and use the word “evolution” to refer to the total sequence of species changes over time, but let it be remembered that this is not the usage of the second quarter of the nineteenth century.

The idea of species change was not new, or rather, the idea of developing variation in successive generations of living things was not new. It is easy to find vague suggestions of the idea in ancient Greece, Rome, and the mediaeval Muslim world. All these, however,
were philosophical, unscientific speculations, since the necessary biological knowledge was not available. And the same is true of what might be described as the first romances of development in natural history, from *Telliamed* to Erasmus Darwin: assertions of a progressive and chronological scale of development from the microbe to man, without any suggestion of a mechanism to account for the changes.

Species change is not a meaningful concept until there are accepted criteria for defining a species. Before the eighteenth century, there was no agreement on the status of taxonomic units; no generally agreed vocabulary for distinguishing genera, species, and varieties; no theory of plant reproduction, and little recognition of sexual differences in plants; and, at a time when the spontaneous generation of cryptogams and invertebrate animals had yet to be rejected, no sense of any necessary limits to the production of variations. Sir Walter Raleigh, in his *Historie of the World* (1614: Book I, chapter vii, section 9), suggested that Noah’s Ark was large enough to hold all the kinds of animals,¹ because the great variety of forms found today developed after the Flood; he even drew an analogy from the modification of cultivated plants: “We also see it daily that the nature of fruits are changed by transplantation, some to better, some to worse, especially with the change of climate. Crabs may be made good fruit by often grafting, and the best melons will change in a year or two to common cucumbers by being set in a barren soil” (Raleigh, 1829: 214–215). So long as this was the available standard of information, ideas of transformation posed no theoretical challenge.

¹ Creationists never seem to address the question, what was the state of the world’s vegetation after some eleven months’ submersion in salt water? An olive leaf, presumably in good condition, is the first sign that the waters are abating; how had it survived? There is no reference to Noah having maintained a potted arboretum on board the Ark, yet before we know it, Noah is cultivating grape vines.
So it was not until plant taxonomy had become an established discipline that species change could be meaningfully discussed. The first scientific theory of evolution was proposed by Lamarck (*Philosophie Zoologique*, 1809). Much ink has been spilt over the question of the philosophical underpinnings of his theory, and the extent to which he was influenced by the ancient notion of the Chain of Being. Suffice it to say that the only direct mechanism of alteration he described was that of organisms’ changing habits resulting in inheritable alterations to bodily structures. Famous example: giraffes, having eaten the leaves within reach, stretched their necks to reach higher leaves, and as a result their offspring were born with longer necks. This theory assumed that the range of variation available to an organism was virtually limitless. Lamarck’s ideas were condemned by Cuvier, the foremost zoologist of the day, who pointed out that the lengthening of a giraffe’s neck would have required changes in shoulders and general body shape to keep the animal balanced: changes of the sort Lamarck envisaged would require a general alteration of the entire organism, not of isolated structures. While Lamarck had followers until the middle of the nineteenth century, the majority viewpoint was that Cuvier had defeated him.

The central issue in this debate was the reality of species. Cuvier’s celebrated ability to diagnose an animal’s total bodily structure from an isolated part seemed robust evidence that species had a real existence, unalterable by normal natural processes, whereas in Lamarck’s theory the status of species was ambiguous. Lamarck, at least in his early years, professed to accept the real existence of species, and in his *Flore Française* he found no difficulty in distinguishing the French plant population into genera and species, but it may be that he thought of them as having only a local or a temporally limited existence.

Today, “Lamarckianism” is used to refer to the theory of the inheritance of characteristics acquired during an organism’s lifetime,
but this was not what the label implied during Darwin’s time. From this point of view, Darwin could be as Lamarckian as the next biologist, and so for that matter could Maxwell T. Masters, who came close on occasion to denying the existence of species; indeed, argument still rages about the extent to which Darwin really believed in species or regarded them as a convenient fiction (Stamos, 2007). Such a statement as “each successive modification being retained as far as that is possible through the force of inheritance” (Darwin, 1871) leaves more than enough room for any follower of Lamarck to feel comfortable. It was not until after Darwin’s death that Weismann’s theory of the “continuity of the germ-plasm” was promulgated, with its implication that characteristics acquired during an organism’s lifetime could not be inherited by its offspring. When Darwin and his coevals rejected Lamarck, it was because of his assumption of limitless variability, not because of the inheritance of acquired characteristics.

The status of “species” continued to be much debated in the early nineteenth century, with many authorities accepting species as something existing in nature, but regarding all higher-order classifications as artificial, human speculations rather than real entities. The major textbook of logic used in English universities in the second quarter of the century represents this stage of the discussion:

If, e.g., two Naturalists differed in the one placing (as Linnaeus) all the Species of Bee under one Genus, which the other subdivided (as later writers have done) into several genera, it would be evident that there was no question of fact debated between them, and that it was only to be considered which was the more convenient arrangement; if, on the other hand, it were disputed whether the African and the Asiatic Elephant are distinct Species, or merely Varieties, it would be equally manifest that the question is one of fact; since both would allow that if they were descended (or might have descended) from the same
stock, they were of the same species, and if otherwise, of two
(Whately, 1826: 262).

By that time most naturalists accepted the reality of genera as well;
the focus of argument by the 1830s had shifted to families, with the
attempts of Lindley, Hooker, et al. to introduce natural classification
into England and overturn the dominance of Linnaeus’ artificial
system. But it was one thing to accept the existence of species, and
another to create a satisfactory definition of species as a taxonomic
unit, let alone provide unambiguous instructions on how to
determine one. Take, on the eve of the announcement of Darwin’s
theory, the pragmatic definition offered by William Benjamin
Carpenter: “The Naturalist, then, regards as distinct species those
races of Plants, the differences between which are evident, and are
such as are not likely to have resulted from cultivation or any other
external cause, and do not exhibit any tendency to alteration in
progress of years” (Carpenter, 1858: 23).

If taxonomy seemed to militate against biological evolution, what of
the nascent discipline of palaeobotany? Fossils had attracted
scientific attention for generations, but until the nineteenth century
the principal problem that fossils posed was that of the mechanism
of preservation, not the characteristics of the organisms themselves:
the Biblical flood offered a sufficient explanation for their presence.
Cuvier’s theory of a succession of catastrophes, each corresponding
to a radical discontinuity in stratification, each heralding a significant
change in the nature of the fossils preserved, allowed geologists and
biologists a framework for classifying fossil remains and building up a
picture of different ages, without requiring any speculation about
inheritance from one epoch to the next (Andrews, 1980). A	
tendency towards greater perfection in each succeeding epoch could
be remarked upon without requiring any speculation about a
mechanism of development. Lindley, for example, in his Fossil Flora
of Britain, could regard it as “a fact beyond all dispute” that
the face of the globe has successively undergone total changes, at
different remote epochs… that long anterior to the creation of man,
this world was inhabited by races of animals, to which no parallels are
now to be found; and that those animals themselves only made their
appearance after the lapse of ages, during which no warm blooded
creatures had an existence… Similar peculiarities have been also
found to mark the vegetation of corresponding periods… (Lindley
1831–1833: I, ix–x)

But Lindley set his face against any notion of what we would now
call an evolutionary development:

Of a still more questionable character is the theory of progressive
development, as applied to the state of vegetation in successive ages.
The opinion, that in the beginning, only the most simple forms of
animals and plants were created, and that, in succeeding periods, a
gradual advance took place in their degree of organization, till it was
closed by the final creation of warm blooded animals, on the one
hand, and of Dicotyledonous Trees, on the other, is one that very
generally prevails. How far this may be admissible in the animal
world, is for Zoologists to determine; but, in the Vegetable Kingdom,
it cannot be conceded, that any satisfactory evidence has yet been
produced upon the subject; on the contrary, the few data that exist,
appear to prove exactly the contrary. (Ibid., xvii).

Lindley notoriously attempted to identify all the fossil plants he
described with currently existing plant groups. Confronted by the
absence of grasses from the fossils of the coal measures, he first
produced an essentially theological explanation – “It may, indeed,
be conjectured, that before the creation of herbivorous animals,
Grasses and Sedges were not required” (ibid., xiv) – but then
produced an experimental explanation, that only certain types of
plant tissue were capable of fossilisation, so that gaps in the fossil
record did not constitute evidence for non-existence (ibid., xvii–xxii,
Within a couple of decades the assumption of a progressive sequence of organisms had been generally adopted; Sir Richard Owen could blithely say that “we presume it will be admitted that Cryptogamia, Phaenogamia, Gymnosperms, and Dicotyledonous Angiosperms constitute a succession and a progressive one” (Owen, 1851: 421). This succession did not involve any notion of ancestry.
Proponents of evolutionary theories tended to be zoologists, or at least to concentrate on zoological examples; consideration of botany seldom extended farther than the addition of “plants and” to discussions of animals. This is true even of the most notorious proposal of an evolutionary theory in the second quarter of the nineteenth century: Robert Chambers’ *Vestiges of the Natural History of Creation*. As this work helped to discredit evolutionary thinking even while Darwin was working on his theory, it is worth making a few comments on it here. Chambers’ work was published anonymously in 1845; his authorship was not revealed until the 12th edition, in 1884. The first edition relied heavily on Alexander Macleay’s quinarian (five-part) system of classification ([Chambers], 1845: 236–276); this entire section was dropped from later editions in favour of a less programmatic chapter on “Affinities and geographical distribution of organisms”, (Chambers, 1884: 238–334). Chambers

Fig. 5. Darwin’s alternative: the tree diagram from the *Origin of Species*. 
did not think it necessary to augment Macleay with a classification scheme for plants, even though he could have found comparable ones in Lindley or Baskerville. What little material there was on plants was largely added after the shift away from Macleay. While abandoning Macleay may have allowed the successive editions of the book to adapt to changing fashions in science, it also sapped something of the energy found in the first edition; much of the progressive rewriting eroded the force of his original phrasing.¹ Chambers’ arguments were most effective in undermining the idea of special creation: “the idea of a separate exertion for each [organism] must appear totally inadmissible. The single fact of abortive or rudimentary organs condemns it; for these, on such a supposition, could be regarded in no other light than as blemishes or blunders” ([Chambers], 1845: 197–198; see Chambers, 1884: 188 for a watered-down version). But as for a mechanism for the transformation of species, there was no concrete suggestion. This absence of definable causative factors meant that, whatever the book’s effect on the general public, it was roundly rejected by the scientific community, and became a model for how a theory of evolution should not be presented.

