The Cambridge Companion to
THE "ORIGIN OF SPECIES"

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12 Darwin's Botany in the *Origin of Species*

> He moons about in the garden, and I have seen him standing doing nothing before a flower for ten minutes at a time. If he only had something to do, I really believe he would be better.
>
> – Charles Darwin's gardener[1]

DARWIN'S BOTANY: INTRODUCTION

Taxon-based studies defined much of natural history in the nineteenth century, with botany and zoology serving as the two major realms of such inquiry. Darwin himself was taxonomically promiscuous, flitting from organism to organism much as his curiosity dictated but also out of a utilitarian need for particular examples to support a generalizable theory that explained the diversity of living organisms. Thus, in the course of his scientific career Darwin studied a range of organisms and familiarized himself with related sciences like geography and geology. But increasingly after the *Origin*, his lifelong interest in botany not only revealed itself but came to dominate his research.

That interest had started early. In fact, one could say that he inherited it; his grandfather Erasmus was a translator of Linnaeus, while another relative, John Wedgewood, was one of the founders of the Royal Horticultural Society. Almost serving as a prophetic image of the role that botany would play in his life, an early portrait of the young Charles shows him seated next to his sister Catherine holding a pot of plants. At the age of twelve or so, he was given the task

[1] As cited in Morris et al. (1987, 48).

of counting peony blossoms in his father's garden; and later, while engaged in what became a failed study of medicine, he was exposed to the study of *materia medica* (or plants known to be useful for medical or healing purposes) (Kohn 2008b). As a young Cambridge student, Darwin formally studied with John Stevens Henslow and spent so much time with him that he became known as "the man who walks with Henslow." Under Henslow's tutelage, he performed anatomical dissections on plants like *Geranium*, and familiarized himself with taxonomic studies (Kohn 2008b). His exposure to Henslow's herbarium and to its special emphasis on "collated" specimens, which stressed multiple collections, was especially important. It helped lay the groundwork for his understanding of variation and indeed for his understanding of speciation (Kohn et al. 2005).

Later, while exploring unfamiliar terrain during the *Beagle*'s various layovers in South America, Darwin collected numerous specimens of local floras and sent them back home for permanent storage as well as identification. Later still, while enjoying his life as the celebrated "squarson-naturalist" of Downe, he began to undertake detailed observational and experimental studies on select plants. Recognizing their importance to his larger theoretical project, Darwin also formed strong professional ties with leading systematic botanists of his day such as Joseph Hooker, the director of Kew Gardens, and Asa Gray, a botanist at Harvard University. He also cultivated an extensive correspondence network with breeders, horticulturalists, collectors, and compilers of floras the world over. These professional networks helped fuel his growing interest in plants, especially by providing some of the best examples in support of his theory of descent as set forth in the *Origin of Species*.[2]

Plants lent themselves readily to Darwin's investigations as examples in support of his theory, but they were especially valuable for the kinds of observational and experimental studies that characterized his research in the mature phase of his career. They were tractable "model organisms" (to use a presentist term), easy to grow (depending on the plant chosen) and stationary (and therefore easy to observe); knowledge of them from horticultural, agricultural, and

[2] The critical year for Darwin's shift to botany is 1860. See David Kohn, "Darwin's Botanical Research," in Morris et al. (1987, 50–9). For an overview of Darwin's life and work, see Janet Browne (1995 and 2002).

breeding practices was well developed by the middle decades of the nineteenth century, as was knowledge of their morphology, anatomy, and even cytology thanks to new microscopic, sectioning, and staining techniques. Plants additionally bore a staggering assortment of vegetative and reproductive structures, with complex mating patterns that included self-fertilization, cross-fertilization, and elaborate pollination mechanisms. These last often required other organisms, like insects and birds, thus making them ideal for studies of co-adaptation. And with what we now recognize as "open" or indeterminate growth patterns that reflected readily the direct effects of the environment, plants also drew attention to the general process of adaptation, making them ideal systems for exploring the direct and indirect effects of the environment (Briggs and Walters 1997). For all these reasons, Darwin increasingly devoted his efforts to drawing on the study of plants not only to fortify, but also to extend his theoretical insights as first developed in the *Origin*.

Though it would be hard to consider Darwin a botanist in the strict sense of the term, he employed examples of plants in at least three interrelated ways: (a) in his thinking about evolution, (b) in his own researches, and (c) in his professional life as a whole. By the end of his long and productive career, he had completed no less than six books exclusively devoted to botanical subjects, published between the years 1862 and 1880, in addition to botanical articles published in the weekly *Gardener's Chronicle* and journals like the *Agricultural Gazette* (Ornduff 1984). Some drew extensively on the work of colleagues, while others drew exclusively on his own observations and experiments performed in the hothouses and experimental gardens of his home in Downe (Morris et al. 1987).

