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The Darwinian Revelation: Tracing the Origin and Evolution of an Idea

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The idea of evolution by natural selection formulated by Charles Darwin and Alfred Russel Wallace is a cornerstone of modern biology, yet few biology students or professionals are familiar with the processes of discovery behind the idea. Focusing on Darwin, I draw on letters, notebooks, and other resources to trace key insights and put them into historical context, illustrating how major elements of Darwin's theory came to him over many years. I further consider how Darwin came to formulate the logical argument structure of his Origin of Species, *discussing the philosophical arguments inherent in the book's structure and how this and Darwin's other works can be seen as part of a larger argument and way of looking at the world. I suggest that in teaching evolution today, educators could profitably draw on both Darwin's personal intellectual journey in coming to his ideas, and the compelling argument structure he devised in presenting his theory.*

Keywords: Charles Darwin, transmutation, natural selection, vera causa, evolution education

Deep in the opening chapter of *On the Origin of Species* is a passage that has always struck me as having a slightly exasperated tone: Seemingly frustrated with animal breeders' unwillingness or inability to see that they create their remarkably divergent breeds gradually through a process of selection, Darwin laments that breeders "refuse to sum up in their minds slight differences accumulated through many generations" (Darwin CR 1859, p. 29). Appreciating the slow and stepwise nature of change under domestication is central to understanding the natural process of species change, Darwin argues. A focus on the end product by these breeders is understandable, given the slow process of change. There is a similar tendency to focus on the end product in the realm of ideas, including the fruitful products of Darwin's own thinking.

The idea of evolution by natural selection, a central pillar of the biological sciences, might be too easily perceived by modern readers as a monolithic idea grasped more or less at once by Darwin. This notion stems at least in part from Darwin's own presentation of his theory as a logical whole in the *Origin*. Darwin's description of his epochal work as "one long argument" in the opening line of the book's final chapter has long served as a general guide to the way in which Darwin conceptualized his theory, but the fuller picture of Darwin's creative process was possible only as his correspondence, notebooks, and other private writings became available for study (Eldredge 2005). Considered from our vantage point 150 years after the *Origin*'s publication in 1859, telescoped by time, it is often unappreciated that key elements of Darwin's thinking unfolded over a dozen or more years—with even his central mechanism of species diversification, his "principle of divergence," not coming to him until well into the 1850s. Darwin scholars have long appreciated this, of course (e.g., Hodge 1977, 1992, Kohn 1980, Mayr 1991, Browne 1995, Waters 2003), just as they have seen Darwin's post-*Origin* works as a continuation of his argument in the *Origin* in the form of explorations and applications of his theory. Yet the common problem of truncated treatment in many science textbooks, with their focus on products, not processes, limits the broader understanding of Darwin's creativity (Kuhn 1962, Marcum 2005). As with Darwin's breeders, it is instructive for the rest of us to analyze how he got there to better appreciate the process. Students of evolutionary biology at all levels would profit from better understanding Darwin's intellectual odyssey and mode of investigation, with its interplay of the inductive and deductive, and historical methodology. The double Darwin anniversary of 2009 thus presents an opportunity not only to celebrate Darwin's achievements but also, in appreciating the development of these ideas, to consider how we might learn from his approach in the way we teach evolution today.

Darwin may have believed in species fixity throughout the *Beagle* voyage (Sulloway 1982a, 1982b), but during this period he reflected on the nature of species and the meaning of their geographical distributions, particularly in the voyage's final year. In Darwin's time most "philosophical naturalists" engaged questions such as the number of "centers of creation" in the world, the nature and age of the Earth, and the nature

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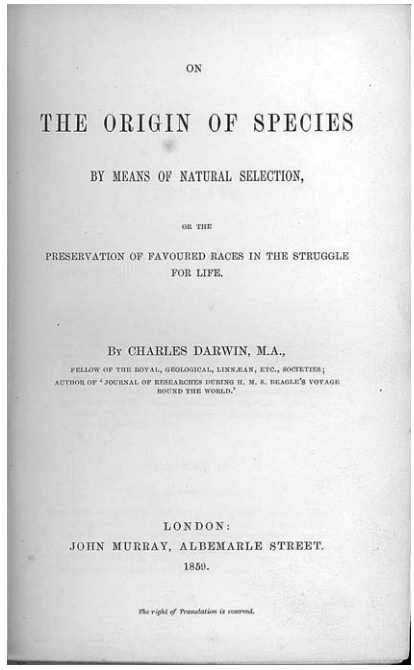
and meaning of fossils (Browne 1983, Sloan 2003, Rudwick 2005, Thomson 2005, Williams and Ebach 2008). The characterization of species and the limits of variation were integral to this quest. Alexander von Humboldt, the polymath German explorer and naturalist who influenced both Darwin and fellow naturalist Alfred Russel Wallace in profound ways (see Sloan 2003), urged the detailed study of biogeography. He established the technique of "botanical arithmetic" to quantify species richness relative to genera, a technique elaborated by others to study levels of endemism (Browne 1980), and suggested that a comparative analysis of New and Old World biota would yield insights into the larger philosophical questions concerning species. Swiss botanist Augustin Pyramus de Candolle expressed the importance of the matter in his *Essai élémentaire de géographie botanique* of 1820: "All of the theory of geographical botany rests on the particular idea one holds about the origin of living things and the permanence of species."


ON

THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

OR THE

PRESERVATION OF FAVOURED RACES IN THE STRUGGLE FOR LIFE.