Much of the activity of taxonomists during the second quarter of the century lay in a form of diagram-making: the arrangement of taxa in a pattern which would present a visually clear demonstration of the relations between their various characters. This activity has been well documented by historians of zoology (Winsor, 1976), less so by historians of botany, but the same projects, and sometimes the same theories, had botanists drawing circles and triangles as enthusiastically as their present-day successors draw cladograms. Alexander Macleay had proposed a quinarian classification for animals, and quinarian

¹ A variorum edition of the *Vestiges* (including its supplement, the *Explanations*, whose text was variously incorporated into later editions) is badly needed. It is over fifty years ago that Morse Peckham first called for such a project; we have now had a critical study (Secord, 2001); it’s about time that a proper variorum edition was compiled.
Fig. 6. Tree diagram of the plant kingdom from Ernst Haeckel, Generelle Morphologie der Organismen, 1866.

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schemes for plants appeared in the 1830s, whether star-shaped (Lindley, 1838: fig. 4, p. 22) or circular (Baskerville, 1839).

Darwin, generally speaking, accepted the principles of “natural classification” that Candolle, Lindley, Hooker et al. had developed, but argued that this classification was the result of descent rather than of morphological principles or an overall plan: “propinquity of descent, – the only known cause of the similarity of organic beings, – is the bond... which is partially revealed to us by our classifications” (Origin, chapter 13; and see Winsor, 2009). In place of the circular or star-shaped classification diagrams of the previous generation, he introduced a tree diagram to show the spreading of species from a common ancestor. Darwin’s example was purely suggestive of how to do it; the first attempt I know at arranging the plant kingdom in a tree diagram was made seven years later by Haeckel (Haeckel, 1866: II tab.2; Dayrat, 2003; see fig. 5, p. 23, and fig. 6, p. 25).

*The Origin of Species, 1859*

The first public revelation of Darwin’s theory was made at a Linnean Society meeting on 1 July 1858, when a joint paper by Darwin and Alfred Russel Wallace was read; it received no notice in the *Journal of Horticulture*, and in the *Chronicle* it appeared only as an item in the list of papers delivered. Darwin then hurriedly got to work writing a paper to give a more detailed abstract of his theory. Originally intended to be 30 pages, it kept resisting his attempts to abridge it, and finally it became the book-length *Origin of Species*.

The *Gardeners’ Chronicle* published a two-part review on 31 December 1859 and 21 January 1860; it was formerly thought that Lindley, as the editor, was the reviewer, but Lindley in fact asked Joseph Hooker to do the review. This was followed on 3 March by a reprinting of Thomas Huxley’s review from *The Times*, which the *Chronicle* hailed as a “brilliant notice” ([Hooker] 1859–1860; Huxley 1860).
Darwin’s theory received its first well-publicised public discussion at the annual meeting of the British Association for the Advancement of Science, in the summer of 1860. The Gardeners’ Chronicle reported the proceedings in extensive detail. What has entered public consciousness is Huxley’s rejoinder to Bishop Wilberforce, but Huxley’s remarks were not quoted in the Chronicle; instead, a telling rejoinder from Joseph Hooker was given at length, Hooker by this time having secured fame both as a plant collector in the Himalayas and as the greatest authority on the botany of Australia and New Zealand:

Dr. Hooker, being called upon by the President to state his views of the botanical aspect of the question, observed, that the Bishop of Oxford having asserted that all men of science were hostile to Mr.
Darwin’s hypothesis – whereas he himself was favourable to it – he could not presume to address the audience as a scientific authority. As, however, he had been asked for his opinion, he would briefly give it. ... As regarded his own acceptance of Mr. Darwin’s views, he expressly disavowed having adopted them as a creed. He knew no creeds in scientific matters. ... For many years he had held to the old hypothesis, having no better established one to adopt, though the progress of botany had, in the interim, developed no new facts that favoured it, but a host of most suggestive objections to it. On the other hand, having fifteen years ago been privately made acquainted with Mr. Darwin’s views, he had during that period applied these to botanical investigations of all kinds in the most distant parts of the globe, as well as to the study of some of the largest and most different Floras at home. Now, then, that Mr. Darwin had published it, he had no hesitation in publicly adopting his hypothesis, as that which offers by far the most probable explanation of all the phenomena presented by the classification, distribution, structure, and development of plants in a state of nature and under cultivation; and he should, therefore, continue to use his hypothesis as the best weapon for future research, holding himself ready to lay it down should a better be forthcoming (Anon., 1860b: 714).

Darwin’s theory was added to over subsequent editions and in supplementary works; one particularly significant addition was his incorporation of Herbert Spencer’s phrase “survival of the fittest” in the fifth edition (1869). It might therefore be useful to give the briefest of summaries of the theory as presented in 1859. Darwin’s theory was stimulated by observing the breeding of varieties of domesticated plants and animals. By carefully selecting the individuals they allowed to mate, breeders had produced varieties that were hard to recognise as the same species (e.g. toy poodles and Great Danes, cabbages and cauliflowers.) Darwin reasoned that anything that human beings could do by selecting parentage could also, given sufficient time, happen in nature without deliberate intention.
Within any species there is a range of variation. Under ordinary circumstances, these variations do not develop into distinct varieties, because mating throughout the population keeps them in check. (If poodles and Great Danes mate, the result is a mongrel, and progressive mongrelisation results in the distinct varietal characters being lost.) But any variations that increased an organism’s chances of survival, and of successfully mating, would tend to be preserved in future generations. Competition for survival would have the same effect in the wild that the deliberate selection of individuals for mating had in domestic breeding: it encouraged the preservation of varieties distinct from their parent stock. As long as these varieties could continue to breed with the normal population, they would remain merely varieties. But if varieties became geographically isolated from the rest of the population, or intermediate forms died out, they could be considered as separate species.

**In the wake of the *Origin*: press debates**

During the years immediately succeeding the publication of the *Origin*, Darwin had to step into the public arena by way of the gardening magazines.

First of all came the priority dispute. Patrick Matthew’s claim to priority in discovering the theory of natural selection was published in the *Gardeners’ Chronicle* on 7 April 1860, and Darwin replied two weeks later acknowledging Matthew’s “anticipation” (Matthew 1860; Darwin 1860a; Dempster 1983: 28–43). Scholars have differed in their assessments of the likelihood of Darwin having encountered Matthew’s *On Naval Timber and Arboriculture* (1831); the fact that Darwin ordered a copy after seeing Matthew’s letter in the *Chronicle* argues strongly for a lack of previous acquaintance with the work, and it must be said that the title was unlikely to recommend it as a source of speculation about speciation. It received one notice in the horticultural press. Loudon’s *Gardener’s Magazine* noticed it briefly in February 1831, promising a detailed review to follow, but for whatever reason that review was delayed, and when it did appear (in
Fig. 9. George Maw (1832–1912), tile manufacturer and botanist; carte-de-visite photograph by Maull & Co., London, 1874.
December 1832, while Darwin was at sea) it was accompanied by apologies both for tardiness and brevity. All it offered on the subject of speciation was a single sentence: “One of the subjects discussed in this appendix is the puzzling one, of the origin of species and varieties; and if the author has hereon originated no original views (and of this we are far from certain), he has certainly exhibited his own in an original manner” (Loudon, 1831; Loudon, 1832: 703). This might have attracted Darwin’s attention a decade later, had he encountered it; but there is no evidence that he ever looked at the Gardener’s Magazine.

Other claimants to priority would arise in more zoological circles, and Darwin added an historical excursus on his predecessors in later editions of the Origin. It was not long, either, before national pride began to muddy the waters. The Chronicle reported in 1865 that, at a conference in Germany, C. H. Schultz-Schultzenstein had presented a paper which “boldly claimed all that was sound in DARWIN’s theory as German property, treated long ago by German savants in a more satisfactory scientific manner” (Anon., 1865b). A similar claim on behalf of the French was made a few years later in Quatrefages de Bréau’s Charles Darwin et ses Précurseurs Français, which was reviewed, fairly positively, in the Chronicle by a reviewer signing himself “H.” (“H.”, 1871).

As for the reviews that appeared in the various magazines, Darwin did not generally respond in the press, although he might reply privately. One such case was that of George Maw. Maw (1832–1912) was a noted tile manufacturer, but also an amateur botanist who collected plants in Eastern Europe, the Levant, and North Africa, and would eventually publish a major monograph on The Genus Crocus (1886). In 1861 he reviewed the third edition of the Origin for The Zoologist, praising Darwin’s writing –

no difficulties that strike him are slurred over; each one is fairly and boldly met; entire chapters are devoted to self-imposed objections to
the theories advanced; indeed, the whole work has more the
carder of an equally-balanced controversy than the pleading of an
author on behalf of his subject (Maw, 1861: 7578).

– and allowing his arguments a (very) limited degree of viability:

there is a measure of truth in Mr. Darwin’s deductions, that
genealogical relationship between species is here and there true to a
limited extent, – just to that extent to which naturalists are puzzled in
discriminating forms which rank below what are universally
acknowledged as good species (Maw, 1861: 7611).