PLANTS IN DARWIN'S *ORIGIN OF SPECIES*

The importance of plants for Darwin's theory is manifested by their prominent appearance in the first four chapters of the *Origin*, the chapters that lay the groundwork for his theory of descent. Plants do not figure significantly in the chapters on geology (Chapters 9 and 10) or in the chapter dealing with instinct (Chapter 7); but in all other chapters of the *Origin*, plant examples appear frequently, customarily following mention of a phenomenon demonstrated in animals.

As early as the very introduction to the *Origin*, Darwin set this comparative rhythm in motion by making reference to how "preposterous" it would be to attribute to "mere external conditions, the structure, for instance of the woodpecker, with its feet, tail, beak, and tongue, so admirably adapted to catch insects under the bark of trees" (*Origin*, 3). He immediately followed the animal example with a comparable plant example, the "misseltoe" (or mistletoe), which "draws its nourishment from certain trees, which has seeds that must be transported by certain birds, and which has flowers with separate sexes absolutely requiring the agency of certain insects to bring pollen from one flower to the other." It was "equally preposterous," Darwin concluded, "to account for the structure of this parasite, with its relations to several distinct organic beings, by the effects of external conditions, or of habit, or of the volition of the plant itself" (*Origin*, 3).

Chapter 1: Cultivated Plants

Chapter 1, titled "Variation under Domestication," relied heavily on examples from cultivated plants. Darwin focused at great length on the interplay of two well-known aspects of the biology of plants: their vegetative reproductive habits and their variability in different environments. Variability was especially problematic. Darwin pointed out that "seedlings from the same fruit and young of the same litter, sometimes differ considerably from each other," though they have had exactly the same conditions of life; but determining how much of this variability to attribute to the direct action of the environment was not easy. Darwin nonetheless maintained that "some slight amount of change, may I think, be attributed to the direct action of the conditions of life – as, in some cases, increased size from food, colour from particular kinds of food and from light, and perhaps the thickness of the fur from climate" (*Origin*, 10).

When seeking "laws of variation" or attempting to explain the causes of such variation, Darwin acknowledged that they were "quite unknown, or dimly seen," though he thought it worthwhile to explore historical treatises on older cultivated plants like the potato, the hyacinth, and the dahlia for what they revealed. He was surprised especially by the "endless points in structure and constitution in which the varieties and subvarieties differ slightly from each other" in these genera. This was especially striking to Darwin: "The whole organization seems to have become plastic, and tends to depart in some degree from that of the parental type" (*Origin*, 12). Darwin's use of the word "plastic" to describe plant variation deserves special notice, for it presaged the notion of plasticity in general and of phenotypic plasticity in particular, a phenomenon observed especially in the plant world and understood only well after the 1920s and 1930s (Smocovitis 1997). But Darwin, of course, knew little about the laws of inheritance, let alone the distinction between genotype and phenotype; he expressed his frustration with the well-known remark that the "laws governing inheritance are quite unknown" (*Origin*, 13). He simply stipulated that "any variation that is not inherited is unimportant for us" (*Origin*, 12).

The chapter then turned to "man's selection," where Darwin employed examples of human modification of animals and plants. He considered "man's" ability to accumulate in organisms traits useful to himself:

> We cannot suppose that all the breeds were suddenly produced as perfect and as useful as we now see them; indeed, in several cases, we know that this has not been their history. The key is man's power of accumulative selection: nature gives successive variations; man adds them up in certain directions useful to him. In this sense he may be said to make for himself useful breeds. (*Origin*, 30).

In this way Darwin stated that new forms have come into being, summoning up Youatt's famous metaphor of "the magician's wand, by means of which he may summon into life whatever form and mould he pleases" (*Origin*, 31). As in the case of animals, new forms of plants have so arisen; but in plants, the "variations are . . . more often abrupt" (*Origin*, 32).

Plants also evinced a staggering diversity of parts within the same species. While Darwin made allowances for "the laws of the correlation of growth," he stated that "as a general rule, I cannot doubt that the continued selection of slight variations either in the leaves, the flowers, or the fruit, will produce races differing from each other chiefly in these characters" (*Origin*, 33). He further added that the horticulturalist, however, must have patience, since changes, even in plants, can occur only slowly over many generations (*Origin*, 36). Darwin concluded the chapter with the following closing thought: "Over all these causes of Change, I am convinced that the accumulative action of Selection, whether applied methodically and more quickly, or unconsciously and more slowly, but more efficiently, is by far the predominant Power" (*Origin*, 43).