Darwin was pleased with the careful presentation of his arguments,
and wrote to Maw that “My opponents would have lost nothing if
they had all treated me as fairly as you seem to have done” (letter,
13 July 1861). But Maw’s final judgment was that Darwin’s theory
was inconsistent with the Bible, and must therefore be jettisoned;
further, that Darwin had deliberately challenged Christianity: “these
passages pain us, because we believe their thoughtful author must
have considered their bearing upon Revelation” (Maw, 1861: 7609).
Darwin chided Maw: “I think it is a pity to mingle science &
religion”, and won Maw’s respect sufficiently for the two of them to
carry on a friendly correspondence that lasted until 1880, with
fifteen surviving letters from Darwin preserved in the RHS Lindley
Library, along with one from Emma Darwin on Charles’ behalf.

One press commentator, however, did spur Darwin into public
action. Donald Beaton (1802–1863) was probably the most important
gardening journalist at mid-century. Born into a Gaelic-speaking
Highland family, he learned English only as an adult and, in common
with various other writers who made their careers in English as a
second language, he developed a flamboyant style of writing which
made his weekly contributions to The Cottage Gardener (and, after it
changed title, the Journal of Horticulture) entertaining whether his
subject matter was plant breeding, garden design, or the use of coir
Fig. 10. Donald Beaton (1802–1863), head gardener at Shrubland Park, Suffolk, and columnist of *The Cottage Gardener*; unattributed carte-de-visite photograph dated 1860.
for mulching. In the 1840s he was the first successful breeder of bedding pelargoniums, and he hypothesised continually about the biology of cross-breeding from the point of view of an active propagator (Elliott, 1991). In 1860 he launched an assault on Darwin, by contesting the validity of the idea of fixity of species (and thus rendering the process of speciation unproblematic). “I have not read Mr. Darwin’s work on the origin of species; but I can originate botanical species almost at will – that is, produce a plant different from all other plants, which will reproduce itself pure from seed to the end of time – that I am quite certain of… there is not the slightest natural difference between a botanical species and a cross-bred variety which will reproduce itself from seeds” (Wooler & Beaton, 1860: 211). In a statement elsewhere in the same issue, he wrote that “All the attempts at classifying, and the pretended results of classifying, the results of crossing species and varieties, and all that is written on the reversion of crossed species and varieties, and the whole theory of mules, are absolutely and altogether the very reverse of innumerable facts within my own personal knowledge” (Beaton, 1860).

Darwin challenged Beaton the following year; his letter appeared in the Journal of Horticulture on 14 May 1861, with a reply from Beaton appended, saying that “I do not know an instance ‘of the natural crossing of varieties’” (Darwin & Beaton, 1861a: 113). Darwin wrote to Hooker that same day that

I have been going through the Cottage Gardener of last year, on account chiefly of Beaton’s articles: he strikes me as a clever but d—d cock-sure man (as Lord Melbourne said) & I have some doubts whether to be much trusted. I suspect he has never recorded his experiments at the time with care. He has made me indignant by the way he speaks of Gärtner, evidently knowing nothing of his work. – I mean to try and pump him in the Cot. Gard. [i.e. Journal of Horticulture – it had only changed its title the previous month], & perhaps defend Gartner [sic]. – He alludes to me occasionally, & I
cannot tell with what spirit. He speaks of “this Mr. Darwin”, in one place, as if I were a very noxious animal (Darwin, 1994: 126–127; see also [letter 3152]).

Gärtner’s defence had to wait. Darwin first of all replied that Beaton must be confining “his remark to the plants of the flower garden”, and pointing out the phenomenon of crossing in cabbages, radishes and onions (Darwin, 1861a). At this point the Reverend Henry Honywood Dombrain, who contributed regularly to the *Journal of Horticulture* under the name “D., Deal”, proposed a query in a survey of auriculas:

How comes it to pass, that if an Auricula throws up a side bloom it is pretty sure to be in character; but that if it be from the heart of the flower – no matter what the edge may be, green, grey, or white – it is just as likely to come in any other class as the one it belongs to? Again: I have had kinds which one year have come all green-edged, the next year all grey. Can Mr. Darwin, or Mr. Beaton, or anybody enlighten me on the first of these points? ([Dombrain], 1861: 174).

Darwin replied asking for more details, and suggesting that “if the many acute observers who read *The Journal of Horticulture* would contribute their knowledge on such points”, light could be thrown on the laws of variation; his attempted explanation involved an analogy with the tendency of peloria to be most frequent in terminal flowers (Darwin, 1861b). Beaton’s reply, a few weeks later, began, “There is a greater harvest to be reaped out of that question than any one of us is yet aware of”, and proceeded (with a confusion of vocabulary between genus and species):

Well, I have seen two things since Mr. Darwin put the question about the central flower, and one of them has made a revolution in my own ideas on a branch of my daily work – a branch in crossing. And I shall make a clean breast of it to save the back. I saw two flowers growing in one head, and they represented two good botanical genera. The
origin of two genera were in that head. The central flower represented the Geraniums of Europe, and the rest of the flowers were of true Pelargoniums; the first with regular and the second with irregular flowers... The other flower [a shamrock clover obtained from John Salter of the Versailles Nursery, Hammersmith] was in my own garden, and it also represented two different botanical genera, if not three... (Beaton, 1861: 311).

Beaton concluded by advising anyone who found such apparent anomalies to send them to Maxwell T. Masters, who was working on his magnum opus, *Vegetable Teratology*. Darwin became positively jovial:

As Mr. Beaton alludes to some mistake which he has made, might I venture to suggest to him to punish himself by telling sooner than he intended by what means he can produce from pollen of the same flower placed on the stigmas of the same variety two different sets of seedlings? That is a mystery which it is tantalising to wait for (Darwin, 1861c: 281).

And the two managed to correspond without acrimony on the parentage of *Gladiolus* hybrids (Darwin & Beaton, 1861b). But Beaton’s imputations against Gärtner still simmered, and in 1863 Darwin returned to the fray, referring to “the well-ascertained influence of the pollen of one species or variety on the seed and fruit of another species or variety whilst still attached to the female plant”, giving Gärtner as his source. Beaton replied that “Gärtner never proved that – he only asserted it”, citing William Herbert to the contrary, and claiming that he himself had repeated all of Gärtner’s experiments without replicating his results (Darwin & Beaton, 1863: 70). Darwin in turn began with mock deference – “I should be sorry to lie under the imputation of having made an entirely incorrect statement” – and then twisted the knife: “It is painful to see a long life of honest labour repaid by contumely from a fellow-experimentalist, who, I suppose – anyhow I hope – never
read one page of the great original work” (Darwin, 1863). Beaton’s reply was delayed by his ill health, and appeared toward the end of the year, appended to the announcement of his death: “This seems the best place for me to make a suitable apology to Mr. Darwin, and to ask a thousand pardons for my seeming contradiction; but I had not the slightest idea even of contradicting him, much less of discourtesy”, while continuing his derogation of Gärtner (Beaton, 1863).

Darwin and ecology

In all the responses, commentary, and debates that the Origin triggered, one of Darwin’s innovative ideas that met with no response was what has been seen in retrospect as the invention of ecology. The locus classicus is in chapter III, on the “Struggle for existence”:

But how important an element enclosure is, I plainly saw near Farnham, in Surrey. Here there are extensive heaths, with a few clumps of old Scotch firs on the distant hill-tops: within the last ten years large spaces have been enclosed, and self-sown firs are now springing up in multitudes, so close together that all cannot live. When I ascertained that these young trees had not been sown or planted, I was so much surprised at their numbers that I went to several points of view, whence I could examine hundreds of acres of the unenclosed heath, and literally I could not see a single Scotch fir, except the old planted clumps. But on looking closely at between the stems of the heath, I found a multitude of seedlings and little trees, which had been perpetually browsed down by the cattle. In one square yard, at a point some hundred yards distant from one of the old clumps, I counted thirty-two little trees, and one of them, judging from the rings of growth, had during twenty-six years tried to raise its head above the stems of the heath, and had failed. No wonder that, as soon as the land was enclosed, it became thickly clothed with vigorously growing young firs...
Here we see that cattle absolutely determine the existence of the Scotch fir; but in several parts of the world insects determine the existence of cattle. Perhaps Paraguay offers the most curious instance of this; for here neither cattle nor horses nor dogs have ever run wild, though they swarm southward and northward in a feral state; and Azara and Rengger have shown that this is caused by the greater number in Paraguay of a certain fly, which lays its eggs in the navels of these animals when first born. The increase of these flies, numerous as they are, must be habitually checked by some means, probably by birds [altered in third edition to: probably by other parasitic insects].

Darwin concluded that “plants and animals, most remote in the scale of nature, are bound together by a web of complex relations”. Seven years later, his German admirer, the young Ernst Haeckel, coined the term “Oecologie” for this mode of investigation in his Generelle Morphologie der Organismen, acknowledging as his inspiration the way in which Darwin had shown “the infinitely entangled and diverse relations” of animals and plants (Haeckel, 1866: ii 286–289).¹ Despite Haeckel’s later fame, this work was never translated into English, so the first appearance of the word in English had to wait for 1876 and Ray Lankester’s translation of his History of the Creation (Haeckel, 1876: ii 354). Eugen Warming acknowledged Haeckel as the founder of the discipline in his 1894 textbook, translated as Oecology of Plants in 1909, and Warming’s work underlay that of Tansley, who was eventually to establish the concept of the ecosystem. But through all this English ecologists seldom looked back beyond Warming, and it was left to more recent historians of science to trace the line of descent all the way back to Darwin (McIntosh, 1985: 11–21). This despite the fact that as early

¹ In the same pages, Haeckel introduced the term “Chorologie” for the study of the geographical distribution of populations, another coinage for which he gets insufficient credit. In this instance his formulation owed more to Humboldt than to Darwin.
as 1875 the Gardeners’ Chronicle was able to claim as one of Darwin’s contributions to science the principle of the “inter-dependence of organisms” (Anon., 1875a: 308).

**The Fertilisation of Orchids, 1862**

In 1862, Darwin published his first purely botanical book, on *The Various Contrivances by which Orchids are Fertilised by Insects*. He had already become interested in the cross-pollination of orchids by 1840, having concluded that cross-fertilisation played an important role in the stability of species. A few hundred yards from his house at Down was a bank full of orchids, on which he made observations for the rest of his life. In 1860 he published an article in the *Gardeners’ Chronicle* on the fertilisation of British orchids (Darwin, 1860b), requesting information, which was followed by some correspondence with William Marshall in the issues for 26 January and 9 February 1861. Nonetheless, the arrival of a book by Darwin – even though he was “amongst the oldest and most valued of our correspondents” – on a purely botanical matter, let alone orchids, took the *Chronicle* “completely by surprise” (Lindley, 1862: 789).

The *Chronicle* review was delayed for three months, while John Lindley studied the book attentively. Lindley was the world’s foremost authority on orchids at the time, the author of six books and various articles on the subject, the creator of around forty generic names still recognised today (including *Cattleya*, *Miltonia*, *Laelia*, and *Lycaste*), and the first botanist to draw up a workable classification of orchids. His review stretched across three separate issues of the magazine in August and September 1862, and covered seven densely printed columns.

The *Fertilisation of Orchids* was divided into two sections, one on British and one on exotic orchids, reflecting the material Darwin had available for study: close observation of insect activity in the one, conjectural reconstructions of insect activity in the other. The *Journal of Horticulture* reviewer felt the reader could “congratulate himself on
Fig. 11. Darwin, *Fertilisation of orchids*, 1862: pollination morphology of a catasetum.
the fortunate want of space in the first volume [i.e. the *Origin*], for had Mr. Darwin attempted then to bring forward his authorities from the bosom of nature, he would probably have confined his matter to his own personal knowledge of how fertilisation is effected among our British orchids only” (Anon., 1862). Insect penetration of orchid flowers had often been observed, but, as Lindley put it, “the insect alone was believed to benefit by the plant, to whose peculiarities of structure its own were consequently specially adapted” (Lindley, 1862: 790); it was left to Darwin to argue that the orchid flowers had adapted to suit the anatomy of the insect. Much of the first part was accordingly dedicated to proving that insects were virtually the sole means by which orchids were pollinated (at least until nurserymen and plant breeders began attacking them with pollen brushes).

Turning to the discussion of exotic orchids, Lindley exulted in the treatment of *Angraecum sesquipedale*, a Madagascar orchid with a nectar receptacle “eleven and a half inches long, with only the lower inch and a half filled with nectar” (see cover). Darwin speculated that it was pollinated by a moth with an eleven-inch tongue; and such a moth (*Xanthopan morganii praedicta*) was indeed discovered early in the twentieth century. For Lindley, “The answer is necessarily conjectural in a great degree, but every hypothetical step in his reasoning being shown to be founded on observation of what occurs in analogous forms of Orchids, we are compelled to acknowledge that the explanation is in the highest degree probable” (Lindley, 1862: 863). But even greater wonders awaited. “Fifty-eight pages are devoted to Catasetum, Myanthus, Mormodes, Monachanthus, and Cycnoches, literally teeming with curious and interesting matter, which alone would establish the reputation of its author as a master of scientific research.” *Catasetum* was “the most extraordinary and complicated case in the whole order of Orchids”, and Lindley quoted three paragraphs on the subject, lamenting that considerations of space prevented him from quoting more. The following extract gives the flavour of the detail and ingenuity of Darwin’s experiments:
When the left-hand antenna is touched, the edges of the upper membrane of the disc instantaneously rupture, and the disc is set free. The highly elastic pedicel then instantly flirts the heavy disc out of the stigmatic chamber with such force, that the whole pollinium is ejected... I imitated this action with a minute strip of whalebone, slightly weighted at one end to represent the disc; and by bending it round a cylindrical object, gently holding at the same time the upper end under the smooth head of a pin, to represent the retarding action of the anther, I then let the lower end suddenly free, and the whalebone was pitched forward, like the pollinium of the Catasetum, with the weighted end foremost (Fertilisation, chapter 6).

Lindley concluded that Darwin had “abundantly” proved his case as far as orchids were concerned: they were pollinated by insects, almost exclusively so; the structure of their flowers was adapted to the anatomy of the insects in question. As to whether all this provided evidence for the theory of the origin of species by natural selection, Lindley thought that Darwin had made a good case, but that the question hinged fundamentally on the definition of a species, which Darwin’s work had thrown into some confusion:

And this physiological element confounds our ideas of species rather than the contrary, for if Catasetum and Monachanthus are shown to be structurally different genera but physiologically the same species [i.e. have been classified as different genera on morphological grounds but can interbreed], and Habenaria chlorantha and bifolia are to be considered structurally the same species, but physiologically distinct ones [i.e. are considered the same species on morphological grounds but can’t breed], we may naturally suppose that the infertility of two forms inter se is simply the effect of the differences induced between their reproductive organs by variation and natural selection. If these differences are accompanied by others in other organs, the forms are acknowledged to be species by all; if not the question is still a moot one, for one party insists on the positive argument that they are never known to breed together, and are
therefore species; and the other must be content to demand proof of
the negative, that they never did breed together and never will
(Lindley, 1862: 910).

Followers of the ongoing reclassification of orchids in *Genera Orchidacearum* may be experiencing a twinge of *déjà vu*.

Lindley’s enthusiasm was won both by the unprecedented quality of the experiments – “The present work is one of a class of which Botany possesses singularly few examples”, “no author hitherto… has written a book relating to vegetable physiology to compare with Mr. Darwin’s in point of engrossing, fascinating interest” – and from the marshalling of evidence to solve a biological problem: “Mr. Darwin has met every difficulty” (Lindley, 1862: 789–790, 910). Darwin had given botany one of its greatest classics, and it was the orchid book more than the *Origin* that sealed his reputation for the gardening press. Joseph Hooker wrote to Brian Hodgson in December 1862:

Darwin still works away at his experiments and his theory, and startles us by the surprising discoveries he now makes in Botany; his work on the fertilisation of orchids is quite unique – there is nothing in the whole range of Botanical Literature to compare with it, and this, with his other works… raise [sic] him without doubt to the position of the first Naturalist in Europe, indeed I question if he will not be regarded as great as any that ever lived; his powers of observation, memory and judgement seem prodigious, his industry indefatigable and his sagacity in planning experiments, fertility of resources and care in conducting them are unrivalled (Huxley, 1918: ii 32).

*The Variation of Plants and Animals under Domestication, 1868*

Darwin’s two-volume compilation of evidences for the selective perpetuation of variations met with a muted reception in the press: it was, after all, a supplement, the main arguments having already
been made. The *Journal of Horticulture* did not notice it at all – oddly, since every week it offered practical advice about poultry and bees. The *Gardeners’ Chronicle*, however, made up for any lack of enthusiasm elsewhere:

Written in admirable English, using no scientific terms but such as are comprehensible to men of fair education, lucidly arranged, and indexed with scrupulous care [unlike the *Gardeners’ Chronicle*, it has to be said], there is not a gardener in the country who has any taste for the history or theory of his art but will peruse it with pleasure and profit, and find it difficult to say whether he values it more as a storehouse of facts or as an incitement to observe and to think. Is his employer a sportsman? he will find in Mr. Darwin’s pages such information regarding dogs and horses, their breeds and individualities, as never entered the brain of the gamekeeper, equerry, or master of the hounds. Is he a farmer? here are anecdotes and observations regarding cattle, pigs, sheep, and goats, which no professional breeder can match for number or truth, and which too few of these will believe or care about, not because they are not true, but because most so-called practical men take no interest in animals beyond what immediately concerns themselves. Is my lady a fowl fancier, or has she an aviary? her gardener will here find a wealth of information on domesticated birds of all sizes, voices, and uses, from the canary bird and peacock to the turkey and goose. Lastly, do his master’s children seek his advice about their rabbits, pigeons, honey bees, goldfish, or silkworms? If they do, here are curiosities of natural history about each and all, treated with masterly skill and originality (Anon. 1868a).

And when the revised edition appeared in 1876, the *Chronicle* noted that Darwin had listed all his additions and corrections in a separate table: “a piece of literary honesty” (Anon., 1876a).

The *Chronicle* reviewer did find theoretical problems with the work: a confusion between variation and modification, and an ambiguity over the causes of variation, while acknowledging that these may
have had more to do with the means of expression than with the underlying concepts:

It is difficult to follow this reasoning: if altered conditions cause variability, and man alters a plant’s condition, he may fairly be charged with causing variability – just as fairly as a man who so places a sovereign before a thievish boy, as that the boy will certainly steal it. We have alluded to these apparent obscurities not by way of hypercriticism, but to show how difficult a matter it is, to treat of such a subtle subject as the genesis of variation without ambiguity (Anon., 1868a).

Fig. 12. Herbert Spencer (1820–1903); undated carte-de-visite photograph by the London Stereoscopic Company.
The use of the work as a source of information on varietal history received testimonials over the years. William Robinson’s magazine *The Garden* did not yet exist in 1868, but when the revised edition appeared it extracted a passage about strawberry breeding for publication (Darwin, 1876). Darwin’s obituarist in *The Garden* summed up the importance of the work:

> It may be said the theories were giants, and needed a broad basis of facts to rest upon, and this is true, but in this age of bold assumption on slender premises it is refreshing to turn to Darwin’s array of facts in such works as “The Variation of Animals and Plants under Domestication,” where the facts alone are left, as with the consciousness that they are sufficiently strong to make their own impact (Fish 1882b).

But the value of the work as in effect a database of plant breeding had an immediate consequence for Darwin. A couple of months after the publication of the *Variation*, the Royal Horticultural Society announced the formation of its Scientific Committee, “whose special functions shall be to promote and encourage the application of physiology and botany to purposes of practical culture, and to originate experiments which may assist in the elucidation of horticultural subjects” (Anon., 1868b). Darwin, along with Herbert Spencer, was included in the list of founding members. The minutes of the early years of the Committee have not survived, so it is not known how many meetings Darwin actually attended, if any; but his inclusion was at least a testimony to his perceived importance for horticulture.