Chapter 2: Importance of Data from Floras to the Argument That Varieties Are Incipient Species

Plants figured most prominently, and were most important in laying out the argument for Darwin's theory, in Chapter 2, "Variation under Nature." In this chapter, Darwin explored the nature and character of variation in the natural world. This is where he explored the notion of individual differences and argued for continuous gradations going from individual differences to varieties, incipient species, and "good" species. Early on in the chapter, Darwin recognized the puzzling phenomenon of "protean" or "polymorphic genera." These were widely varying species with multiple forms of "inordinate variation" that were especially prevalent in plant genera like *Rubus*, *Rosa*, and *Hieracium* (this last plant, known as the hawkweed, was later to give Mendel a headache and possibly led him to drop his experimental studies of inheritance in plants), as well as in some insects and Brachiopod shells. For Darwin, these were "perplexing cases" because they appeared to be polymorphic in all "countries" and therefore seemed to vary independently of the conditions of life. He wrote, "I am inclined to suspect that we see in these polymorphic genera variations in points of structure which are of no service or disservice to the species, and which consequently have not been seized on and rendered definite by natural selection, as hereafter will be explained" (*Origin*, 46). The preponderance of polymorphic genera in some large plant genera aside, Darwin drew heavily on botanical data, notably from the huge number of flora that had been compiled or were actively being compiled by systematic botanists. That data, in Darwin's mind, was crucial in supporting his argument that varieties are incipient species.

As Karen Parshall (1982) has shown, Darwin relied on mathematical calculations based on a series of floras compiled by botanists like Joseph Hooker (and his flora of New Zealand), Asa Gray (and his celebrated flora of temperate North America), Hewett C. Watson, and others to lay the groundwork for his belief that varieties were indeed incipient species (see also Browne 1980). From the summer of 1857 to the spring of 1858, Darwin worked studiously on an enormous compilation of botanical data that he then analyzed mathematically. He knew that such use of numerical data to determine relationships of genera, species, and varieties was actually fairly common at the time: Alphonse de Candolle had compiled extensive data in his *Géographie biologique raisonnée*, and Asa Gray had written "Statistics of the Flora of the Northern United States."[3] Though he was not mathematically inclined, Darwin was aware of these studies and looked to them to provide numerical evidence of a correlation between extensiveness of plant distribution and variability. The larger the genus, the larger the species that it contained, or so his theory suggested.[4]

Darwin was of course famously vague about the definition of 'species,' writing on page 44: "No one definition has as yet satisfied all naturalists: yet every naturalist knows vaguely what he means when he speaks of a species. Generally the term includes the unknown element of a distinct act of creation. The term 'variety' is almost equally difficult to define; but here community of descent is almost universally implied, though it can rarely be proved." He held that "the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms" (*Origin*, 52). For Darwin, therefore, species did not differ in kind from varieties; and while the naturalist's definition of species appeared "vague," it served his purposes well: it supported his argument that that there were no clear lines separating species from varieties or varieties from individual differences. Taken as a whole, furthermore, such a view

[3] Both had been recently published. See Alphonse de Candolle (1855) and Asa Gray (1856–57).

[4] There were three additional patterns possible: large genera having small species, small genera having large species, and small genera having small species. Darwin argued that the pattern of large genera having large species would be the likely outcome if his theory were true.

also argued against the notion that species were the products of special acts of creation.

To illustrate these points, Darwin wrote: "Guided by theoretical considerations, I thought that some interesting results might be obtained in regard to the nature and relations of species which vary most, by tabulating all the varieties in several well-worked floras" (*Origin*, 53). He considered first what he termed "dominant species," or those that were at the same time the most widely diffused and the most common in a particular geographical region. It was generally known that the most widely ranging species exhibited the most varieties, but Darwin's use of available data in the context of his theory took this point even further:

> in any limited country, the species which are most common, that is abound most in individuals, and the species which are most widely diffused within their own country (and this is a different consideration from wide range, and to a certain extent from commonness), often give rise to varieties sufficiently well-marked to have been recorded in botanical works. Hence it is the most flourishing, or, as they may be called, the dominant species, – those which range widely over the world, are the most diffused in their own country, and are the most numerous in individuals, – which oftenest produce well-marked varieties, or, as I consider them, incipient species. (*Origin*, 53–4)

The data also indicated to Darwin that these "dominant species" tended to belong to genera that were of proportionately larger size. Based on his belief that species differed from varieties in degree rather than in kind, Darwin finally conjectured that species in larger genera presented more varieties than species in smaller genera, just as he had postulated if his theory held true. And since his theory held true, it could account for these phenomena better than any creationist interpretation of species.