*Insectivorous Plants*, 1875

It had been known since the early nineteenth century that certain plants, like the sundew (*Drosera*), often had quantities of dead insects sticking to them. As late as the 1860s, textbooks continued to deny the possibility that the plants derived any nutrition from the insects; similarly, although the mechanism of trapping insects in the
### Table 3. Membership of the RHS Scientific Committee, as originally announced in the *Gardeners’ Chronicle*, 25 April 1868

<table>
<thead>
<tr>
<th>Name</th>
<th>Position, Years</th>
</tr>
</thead>
<tbody>
<tr>
<td>Duke of Buccleuch (1806–84)</td>
<td>Chairman, President of the RHS</td>
</tr>
<tr>
<td>Warren de la Rue (1815–89)</td>
<td>Vice-chairman, Astronomer and chemist</td>
</tr>
<tr>
<td>William Wilson Saunders (1809–79)</td>
<td>Vice-chairman, former Secretary of the RHS, famous for his collection of exotic plants</td>
</tr>
<tr>
<td>Thomas Thomson (1817–78)</td>
<td>Vice-chairman, former superintendent of the Calcutta Botanic Garden</td>
</tr>
<tr>
<td>Rev. Miles J. Berkeley (1803–89)</td>
<td>Secretary, Editor of the <em>RHS Journal</em> and mycologist who identified the potato blight as caused by a fungus</td>
</tr>
<tr>
<td>Frederick Augustus Abel (1827–1902)</td>
<td>Chemist</td>
</tr>
<tr>
<td>Isaac Anderson-Henry (1800–84)</td>
<td>Plant breeder and President of the Botanical Society of Edinburgh</td>
</tr>
<tr>
<td>J. G. Baker (1834–1920)</td>
<td>Of Kew Herbarium</td>
</tr>
<tr>
<td>James Bateman (1811–97)</td>
<td>Of Biddulph Grange, orchid collector and monographer</td>
</tr>
<tr>
<td>George Bentham (1800–84)</td>
<td>Former Secretary of the Society and President of the Linnean Society, author with Hooker of <em>Genera Plantarum</em></td>
</tr>
<tr>
<td>Robert Bentley (1821–93)</td>
<td>Professor of Botany at King’s College and future author with Trimen of Medicinal Plants</td>
</tr>
<tr>
<td>Isaac Anderson-Henry (1800–84)</td>
<td>Deputy Inspector of Hospitals</td>
</tr>
<tr>
<td>Major Trevor Clarke (1813–97)</td>
<td>Plant hybridist</td>
</tr>
<tr>
<td>Charles Darwin (1809–1882)</td>
<td></td>
</tr>
<tr>
<td>Rev. Joshua Dix (c.1811–71)</td>
<td>Chairman of the RHS Floral Committee</td>
</tr>
<tr>
<td>Robert Fortune (1812–80)</td>
<td>Plant collector in China</td>
</tr>
<tr>
<td>Professor Edward Frankland (1825–99)</td>
<td>Professor of Chemistry at the Royal Institution</td>
</tr>
<tr>
<td>B. T. Brandreth Gibbs (1821–85)</td>
<td>Agriculturist and director of the Royal Show</td>
</tr>
<tr>
<td>Joseph Henry Gilbert (1817–1901)</td>
<td>Agricultural chemist at Rothamsted</td>
</tr>
<tr>
<td>James Glaisher (1809–1903)</td>
<td>Meteorologist</td>
</tr>
<tr>
<td>Robert Hogg (1818–97)</td>
<td>Editor of the <em>Florist and Pomologist</em>, and co-editor of the <em>Journal of Horticulture</em></td>
</tr>
<tr>
<td>Joseph Dalton Hooker (1817–1911)</td>
<td></td>
</tr>
<tr>
<td>John Eliot Howard (1807–83)</td>
<td>Authority on quinine</td>
</tr>
<tr>
<td>George W. Johnson (1802–86)</td>
<td>Founder-editor of the <em>Journal of Horticulture</em></td>
</tr>
<tr>
<td>William Marshall (1835–1917)</td>
<td>Orchid grower</td>
</tr>
<tr>
<td>Maxwell T. Masters (1833–1907)</td>
<td>Editor of the <em>Gardeners’ Chronicle</em> and author of <em>Vegetable Teratology</em></td>
</tr>
<tr>
<td>John Miers (1789–1879)</td>
<td>Authority on South American flora</td>
</tr>
<tr>
<td>Thomas Moore (1821–87)</td>
<td>Curator of the Chelsea Physic Garden</td>
</tr>
<tr>
<td>Giles Munby (1813–76)</td>
<td>Botanist and plant collector in Algeria</td>
</tr>
<tr>
<td>Andrew Murray (1812–78)</td>
<td>Entomologist and former Assistant Secretary of the RHS</td>
</tr>
<tr>
<td>J. Russell Reeves (1804–77)</td>
<td>Former East India Company official in China, and authority on Chinese plants</td>
</tr>
<tr>
<td>Sigismund Rucker (c.1809–75)</td>
<td>Grower of exotic plants in Wandsworth</td>
</tr>
<tr>
<td>Henry Young Darracott Scott (1822–83)</td>
<td>Secretary of the RHS and completing architect of the Royal Albert Hall</td>
</tr>
<tr>
<td>Herbert Spencer (1820–1903)</td>
<td></td>
</tr>
<tr>
<td>Augustus Voelcker (1822–84)</td>
<td>Agricultural chemist</td>
</tr>
<tr>
<td>Friedrich Welwitsch (1806–72)</td>
<td>Plant collector in Angola</td>
</tr>
<tr>
<td>George Fergusson Wilson (1822–1902)</td>
<td>Treasurer of the RHS; later founder of Wisley</td>
</tr>
</tbody>
</table>
pitchers of sarracenas had been well studied before 1820, the idea that the plant benefited directly from the insects was ridiculed when mooted (Juniper, 1989: 12–20).

Darwin became interested in this phenomenon in 1860; he had the advantage of colonies of Drosera in the fields near Down. He soon wrote to Lyell, “I care more about Drosera than the origin of all the species in the world” (24 November 1860). When he learned that George Maw was going to collect plants near Gibraltar, he entreated him to hunt out living specimens of Drosophyllum lusitanicum (letters to Maw, 13 and 17 January, 27 April, and 22 May 1869). Over the next decade, he tested these and other plants to see what chemicals were secreted by their leaves, what types of organic matter the plants could absorb and with what speed, and how insects were captured. By the 1870s the similarity in reaction between the behaviour of sundew leaves and animal muscle was being argued on an experimental basis by Burdon Sanderson, and the time-honoured concept of irritability invoked. “Irritability” was a concept introduced over a century earlier by Albrecht von Haller as one of the characteristics of animal tissue; its application to the plant kingdom challenged the most basic premises of botany, that plants were passive, dare one say mechanical, in their principles of operation.

In 1874 Hooker, in address to the British Association for the Advancement of Science, referred to Darwin’s experiments, and the way in which he had shown that insectivorous plants operated by tissue contractions, just like animal muscles. The world was thus ready for the revelations in Darwin’s book published the next year. The results impressed most; some remained sceptical; but within a few years further examples were discovered in tropical countries. (A fad for growing such plants was already beginning: the Veitch nurseries were advertising exotic droseras in the year of publication.)

Fig. 13 (opposite). Insectivorous plants sold by Veitch nurseries, from the Gardeners’ Chronicle, 24 July 1875.
© Royal Horticultural Society
The *Gardeners’ Chronicle*, reviewing the book on 10 June 1875, remarked that it was marked in a very strong degree with many of those characteristics which have made Dr. Darwin’s previous works so remarkable. We have the same clear statement of facts, the same evidence of patient and laborious research, the same simple modesty of expression, the same scrupulous care to give due credit and acknowledgment to the researches of others, the same excellent practice of repeating and summarising important details, the same weaving together into one strand of all the facts and all the inferences; the same unconsciously exerted persuasiveness, which leads the reader on from point to point, and at the end leaves him no choice but to adopt the author’s conclusions (Anon., 1875b: 44).

A flaw in Darwin’s work then emerged. Andrew Murray, the former Assistant Secretary of the Royal Horticultural Society, who had been an opponent of Darwin a decade and a half earlier, giving the *Origin* one of its more damning scientific reviews (Murray, 1860), reviewed *Insectivorous Plants* for William Robinson’s magazine *The Garden*. He began with the usual praise for Darwin as a stylist and an experimenter:

Mr. Alexander Dumas makes his great hero, the Count of Monte Christo [sic], say that whatever he does he does well. With much better warrant may we say this of Mr. Darwin, and, notwithstanding our different views, of none of his works with more truth than that at present under review.

But he then proceeded to point out that Darwin, while establishing the capacity of the plants to digest insect matter, had not demonstrated the advantage to the plant: “Let two plants of Drosera be grown under the same conditions, the one well supplied [with] flies, and the others [sic] protected from them, and see which thrives best” (Murray, 1875). Murray was seconded by Alexander Forsyth,
formerly Brunel’s head gardener, whose own experiments had yielded no evidences of digestive power (Forsyth, 1875).

The spectacle of Darwin kicking himself for having omitted this little detail was brought to an end three years later, when his son Francis Darwin launched his own botanical career with a series of experiments designed to test exactly this point (F. Darwin, 1878). The Gardeners’ Chronicle reported the meeting of the Linnean Society at which the paper was read, concluded that the point had been proven, and said of the Darwins’ work that it was “the starting point, if not of a revolution, at least of an entirely new departure, in vegetable physiology, and one, moreover, in which practical cultivators are very greatly concerned” ([Masters], 1875b). A few months later, having had an opportunity to watch the responses of the horticultural world, the magazine issued the sardonic statement:

Previous to [Francis Darwin] the statement had been received first with doubt (as usual and proper under the circumstances), next with the assertion that the plants derived no benefit from the insect or meat diet, and did as well without as with it; and now that the matter is duly substantiated, we are quite prepared to hear that there is nothing new in the matter, and that it was all known long ago! (Anon., 1878).