Chapter 3: Plants and the Struggle for Existence

Strangely enough, Darwin began this chapter, titled "Struggle for Existence," stressing the relative unimportance of being able to distinguish the 300 or so species of British plants as species, subspecies, or varieties (*Origin*, 60). Far more important to him was understanding how species arise in nature and the process by which adaptation to the environment and to other interactions with species takes place. Critical to this process was the inevitable competition that took place in the "struggle for existence," a phrase that Darwin stressed was used in a "large and metaphorical sense, including dependence on another, and including (which is more important) not only the life of the individual, but success in leaving progeny" (*Origin*, 62). Once again, Darwin referred to the "beautiful co-adaptations" seen in the woodpecker and the mistletoe, but took special care to use plants to make the point that such competition is subtle as well as inordinately complex:

> Two canine animals in a time of dearth, may be truly said to struggle with each other which shall get food and live. But a plant on the edge of a desert is said to struggle for life against the drought, though more properly it should be dependent on the moisture. A plant which annually produces a thousand seeds, of which on an average only one comes to maturity, may be more truly said to struggle with the plants of the same and other kinds which already clothe the ground. The missletoe is dependent on the apple and a few other trees, but can only in a far-fetched sense be said to struggle with these trees, for if too many of these parasites grow on the same tree, it will languish and die. But several seedling missletoes, growing close together on the same branch, may more truly be said to struggle with each other. As the missletoe is disseminated by birds, its existence depends on birds; and it may metaphorically be said to struggle with other fruit-bearing plants, in order to tempt birds to devour and thus disseminate its seeds rather than those of other plants. In these several senses, which pass into each other, I use for convenience sake the general term struggle for existence. (*Origin*, 62)

Darwin thus painted an ornate picture of interactive relations among organisms in nature; in the process of doing so, he also drew the distinction between interspecific and intraspecific competition, only later formally recognized by twentieth-century ecologists. But the plant examples he noted also served to give a more nuanced meaning to his use of the metaphor "struggle for existence." As he noted, plants could not rightly be said to struggle against drought, but only against other similar plants; nor could they be properly said to "struggle" at all, since that employed a kind of anthropomorphism difficult to uphold in the case of nonsentient organisms like plants. The "convenient" metaphor of "struggle" was thus subject to critical interpretation; Darwin used it loosely to depict the frequently unseen interactive forces at work in the natural world. Indeed, this chapter as a whole, which was devoted to the complex relations of living organisms, made especially notable use of such metaphors, which later scholars from ecologists to literary critics have scrutinized (Beer 1983, 2000 revised edition).[5]

The chapter also revealed Darwin's own clever experiments that eventually inspired the field of plant ecology (Harper 1967). In one critical experiment, Darwin followed the fate of native seedlings on a cleared piece of ground three feet long by two feet wide. Out of 357 seedlings that germinated, 295 were destroyed by organisms like slugs and insects. In yet another experiment on a little plot of turf (three feet by four feet) that had been mowed for some time, he followed the fate of plants allowed to grow freely without mowing and grazing. Darwin found that under these conditions, the more vigorous plants gradually killed the less vigorous plants, even though the latter were fully grown. He counted some nine species that perished as a result of competition from other species that were allowed to grow freely. Such complex interactions were also seen as a result of the enclosure of the heathlands, where Darwin had observed a takeover by the Scotch fir tree. This was due to the protection such enclosures afforded from grazing cattle. In yet other examples, Darwin showed how insects were required for the existence of various plants such as orchids, which required visits from moths to remove pollen masses for fertilization. He also noted yet another set of experiments and observations he conducted on common red clover pollination from humble-bees.[6] One of the most ecological chapters of the *Origin*, it culminated with the famous description on page 74 of the "entangled bank." A metaphor for the complex relations among diverse organisms, the entangled bank described by Darwin was the result of a natural process that obeyed well-defined laws. Thus, an image that appeared disordered or chaotic on the surface

[5] The most famous of these evokes a disturbing image: "The face of Nature may be compared to a yielding surface, with ten thousand sharp wedges packed close together and driven inwards by incessant blows, some one wedge being struck, and then another with greater force" (*Origin*, 67).

[6] Darwin performed a series of experiments on the nectary structure and on various flowers and insect pollinators that he published as brief articles or reports for the *Gardener's Chronicle* in the 1850s.

was in fact deeply structured, orderly, and emerged from well-defined natural laws. Its importance not only to this chapter but also to Darwin's thinking in the *Origin* overall is made apparent by its appearance (though somewhat altered in form) in the final dramatic paragraph closing the book.