Climbing Plants, 1865, and The Power of Movement in Plants, 1880
It makes sense to treat Darwin’s two books on the motions of plants together, though their publication was separated by fifteen years, and to treat them after Insectivorous Plants. The results of Darwin’s experiments on climbing plants were published in the Journal of the Linnean Society for 1865 (Darwin, 1865), and filtered through to the horticultural public by the Gardeners’ Chronicle (Anon., 1865a). Darwin’s researches did not reach their widest audience until 1875, when his paper was republished in book form as The Movements and Habits of Climbing Plants (second edition). It sold well, but in that year it was Insectivorous Plants that captured the attention of the
press. So while Darwin’s treatment of plant movement was known to the horticultural world, it did not have its full impact until the publication of the sequel, *The Power of Movement in Plants*, in 1880.

In the late 1850s Asa Gray had sent Darwin seeds of *Echinocystis lobata*, a plant that climbed by tendrils; Gray had written a paper attributing its movements to irritability excited by contact. The earliest investigators of plant movements (Hales, Bonnet, *et al.*) had explained them as consequences of changes in temperature or moisture levels. Candolle introduced the concept of heliotropism (Candolle, 1832: 1069–1087), but without attempting an explanation for the tendency of plant organs to follow light. Irritability seemed to account for the facts, and Gray’s concept gradually won a
provisional acceptance. It was left for Darwin to treat such movements as a goal-directed activity on the part of the plants.

Darwin’s experiments on climbing plants showed him that even without contact, the growing tip was constantly moving, making a circle every two hours. (He coined the term “circumnutation” for this circular movement.) He began to study plant motion in more detail, since no previous scientist had explained how climbing plants worked. Darwin distinguished between plants that climbed by twining (like *Wisteria*), by using tendrils (like *Cobaea*), and by using their leaves (like *Clematis*). He experimented by placing weights on growing tips to see whether movement was affected, by inserting different fabrics and materials to see what surfaces plants climbed most easily, by putting sticks and other objects in the path of tendrils.

After the publication of *Climbing Plants*, Darwin continued to investigate plant movements, extending his study of circumnutation from climbing plants to seedlings: the movements of seed-leaves emerging from the seed, and the daily cycle of movements as plants “slept” for the night. These he investigated by having the plant trace its movements on a piece of smoked glass; his equipment was nothing like as sophisticated as that developed a generation later by J. C. Bose (Elliott, 1994). Circumnutation and curvature of growth, he discovered, occurred in emerging shoots even in the absence of light; so these processes were not a passive response to the presence of light, but in effect an active seeking after it. Having observed an echeveria extending roots even when the general growth of the plant had been checked by dry conditions, he sent the specimen to Maxwell T. Masters, who published it as an example of “Growth under difficulties” in the *Gardeners’ Chronicle* ([Masters], 1877c).

*The Power of Movement in Plants* was greeted in the gardening press as “more entertaining than any fairy tales” ([Hibberd], 1881a: 1), and “a record of minute research and of patient, untiring investigation
which are simply wonderful” (Anon., 1880b). The Chronicle was most excited by the discoveries of the motions of root-hairs and root-tips; the Gardeners’ Magazine rejoiced that a scientific explanation had now been found for the high mortality of seedlings in heavy soils. As for the relationship of all these data to the theory of evolution, it was Shirley Hibberd who made the point most clearly: “these movements tend directly to the advantage of the plants, and each plant performs the kind of movements that are best adapted to promote its own welfare” ([Hibberd], 1881a: 1). As he, or his staff writers on the Gardeners’ Magazine, had put it a few years earlier, “The premiss on which Mr. Darwin’s labours are founded may be put in some such words as these – Nature always has an end in view. And the impulse by which he is guided may be summarised in such questions as, What is that end, and by what means is it attained?” (Anon., 1877: 51). Or in other words: of what advantage is the behaviour to the plant? If it produced an advantage, then it fell within the remit of the theory of natural selection.

Darwin’s work on plant movements only gradually conquered the world. In Germany, the emphasis of Julius Sachs on osmotic water pressure as an explanation for what was coming to be known as “Darwinian curvature” in plant organs tended to undercut the idea of goal-directed activity on the part of plants, and Bose’s work on electrical action potentials in plants was long dismissed on the continent. For a survey of what had been accomplished in the field of plant movement a century after the Origin, see P. R. Bell’s centenary paper (Bell, 1959); for a statement of how things looked less than half a century later, see Paul Simons’ Action Plant (Simons, 1992).

Fig. 15 (opposite). “Growth under difficulties”, Gardeners’ Chronicle, 29 December 1877.
Mr. McNab, now of the Royal Botanic Garden, Edinburgh, made some experiments on the growth of plants in an artificial situation, and which were described in our columns at the time (January 14, 1879). In one case, carried out by Mr. McNab, a hothouse was furnished with 217 plants, which were trained up to an iron frame placed in the north aspect of the house, receiving only the radiance derived from the evaporating operations. For three years, the plants rotted and cast off slant and unhealthy at the close of the report.

A second experiment (fig. 107) was one of the same type, only smaller in extent, being carried out with 27 plants of a hothouse, which were trained up to an iron frame erected in the north aspect of the house. The plants were in a healthy state, the frame was fully exposed to the light.

Another experiment (fig. 105) was hung upside down, and the plants were of a hothouse, and not in the present case. The plants were trained up to an iron frame erected in the north aspect of the house, receiving only the radiance derived from the evaporating operations. For three years, the plants cast off slant and unhealthy at the close of the report.
Fig. 16. F. W. Burbidge (1847–1905), Curator of Trinity College Garden, Dublin; undated carte-de-visite photograph by Robinson & Sons, Dublin.
Cross- and Self-Fertilisation, 1876, and The Different Forms of Flowers, 1877

Darwin’s last two books directly concerned with questions of inheritance and evolution appeared close together: *The Effects of Cross- and Self-Fertilisation* in 1876, *The Different Forms of Flowers on Plants of the Same Species* the following year.

The theme of what Darwin then called “self-impotence” in plants had been a major theme in the second volume of the *Variation of Animals and Plants under Domestication* (1868). In 1871, F. W. Burbidge, the future Curator of the garden at Trinity College Dublin, whose *Cultivated Plants: their Propagation and Improvement* (1877) would become a standard manual for generations, had written to the *Gardeners’ Chronicle* about the fertilisation of *Leschenaultia formosa*, pointing out that “It was Darwin who first pointed out that self-fertilisation was injurious in the long run”, querying an apparently contradictory instance – “I… was agreeably surprised to find it furnished with everything needed in order to insure the most perfect fertilisation of the stigma by pollen from its own flower” – and wondering whether the plant had “degenerated and become sterile in consequence of this invariable self-fertilisation” (Burbidge, 1871).

Darwin had replied, recounting his experiments on the plant in 1862 (see also his letter to Beaton, Darwin 1861a), and concluding that there was an elaborate arrangement for insect pollination, while noting from Thomas Drummond’s observations in Australia that the plant rarely set seed in the wild:

> It appears at first sight a surprising circumstance that in this genus… the pollen, whilst the flowers are still in bud, should be scooped out of the anthers, in which it might have remained ready for use, and then be immediately enclosed in a specially contrived receptacle, from which it has afterwards to be removed, so as to be placed on the stigma. But he who believes in the principle of gradual evolution, and looks at each structure as the summing up of a long series of adaptations to past and changing conditions… will not feel surprise
at the above complex and apparently superfluous arrangement (Darwin, 1871).

That was how matters stood when Cross- and Self-Fertilisation appeared, and it was immediately seized on as a confirmation, in even greater detail, of the principle already proposed:

It is evident that the settled conviction of those who have made a study of crossing as a matter of business, is well confirmed by Mr. Darwin’s experiments, conducted without any view to business, but for purely scientific purposes. That settled conviction is well known to be in favour of artificial fertilization... The general result, indeed, is, that cross-fertilization is beneficial, and self-fertilization injurious (Anon., 1877: 51).

Again, “cross-fertilization by insect agency is likely to originate new forms, while self-fertilizing plants, on the other hand, are more likely to possess fixed characters or sameness of habit and colour” (“B.”, 1876), a formulation which shows clearly the interests of plant breeders.