Darwin concluded this important chapter by once again drawing attention to the subtleness of competition in the plant world, in contrast to that of animals. Just as the structure of the teeth and talons of the tiger served adaptive functions that enabled the animal to compete, and just as the legs and claws of the parasite that clung to the tiger's body enabled it to survive in a competitive world, so too did the "beautifully plumed seed of the dandelion" have competitive value (*Origin*, 77). With reference to such seeds, Darwin then explained that in many plants the store of nutriment therein may at "first sight" bear "no sort of relation to other plants." But then he added: "from the strong growth of young plants produced from such seeds (as peas and beans), when sown in the midst of long grasses, I suspect the chief use of the nutriment is to favour the growth of the young seedling whilst struggling with other plants growing vigorously all around" (*Origin*, 77). Darwin thus also understood the nutritive value of seeds and their role in enabling the plants to survive in a competitive environment.

Chapter 4: Plants and Support for Natural Selection

Chapter 4 finally explored Darwin's "principle of natural selection," following the development of the argument laid out for it in Chapters 1 to 3. Darwin used plant examples in three important sections of this chapter: (a) as illustrations of the action of natural selection; (b) as examples of the intercrossing of individuals; and (c) as examples demonstrating divergence of character.

IMAGINARY ILLUSTRATIONS. Darwin's best evidence in support of his theory was indirect, based on an analogy with "man's selection" and on the geographical distribution of plants and animals on continents and oceanic islands. He had no real direct evidence for natural selection and instead relied in this section on two famously "imaginary illustrations." The first was the case of the predating wolf, while the second, intended to be a more "complex" case, involved the excretion by a plant of a sweet juice that would serve to draw insects for pollination. In the latter example, Darwin devoted over two pages of text to what was mostly a hypothetical discussion on the origin of the complex parts of flowers coadapted as pollinating mechanisms that would serve to enhance cross-fertilization of the plants.

INTERCROSSING OF INDIVIDUALS. The elaborate mechanisms proposed for cross-fertilization then gave way to a discussion of its advantages. Here Darwin built on earlier insights on the subjects of generation, reproduction, and sexuality, broadly construed (*Notebooks*, 170–71). For Darwin, sexual reproduction or intercrossing between unlike individuals was potentially advantageous because it was a means of increasing the variability of organisms. Such variability, alongside generation (which included not just birth but also death), enabled the constant process of adjustment to the changing conditions of life. The alternative mechanisms of vegetative (asexual) reproduction and self-fertilization (inbreeding), though potentially offering temporary advantages (such as enabling organisms to colonize new habitats), limited variability and were in the long term detrimental to organisms. Plants again offered stunning examples of diverse reproductive or mating systems that could serve as examples for Darwin's theory; but what counted as "like" individuals, or what counted as proper, good, or true species, was not easy to ascertain in the plant world, a problem long recognized, and at times also capitalized on, by plant breeders. Indeed, hybridization between "unlike forms," while serving to increase variability, could also disrupt the integrity of species. Darwin was aware of the complex issues raised by hybridization and reserved that discussion for a later chapter devoted exclusively to the subject; in the section on intercrossing, what he needed to show was the advantages of intercrossing, meaning here mostly sexual reproduction. He therefore scoured the works of well-known plant breeders like F. C. Gaertner and J. G. Koelreuter for their knowledge and for relevant examples. He also drew extensively from C. C. Sprengel's work on pollination mechanisms and floral anatomy to engage in a substantive discussion of plant sexuality and the advantages of intercrossing. He was also aware of the phenomenon of hybrid vigour, which was later recognized by twentieth-century geneticists as "heterosis," and used it to explain the advantages of intercrossing:

> In the first place, I have collected so large a body of facts, showing, in accordance with almost universal belief of breeders, that with animals and plants a cross between different varieties, or between individuals of the same variety but of another strain, gives vigour and fertility to the offspring; and on the other hand, that close interbreeding diminishes vigour and fertility; that these facts alone incline me to believe that it is a general law of nature (utterly ignorant though we be of the meaning of the law) that no organic being self-fertilizes itself for an eternity of generations; but that a cross with another individual is occasionally – perhaps at very long intervals – indispensable. (*Origin*, 96)

He also added to the store of knowledge from Sprengel his own observations from experiments on *Lobelia fulgens* (on what twentieth-century biologists call self-incompatibility) and his observations on a contrivance that prevents the stigma from receiving its own pollen. In *Lobelia*, he wrote,

> there is a really beautiful and elaborate contrivance by which every one of the infinitely numerous pollen-granules are swept out of the co-joined anthers of each flower, before the stigma of that individual flower is ready to receive them; and as this flower is never visited, at least in my garden, by insects, it never sets a seed, though by placing pollen from one flower on the stigma of another, I raised plenty of seedlings; and whilst another species of Lobelia growing close by, which is visited by bees, seeds freely. (*Origin*, 98).