Maxwell T. Masters, as editor of the Gardeners’ Chronicle, commissioned George Henslow, the son of Darwin’s mentor John Stevens Henslow, to write an abstract of The Effects of Cross- and Self-Fertilisation; it was published in instalments between 13 January and 5 May 1877, interspersed with editorial commentary (3 March) and letters from Darwin (Darwin, 1877) and Peter Grieve, the head gardener at Culford House, Suffolk, and celebrated breeder of pelargoniums (Grieve, 1877). Darwin acknowledged that Henslow had caught him out in a misprint, but also urged readers not to rely on Henslow for an accurate interpretation of his theory. But the end result was that the work on fertilisation received even greater exposure in the Chronicle than the orchid book had.
But *The Different Forms of Flowers* struck much more acutely at the horticultural community. Generations of florists had produced *Primula* cultivars as ornamental plants, and in the nineteenth century hybridists had turned their attention to them, with mixed results. Donald Beaton had summed up his experience thus: “the cultivated varieties of Primrose and Polyanthus do not yield to the natural laws of cross-breeding, the pollen having little or no influence in the production of new forms or colours” (Beaton, 1859: 137). *Primula* flowers were notoriously either pin-eyed (with long styles) or thrum-eyed (with short styles); but no one before Darwin had noticed that pollen from pin-eyed flowers was sterile on other pins, but fertile on thrums, and vice versa. Darwin first published his results in the *Journal of the Linnean Society* (Darwin, 1869a, 1869b), and a few years later William Robinson published a portion of the text in *The Garden* (Darwin, 1873). So the discovery was not exactly news when it finally appeared in book form, and Masters could invoke the astonishment it had provoked as a testimony to the importance of the book:

It was not without some sense of humiliation and of wasted opportunity that florists and horticulturists found that they had been pottering over “pin-eyes” and “thrum-eyes” for generations, without having the slightest notion of the significance of the variations in question. Even from the restricted point of view of the professed florist, the meaning of the formations in question, and their direct practical bearing on the cultivation and selection of the forms most in consonance with his arbitrarily assumed standard were entirely overlooked. So-called botanists were, with very few exceptions, not one whit better. They had been splitting hairs, counting spots, wrangling whether this was a species and that a variety, discussing whether there were two or fifty British representatives of a particular genus, and so on, without troubling themselves in the least about the causes of the variations they observed in such minuteness of detail ([Masters], 1877b).
The second main issue the horticultural press responded to was the putative hybrid origin of the oxlip, which Darwin had also raised:

Finally, although we may feel confident that *Primula veris*, *vulgaris*, and *elatior*, as well as the other species of the genus, are all descended from some primordial form, yet, from the facts which have been given, we may conclude that they are now as fixed in character as are very many other forms which are universally ranked as species. Consequently they have as good a right to receive distinct specific names as have, for instance, the ass, quagga,¹ and zebra (Darwin, 1869b: 451).

James Britten devoted most of his review in *The Garden* to the oxlip question (Britten, 1877).

Masters, in a leader on *Cross- and Self-Fertilisation*, made the point that in his discussion of the origin of sexes in plants, Darwin seemed to be contradicting his own theory, by suggesting that plants were originally dioecious: “in so doing [he] is considered to be in so far opposed to those great doctrines of evolution and progressive development of which he is the high priest”.

No difference of sex exists in the first instance [i.e. embryologically] in the structure of any plant or animal; it is only after development has proceeded some way that any difference is observable. There is, then,

¹ The quagga, a relative of the zebra with stripes confined to its front quarters, may be unfamiliar to my readers; it became extinct around the end of the nineteenth century. Its former familiarity may be gauged from Saki’s story “The Strategist”, published in the Edwardian period, which describes a group of children deciding on terms for a guessing game: “Mustang’ was no good, as half the girls wouldn’t know what it meant; finally ‘quagga’ was pitched on.” By the time Saki was writing, the last quagga in captivity had already died. Whether it was a separate species or, as many now think, a variety of zebra, may be empirically decided before long, if the Quagga Project succeeds in breeding it back.
in the life of every individual a primordial oneness of sex. What happens in the individual may be true, as Plato surmised, of the race. It may even be the foundation of the myth of the development of Eve from Adam’s rib.

Nonetheless, he concluded, Darwin was right: the geological evidence for development suggested that plants which carried the male and female flowers on different individuals appeared first, with hermaphroditic flowers a later development ([Masters] 1877a). Masters also provided the best general summary of the horticultural consequences of Darwin’s experiments:
The injury from the self-fertilisation of plants, as well as from too close breeding in animals, does not, according to Mr. Darwin, depend on any tendency to disease or weakness of constitution common to the related parents. On the other hand, the advantages of cross-fertilisation depend on the ancestors of the parent-plants having been exposed to different conditions, or from their having been intercrossed with individuals thus exposed. Thus is justified that common practice with horticulturists of obtaining seeds from different localities, and which have been grown under different conditions, so that the error and evil consequences of raising plants for a long succession of generations under the same conditions may be avoided. ... Bearing in mind the immense importance of the subject to raisers of new varieties, or to the growers of old ones, who are lamenting over the vanished constitution of Roses, or the sterility or bad setting of Grapes, Cucumbers, Strawberries, or what-not, it must be obvious how very valuable the record of such a series of experiments, carried on so patiently for so many years, must be ([Masters], 1876).

In the wake of Darwin’s work, pollination studies suddenly became an immense growth area in botany, culminating in Knuth’s magnificent three-volume Handbuch der Blüthenbiologie, translated into English as the Handbook of Flower Pollination (1906–1909). By that time, Mendelism had raised its head, and the next generation was less concerned with the mechanisms of pollination than the mechanics of chromosomes, the problem of apomixis, and the “prepotency of pollen” from different individuals; a survey of the early twentieth century’s directions of research will be found in Whitehouse (1959). Since then, pollination studies have returned to prominence as a branch of ecology.

Darwin as natural theologian
The botanical world in general accepted the idea of speciation through natural selection more readily than the zoological; hybridisation and sporting were, after all, far more familiar
phenomena among plants than among animals. A writer in the Gardeners’ Chronicle in 1875 made the claim that Darwin’s theory was based primarily on his observations of horticultural practice: “Darwin borrowed the idea of ‘natural selection,’ or, as it is more accurately termed, ‘the survival of the fittest,’ from the gardener. The gardener or the florist selects, causes to survive, and propagates varieties showing one particular quality or tendency which he may happen to desire; but in Nature the selection or the survival is not so simple an affair” (Anon., 1875a: 308).

The triumphalist tone is explained by the previous history of horticultural taxonomy. Fifty years earlier, when Joseph Sabine published his pioneering articles on horticultural taxonomy in the Horticultural Society’s Transactions, his work was dismissed for its
attention to fugitive variations: “Was it necessary that a Society should come together for the purpose of printing a volume in quarto on the characters of Sportive Varieties of Chrysanthemums, and figures of fugitive Dahlias?” ([Ker], 1829: 5–6). That was at a time when the commercial production of varieties was in its infancy, and the first systematic programme of hybridisation of garden plants (Cape heaths, by William Rollisson’s nursery) had recently achieved a total of 285 cultivars (Rollisson, 1826). The succeeding half-century had seen plant breeding become the basis of a thriving industry, so that Shirley Hibberd would soon claim that “the hybridist who has thoroughly mastered the art may predetermine, with almost mathematical exactitude, what it is in his power to produce” (Hibberd, 1883: 164). As the Chronicle writer (probably Maxwell T. Masters) put it: “The apparently trifling variations, the variations which it was once the fashion for botanists to overlook, have become, as it were, the keystone of a great theory” (Anon., 1875a: 308).

When the Origin was published, Darwin had a solid reputation as a naturalist, based in the public eye on his Beagle narrative, and in the eyes of taxonomists on his work with barnacles. No writer in the horticultural press felt inclined to dismiss Darwin’s theories out of hand: respect had to be paid to his marshalling of evidence, and his willingness to declare in advance the difficulties and potential stumbling blocks his arguments faced. Nonetheless, when the overt enthusiasm of a Huxley or a Hooker is set aside, there was a general sense of discomfort in the responses, a palpable sense of relief in being able to propose objections, and sometimes a principled rejection, as in the case of Andrew Murray’s review, which concluded: “I cannot believe in such doctrine… I have come to be of opinion that Mr Darwin’s theory is unsound, and that I am to be spared any collision between my inclinations and my convictions” (Murray, 1860: 20). The Gardeners’ Chronicle, under Maxwell T. Masters, took a sympathetic line in defending Darwin against his critics. Of Robert MacKenzie Beverley’s anonymously published pamphlet, The Darwinian Theory of the Transmutation of Species examined by a
Graduate of the University of Cambridge, the reviewer wrote, “The writer succeeds in demolishing Mr. Darwin very much to his own satisfaction, and, if slashing argument without much heed as to its basis be sufficient, his victory is complete” (Anon., 1868a). C. R. Bree’s *Exposition of Fallacies in the Hypotheses of Mr. Darwin* was described – almost certainly by Masters – as “a violent attack, tirade rather, on the Darwinian hypothesis, and on those who have learnt to look on it as a good working-plan, reconciling a greater number of observed phenomena than the older hypothesis” (Anon., 1872). Note the resemblance of this strategy of provisional acceptance to Hooker’s defence at the British Association in 1860. The *Chronicle* even published a review of *The Descent of Man*, the only horticultural journal to do so, and expressed itself in what might be described as a jaundiced manner: “Mr. Darwin, with his usual candour, fails not to insist on what he calls the enormous difference in mental power between the lowest and most degraded savage and the highest ape: indeed, it appears to us that he overrates the difference” (Anon., 1871).

As the 1860s yielded to the 1870s, a shift in the rhetoric of discussions of Darwin in the horticultural press can be perceived. Beginning with the *Fertilisation of Orchids*, reviewers made a point of emphasising the immense practical value of Darwin’s researches, while bracketing the evolutionary speculations as an interesting sideline, metaphysical speculation, or at worst a regrettable excrescence. The *Journal of Horticulture*’s review of the orchid book concluded that “As a contribution of the very highest order to the practical attainment of seeding foreign Orchids, we would recommend the work, apart from all speculations about the origin and progress of the clothing of our planet” (Anon., 1862). A laudatory piece in the *Gardeners’ Chronicle* about Darwin’s contributions to horticulture offered him homage “setting aside, as beside the question we are at present concerned with, all direct reference to his theories as to the origin and progress of species” (Anon., 1875a: 309).
Once evolution could be pushed to one side in the consideration of Darwin’s work, what was left was an immense battery of examples of adaptation – and adaptation, conceived as evidence of benevolent design, had been the mainstay of early nineteenth-century natural theology, the great subject of the Bridgewater Treatises. There has never yet been a proper history written of natural theology, any more than of its predecessor, the physico-theology of the late seventeenth and early eighteenth centuries. When such a history is written, it will reveal that natural theology, however widely
accepted, was never unembattled; there were always hard-line Christians who disdained the attempt to uncover evidences for God in the natural world, and regarded the outright atheist as less dangerous to Christianity than those who undermined the status of revelation by drawing proofs from outside the Bible. George Maw, for example, said: “Dr. [Asa] Gray says that natural selection is compatible with natural theology; this is merely a truism, for who doubts that a religion built up of natural evidences is compatible with natural evidences?” (Maw, 1861: 7610). Nonetheless, natural theology was effectively the cultural mainstream at the time Darwin was writing.