Darwin then noted how varieties of various common vegetables like cabbage, radish, onion, and other plants, if allowed to seed near each other, will see "a large majority . . . of the seedlings thus raised . . . turn out mongrels" (*Origin*, 99). This he confirmed with his own data. Darwin attempted to understand the "mongrelization" of forms by conjecturing that pollen from another variety had a prepotent effect over a flower's own pollen, but he then added that "when distinct *species* are crossed the case is directly the reverse, for a plant's own pollen is always prepotent over foreign pollen" (*Origin*, 99). The flowers of many species, in Darwin's view, therefore had some kind of physiological or structural mechanism(s) in place to ensure that they mated preferentially with their own kind (for the most part, that is). While crosses served to increase variability, they ideally also took place in way that ensured the integrity of species. Darwin thus set the stage for his discussion of hybridization or "hybridism," a phenomenon common in plants but that needed explanation in the context of his theory.

DIVERGENCE OF CHARACTER. By divergence of character, Darwin had in mind a principle of "high importance" to his theory, the process by which individual differences among members of the same species gradually increase so as to form varieties, subspecies, and finally distinct species. Simply stated, the principle was described thus: "the more diversified the descendants from any one species become in structure, constitution and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers" (*Origin*, 112). Outlining the process was crucial to Darwin's theory as it explained how species originated; he devoted some fifteen pages of the *Origin* to the complex subject (see Kohn 2008 for extensive discussion of this topic).

Plants once again figured prominently in Darwin's examples demonstrating this important principle. He described a novel natural experiment he had performed himself on turf plots three feet by four feet in size that followed the diversification of the plants therein. He wrote of his results: "it has been experimentally proved, that if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater weight of herbage can thus be raised" (*Origin*, 113). So too under "natural circumstances" the "greatest amount of life can be supported by great diversification of structure" (*Origin*, 114). Such natural circumstances included small ponds or islets or limited environments where plant and animal inhabitants "jostled" or competed with each other closely. Darwin further noted that introduced or "naturalized" plants that were able to compete and colonize successfully were often of a highly diversified nature, thus presaging insights from the science of the biology of invasive species, the area that is now known as "invasion biology" (*Origin*, 115).

Chapters 5, 6, and 7: Acclimatisation in Plants

In Chapter 5, titled "Laws of Variation," Darwin played on themes referred to especially in Chapter 1, "Variation under Domestication." Only heritable variation was important for his theory, but without detailed knowledge of the laws of inheritance, little could be done to discern variation that was due to direct or indirect actions of the environment (though Darwin did of course also think that direct actions of the environment were often heritable). Darwin nevertheless thought it possible to "dimly catch a faint ray of light" (*Origin*, 132). He repeated his belief that the direct effect of the environment – a Lamarckian process – is extremely small in the case of animals but perhaps rather more pronounced in the case of plants. He yet believed that often the direct effects of the environment would be seized on by natural selection, and so preserved by his principal device.

Chapter 8: Hybridism or Hybridization

Hybridization (and mechanical grafting) in plants was a time-honored agricultural and horticultural practice. By the eighteenth century, plant hybridization had drawn the attention of horticulturalists and practical breeders like Koelreuter and Gaertner, and Darwin relied on their insights extensively in the *Origin*. Darwin once again drew heavily on both for their understanding of hybridization to support his view of the relations among varieties, incipient species, and species. He especially needed to explain why species, which, according to his theory, had descended from each other, usually could not interbreed. Darwin offered a quick survey of the diverse and complex patterns observed in the phenomenon of sterility and its correlate, fertility in hybrids and mongrels (mongrels being the progeny of varieties). He noted especially striking peculiarities in hybridization patterns; species crossing with facility could give rise to sterile hybrid progeny, while species that crossed with difficulty could give rise to fertile hybrid progeny; and reciprocal crosses between two species sometimes gave very different results. The view that barriers to hybridization existed so as to "prevent confusion of all organic forms," the standard explanation of why species did not interbreed, was clearly not a viable explanation (*Origin*, 245). For Darwin, the patterns of sterility and fertility observed instead provided further evidence in support of his theory and the view that there were no clear lines between varieties, incipient species, and species. It was also a way of arguing against special creation. He concluded: "Finally, then, the facts briefly given in this chapter do not seem to me opposed to, but even rather to support the view, that there is no fundamental distinction between species and varieties" (*Origin*, 278). This was to prove crucial in the penultimate chapter on classification.

Chapters 11 and 12: The Geographical Distribution of Plants

In keeping with his observations while aboard HMS *Beagle*, Darwin's best evidence in support of his theory was drawn primarily from the distribution patterns of the plants and animals he had observed while he traveled on the celebrated voyage. The patterns – and the implied relationships thereof – on continents and oceanic islands in particular inspired crucial reflection and provided evidence not so much directly in support of his theory, but against the view that special creation could account for the observable distribution and variation patterns. Plants once again figured prominently in these chapters, especially since the problem of dispersal and dissemination in plants (using seeds or vegetative structures in reproduction) could be readily tested even by gentleman naturalists. Here again, Darwin's experimental efforts to test his theories of dispersal among continental and oceanic forms of plant species figured prominently. He explored what he termed "occasional means of distribution" through experiments on seed survival during ocean dispersal. He tested 87 kinds of plant seeds and found that 64 were able to germinate after an immersion of 28 days in salt water, while a few survived 137 days. He drew distinctions between small seeds (without capsules and fruit, which could increase buoyancy as well as provide reserves) and vegetative structures like branches and leaves, performing experiments that also took into account the rates of Atlantic currents, which he found listed in Johnson's *Physical Atlas*.[7] He even tested the ability of seeds to survive and be transported above flotsam and jetsam

[7] Darwin here was referring to a popular atlas by Alexander Keith Johnson that was available at the time. "Johnson's *Physical Atlas*," as it was popularly known, had been inspired by Alexander von Humboldt. Darwin may have used either the first edition, which appeared in 1848, or the second, extended version, which appeared in 1856; he may have also used both over a period of time. See Alexander Keith Johnson, *Physical Atlas of Natural Phenomena* (London and Edinburgh: W. Blackwood and Sons, 1848 edition and 1856 edition).

in the crops of pigeons and on the feet and in the beaks of birds. He also took into account potential transport on icebergs and then extended his discussion to include historic means of dispersal during the glacial period. The discussion of the diverse means of transport and the survivability of plants stretched to no less than twenty or so pages of the *Origin* and revealed much about Darwin's experimental prowess (see Bowler 2008).

Chapter 13: Classification, Morphology, and Embryology in Plants

Plants make brief – but notable – appearances in Chapter 13 on classification, morphology, and embryology. This was not so much because plants were not important to these concerns, but because Darwin had already given abundant evidence to support the arguments of the chapter. By Chapter 13, the penultimate chapter, Darwin had carefully built his argument for a rethinking of classification based on a more natural plan that took into account community of descent.

Darwin agreed with other systematists that vegetative structures that varied greatly were not ideal characters for classification and that reliance should instead be placed on the reproductive parts. He wrote with some emphasis: "organs of vegetation, on which their whole life depends, are of little signification, excepting in the first main divisions; whereas the organs of reproduction, with their products the seed are of paramount importance!" (*Origin*, 414).[8] In this statement Darwin also revealed an insight from what is now known as "plant developmental biology," which he later developed on pages 418–19. By speaking of "main divisions" Darwin recognized the process by which the fundamental character used in the major division of plants into the Dicots and the Monocots originated embryonically. He wrote:

The same fact holds good with flowering plants, of which the two main divisions have been founded on characters derived from the embryo, – on

[8] Darwin had earlier resisted this idea but changed his mind because his theory of descent upheld the view that essential parts (or characters) were common in related groups. These were therefore the least likely to vary.

the number and position of the embryonic leaves, or cotyledons, and on the mode of development of the plumule and radicle. In our discussion on embryology, we shall see why such characters are so valuable, on the view of classification tacitly including the idea of descent. (*Origin*, 436)

He also recognized yet another significant fact of plant development that was most closely associated with German morphologists like Johann Wolfgang von Goethe:

It is familiar to almost every one, that in a flower the relative position of the sepals, petals, stamens and pistils, as well as their intimate structure, are intelligible on the view that they consist of metamorphosed leaves, arranged in a spire. In monstrous plants, we often get direct evidence of the possibility of one organ being transformed into another; and we can actually see in embryonic crustaceans and in many other animals, and in flowers, that organs, which when mature become extremely different, are at an early stage of growth exactly alike.