And thus we find that the corpus of Darwinian botany, within a decade of the publication of the *Origin*, was being accepted by natural theologians. Some of the proceedings of the 1868 British Association meeting were republished in the *Journal of Horticulture*, and offered the unusual spectacle of a clergyman (Miles J. Berkeley, Vicar of Sibbertoft, and editor of the Royal Horticultural Society’s *Journal*) asking a secular congregation to pray for Darwin’s health: “Nothing can be more unfair, and I may add unwise, than to stamp at once this and cognate speculations with the charge of irreligion. Of this, however, I feel assured, that the members of this Assocation will conclude with me in bidding this great and conscientious author God speed, and join in expressing a hope that his health may be preserved to enrich science with the results of his great powers of mind and unwearied observation” (Berkeley, 1868: 225).

The *Gardeners’ Chronicle* put the paradox forward most succinctly: “No more persuasive apostle of natural theology, no more powerful advocate of the argument furnished by design and adaptation, ever lived than CHARLES DARWIN” (Anon., 1875a: 308). The *Chronicle* continued this tone in later discussions, saying of the *Power of Movement in Plants* that “as a storehouse of facts for the student of Natural Theology it will be found replete” (Anon., 1880). This may not have been advocacy so much as a wry comment on the intellectual
climate, but Shirley Hibberd, the editor of the Gardeners’ Magazine, was personally much attracted to natural theology – see his miscellaneous essays in Brambles and Bay-leaves – and greeted the same book with the encomium: “A finer reading in natural theology the present book season has not brought us” ([Hibberd], 1881a: 2). For those who found evolution incompatible with revelation, Hibberd offered a slap on the wrist:

Mr. Darwin has never assailed any creed or any church, but has sometimes alarmed good people by showing that probably the world has attained to its present form through agencies the existence and nature of which they have not hitherto apprehended. But when they took fright at something Mr. Darwin suggested as a proper deduction from facts they forgot that he and they were equally interested – or should be equally interested – in the object of every scientific inquiry, which certainly is to ascertain the truth. If, through our superficiality of observation, we have taken errors for truths, it must be to our advantage to be untaught and to begin again; for Truth is one of the heavenly things that we shall have to live on when the conflicts of mortality are past ([Hibberd], 1881b: 477).

And Darwin remained for Hibberd, and for the Gardeners’ Magazine under his editorship, “our great observing philosopher, our one great prophet in the region of facts” (Anon., 1881b: 583).

The Formation of Vegetable Mould, 1881
As early as the 1830s, Darwin began making observations on earthworms and their castings; he published his first paper on the subject in 1837, and his first letter on the subject in the Gardeners’ Chronicle in 1844 (Darwin, 1844). In his last years he returned to the subject, with a range of experiments designed not only to study the physiology of earthworms (playing music to them to see if they could distinguish sounds) but also to estimate their effects on vegetation (placing leaves and triangular pieces of paper near earthworm burrows to test their ability to transport them) and soil
Fig. 21. David Taylor Fish (1824–1901), head gardener at Hardwicke Hall, Suffolk, from *The Garden*, 4 May 1901.
(placing a large flat stone, nicknamed the worm-stone, to see how much it moved as a result of the activity of earthworms tunnelling through the soil beneath). Darwin calculated that an acre of garden soil could contain 50,000 earthworms, and their castings could produce 18 tons of humus each year. He concluded that “it may be doubted if there are any other animals which have played such an important part in the history of the world as these lowly organized creatures” (Darwin, 1881: 316).

The primary initial response to Darwin’s ideas was scepticism. Loudon had listed earthworms among garden pests, and discussed means of eradicating them, and this prejudice continued long after Darwin’s time (Satchell, 1983: 5–18). Even before Darwin had completed his experiments, his theory was tested in the press, for the columns of the Gardeners’ Chronicle were the scene of a controversy over his views in 1869. It began with an article by “W. T.” – presumably the zoologist William Thomson (1825–1899), a frequent contributor to the Chronicle – describing the beneficial effect of earthworms on the soil in terms of aeration and drainage ([Thomson], 1869). A reply came a month later from a noted horticultural journalist, D. T. Fish, the head gardener at Hardwicke House, Suffolk (Fish, 1869), challenging these contentions, and arguing that the beneficial effects were more likely the result of the decomposition of grass roots, and “the specific gravity of the marl”. “W. T.” then sent Fish Darwin’s 1837 paper, to which Fish drew attention in a letter, full of expressions of unease at challenging the great naturalist (“No great man will ever respect a little one the less for speaking his mind freely, even though it may be in opposition to him”), but speculating that the activity of plants and their roots counted for more than that of earthworms. Darwin replied defending his theory (Fish and Darwin, 1869). In this instance, Fish’s apprehensions about Darwin’s response were justified, for when his book was finally published, it contained a stinging rebuke:
In the year 1869, Mr. Fish rejected my conclusions with respect to the part which worms have played in the formation of vegetable mould, merely on account of their assumed incapacity to do so much work. He remarks that “considering their weakness and their size, the work they are represented to have accomplished is stupendous.” Here we have an instance of that inability to sum up the effects of a continually recurrent cause, which has often retarded the progress of science, as formerly in the case of geology, and more recently in that of the principle of evolution (Darwin, 1881: 6).

Fish, however, seemed to take Darwin’s remarks with little resentment; in the years since he had continued his own observations, and concluded that “No doubt the mean despised worm is a wonderfully efficient drainer” (Fish, 1881).

Indeed, there was more scepticism expressed in the gardening press about his earthworm researches than about the origin of species. Both the *Gardeners’ Chronicle* and the *Gardeners’ Magazine* made the book the subject of leaders (Anon., 1881a, 1881b), and everyone praised it for its narrative qualities and its accumulation of facts. But the *Journal of Horticulture*, after praising the work for its new facts and immense quantity of experiments, used the phrase “so this naturalist fancies”, to distance itself from his more extreme speculations (“C.”, 1881), while the reviewer in *The Garden* took Fish’s former line that “enough has not been allowed for the great part the decay of vegetation itself plays in the formation of mould” (Anon., 1881c: 489). The *Chronicle’s* assertion of respect for the worm, and suggestions of a transformation in agriculture, turned out to be flashes in the pan. Agricultural colleges ignored Darwin’s work, and interest on the part of zoologists seems to have remained resolutely taxonomic. “Darwin’s work”, wrote Hilderic Friend, “was of no service to the systematist or collector”, and in the 1890s “There were only two men in England... who knew anything about the subject, and they had not paid attention to the native forms” (Friend, 1924:21). A general sentiment gradually percolated...
Fig. 22. Charles Darwin, wood-engraving by Worthington G. Smith from Gardeners’ Magazine, 1881.
that earthworms “are almost without exception our friends and allies” (Friend, 1923: 5), but as late as the 1950s, the RHS Dictionary of Gardening, having remarked on the “beneficial manurial effect” of wormcasts, gave most of its attention to preparations for killing earthworms in bowling-greens and tennis courts (Royal Horticultural Society, 1956: 727). I have found no book before Thomas Barrett’s Harnessing the Earthworm (1949) which made concrete recommendations for encouraging earthworms and using them to make compost in culture beds (not yet known as wormeries).

Valedictory: Darwin and horticulture
Darwin’s death produced uniformly appreciative obituaries in the gardening press. In all, the theme of Darwin the benefactor of horticulture was paramount.

The testimony to Darwin’s general importance to horticulture had begun in the 1870s, when a leader in the Gardeners’ Chronicle described him as “the physiologist who has done the most in our time to advance the science of horticulture”; “since the days of Thomas Andrew Knight, no physiologist has done so much to extend the basis on which successful culture, whether of animals or of plants, depends” (Anon., 1875a). And not long after a writer in The Garden had condemned pre-Darwinian botanists as being “of slight use to horticulture or to art compared with what it might be... therefore it is a pleasure to notice that Mr. Darwin’s work is appreciated” (“Justicia”, 1880: 11). Shirley Hibberd declared that “Horticulturists and botanists owe to Charles Darwin more than to any philosopher of modern times, but their debt, great as it is, seems to be lost in the general indebtedness of the world to this painstaking inquirer, experimentalist, and generalizer” ([Hibberd], 1881b).

The best statement of horticulture’s debt to Darwin comes from an obituary by D. T. Fish – one of two, for he wrote obituaries for both
the *Gardeners’ Chronicle* and *The Garden*. (There is no record of whether the magazines took umbrage at this double-dealing.)

It is astonishing how much one hears in general society of Darwin’s theories and how little of his facts. I do not know how it may have struck other students of his works, but I have been amazed at his reverent timidity in heaping up fact upon fact until they seemed piled to a mountain height, and all pointing to one conclusion; and then, instead of anything like dogmatic conclusions, or assumptions, merely a mild supposition, or “may be so.” Would that we could imitate our great teacher in the strength of our facts and the timidity of our conclusions therefrom.

One trait in his character that endeared him to many of us must not go unnoticed. No practical man, however humble his station, that had a fact to record was considered unworthy of his notice or a note of thanks. He also seemed to have scanned our horticultural literature with an eagle eye, and to have gleaned from thence all the facts that served to illustrate his point or bore upon his purpose, verifying his extracts with references.

No man has done more to raise horticulture than he who has been laid in his right place in the Great Abbey (Fish, 1882a).
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Volume 4 will examine nineteenth-century British literature on fruit-growing, and will include:

- Hogg’s *Fruit Manual*, its rivals and successors: a bibliographic study
- English fruit illustration in the early 19th century: Knight and Ronalds

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