This latter point was especially important because it suggested recapitulation, which was a demonstration of descent. Darwin then resumed his reverse argument in support of his theory, and against special creation, to account for this; he also demonstrated the taxonomic promiscuity and the comparative rhythm that characterized his style of argumentation in the *Origin* overall:

How inexplicable are these facts on the ordinary view of creation! Why should the brain be enclosed in a box composed of such numerous and such extraordinarily shaped pieces of bone? As Owen has remarked, the benefit derived from the yielding of the separated pieces in the act of parturition of mammals, will by no means explain the same construction in the skulls of birds. Why should similar bones have been created in the formation of the wing and leg of a bat, used as they are for such totally different purposes? Why should one crustacean, which has an extremely complex mouth formed of many parts, consequently always have fewer legs; or conversely, those with many legs have simpler mouths? Why should the sepals, petals, stamens and pistils in any individual flower, though fitted for such widely different purposes, be all constructed on the same pattern? (*Origin*, 437)

The answer to all of these questions is that the mentioned structures have been derived from common descent.

CONCLUSIONS

What if any general conclusions can we draw from this brief study of Darwin's botany in the *Origin*? For one thing, plants were absolutely foundational to the development of his argument. Plant examples appear in greatest abundance throughout Chapters 1 to 4, the critical chapters laying out the argument for his theory, and especially in Chapter 2, where Darwin used botanical data in support of his argument that varieties may be seen as incipient species. Darwin's use of hybridization in Chapter 8 played a similar foundational role in establishing varieties as incipient species; it also supported his natural or genealogical (or what we now term "evolutionary") classification.

Yet another conclusion we may draw is that Darwin's own researches into botany deserve more credit than has been given him. Historians have always known that botany figured prominently in his work after the *Origin*, but have not fully appreciated the extent to which the study of plants served a foundational role in formulating the argument for his theory. As one recent study has revealed, historians still have much to learn about the early influences that teachers like Henslow had upon Darwin (Kohn et al. 2005).

Along these lines, historians have also not fully appreciated Darwin's adroitness in the use of experimentation (though his powers of observation have been duly noted and appreciated). A closer reading of Darwin's botanical research in the *Origin* reveals the extent to which he was engaged in clever and crucial experiments to test or buttress key points of his theory well before 1860. Study of Darwin's botany also reveals the more practical, "down-to-earth" aspects of his work, which complements the traditional historical portrait of Darwin as a great theorist and synthesizer (he was, of course, but this was possible because he was also a keen observer and experimentalist).

Taking this point a bit further, historians might wonder why Darwin did not consider himself a botanist, and why botanists did not readily claim him as one of their own, given that it was the one area of natural history where he arguably made the most notable contributions. One reason for this is that his proximity to full-time systematists like Hooker and even Gray (who were entirely devoted to the systematic study of plants) may have thwarted his identification as a botanist. Compared to them, and other like-minded specialists, Darwin lacked the kind of single-minded devotion to one particular taxonomic group. Yet another reason may be that his experiments lacked the kind of laboratory setting that was increasingly taking center stage in botanical practice as it embraced the "new botany" associated with microscopy and table-top instrumentation. In at least one celebrated exchange with the noted German plant physiologist and experimentalist Julius Von Sachs, Darwin was criticized, if not belittled, for his lack of experimental rigor (Heslop-Harrison 1979; De Chadarevian 1996). Caught between the full-time systematists, whose botanical knowledge of individual groups was incomparably greater than Darwin's, and the proponents of the "new botany," whose experimental methods appeared to be more rigorous, Darwin's contributions to botany resided in a peculiar place that did not gain real status or legitimacy until the second half of the twentieth century, with the emergence of the new field known as "plant evolutionary biology." Even his contributions to the area of "evolutionary ecology" or "plant ecology," areas that were clearly articulated in the *Origin*, had to wait until those fields came to fruition in the latter half of the twentieth century. His equally keen insights into the biology of invasive species and his contributions to the new field of "invasion biology" have been recognized only in recent years (Hayden and White 2003).

Plant evolutionary biology itself did not properly come of age until the 1930s and the 1940s, during the period of the "evolutionary synthesis." It was during this period that Darwinian evolutionary understanding was integrated with Mendelian genetics in a manner that could account for the origin of biological diversity. A number of questions and problems that Darwin had encountered were resolved by this integration of heredity and evolution, broadly construed. For plant evolution more specifically, this integration took place in 1950 with the publication of G. Ledyard Stebbins's *Variation and Evolution in Plants*; it was only after this synthesis that many of the phenomena that had piqued Darwin's interest but that had bedeviled him and his contemporaries interested in formulating a general theory of plant evolution were resolved, or at least re-problematized (see Arnold 1997 for new views on hybridization and evolution). Thus, Darwin's botanical efforts did not really come to fruition until enough was understood about the evolutionary biology of plants; just the same, in the context of their day and in the context of the *Origin*, Darwin's insights into plant evolution proved to be critical to formulating the most coherent theory then available for general evolution.