BY CHARLES DARWIN, M.A.,

FELLOW OF THE ROYAL, GEOLOGICAL, LINNÆAN, ETC., SOCIETIES; AUTHOR OF 'JOURNAL OF RESEARCHES DURING H. M. S. BEAGLE'S VOYAGE ROUND THE WORLD.'

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1859.

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***Title page of the first edition of* On the Origin of Species. *Reproduced with permission from John van Wyhe ed.,* The Complete Work of Charles Darwin Online (http://darwin-online.org.uk).**

Darwin had considerable training in the significance of "geographical botany" as a student of the Reverend John Stevens Henslow at Cambridge. Beyond merely cataloging species and varieties of different locales, Henslow sought out and highlighted individual variations. He focused attention on how the limits of variation relate to species boundaries, and undertook experiments to probe the limits of morphological variation of species. Darwin, "the man who walks with Henslow," as he was known by his classmates, assisted in the collection of specimens during the popular weekly botanical rambles Henslow led through the Cambridgeshire countryside (Kohn et al. 2005).

Darwin was thus very much aware of the burning questions of natural philosophy. Yet explicit reflections on the nature of species and the meaning of their geographical distributions are few in his *Beagle* diary. Darwin later asserted (e.g., in his notebooks, the introduction to the *Origin*, and his autobiography) that his nascent evolutionary views were sparked by observations of South American fossils and biogeography made on the voyage. This is true, but he realized the deeper significance of his observations in retrospect—it took the analysis of specialists to lead him to see their true importance. His most spectacular fossil finds came in September 1832, at the eroded sea cliffs near Bahía Blanca in Argentina (Keynes 2001). Anatomist Richard Owen later (in 1837) described these fossils as extinct giant quadrupeds that nonetheless belonged to recognizable extant South American groups. By the time Darwin summarized his fossil findings in his *Journal of Researches* after the voyage, he had become a convinced evolutionist, yet in the *Journal* he remarked only that "the law of the succession of types...must possess the highest interest to every philosophical naturalist.... It is impossible to reflect without the deepest astonishment, on the changed state of this continent" (Darwin CR 1839, p. 210). Darwin's biogeographical observations in South America seem to have had a more immediate effect on him. For example, the flora and fauna of the Galápagos Islands, visited in September 1835, underscored for Darwin how fraught with uncertainty was the nature of species and varieties, and provided him with provocative facts of distribution and affinity. Four months after departing the islands Darwin commented in a letter to Henslow: "I shall be very curious to know whether the Flora belongs to America, or is peculiar," also mentioning that he had "paid also much attention to the Birds, which I suspect are very curious" (Burkhardt et al., vol. 1, p. 484).

He did not dwell on the curious nature of Galápagos species in this letter, yet species and varieties and their larger distribution and relationships stayed on Darwin's mind. From New South Wales he recorded this diary entry in January 1836: "I had been lying on a sunny bank & was reflecting on the strange character of the Animals of this country as compared to the rest of the world. An unbeliever in everything beyond his own reason, might exclaim 'Surely two distinct Creators must have been [at] work.'" Observing an insect he recognized brought him back to the idea of a universal creation; his diary continues: "Whilst thus thinking, I observed the conical pitfall of a Lion-Ant.... Without a doubt this predacious Larva belongs to the same genus, but to a different species from the European one. Now what would the *Dis*believer say to this? Would any two workmen ever hit on so beautiful, so simple and yet so artificial a contrivance? It cannot be thought so. The one hand has surely worked throughout the universe" (Keynes 2001, pp. 402–403; emphasis Darwin's). Species and varieties were very much on Darwin's mind that following summer, when we see more explicit consideration of the significance of Galápagos flora and fauna in his notes. Of the Galápagos mockingbirds he reflected:

> "When I see these Islands in sight of each other and possessed of but a scanty stock of animals, tenanted by these birds but slightly differing in structure and filling the same place in Nature, I must suspect they are only varieties.... If there is the slightest foundation for these remarks, the Zoology of Archipelagoes will be well worth examining; for such facts would undermine the stability of species." (Barlow 1963, p. 262)

Darwin seemed to glimpse the significance of these birds, but he did not yet realize that the finches of those equatorial islands were even more remarkable, nor that the tortoises told a similar story (Sulloway 1982a, 1982b).

Birth of a transmutationist

Following Darwin's return home in October 1836, there is little indication that he gave much thought to these big philosophical questions until early winter of 1837 when, in London and Cambridge, specialists impressed upon him the curious nature of his collections from South America and the Galápagos. Richard Owen received Darwin's fossil mammals sometime between late December 1836 and early January 1837. He wrote geologist Charles Lyell in late January with his findings: Darwin had found extinct giant forms of several South American mammal groups, including edentates, a rodent, and a llama or camel, discoveries that confirmed the "law of succession," which described the sequential replacement of species over time by related, but distinct, forms. Lyell was sufficiently impressed to announce Darwin's findings in his presidential address to the Geological Society the following month: "These fossils," Lyell stated, "establish the fact that the peculiar type of organization which is now characteristic of the South American mammalia has been developed on that continent for a long period" (Herbert 2005).

Over this same period, ornithologist John Gould read a series of papers to the Zoological Society treating Darwin's bird collection from South America and the Galápagos. Gould treated the finches that now bear Darwin's name on 10 January, raptorial birds on 24 January (even citing the Galápagos hawk as a "beautiful intervening link" between the hawk genus *Buteo* and the caracara genus *Polyborus*), Galápagos mockingbirds on 28 February, and the two contiguously allopatric South American rheas on 14 March. Darwin conferred with Gould between 7 and 12 March 1837, learning that more than two-thirds of his Galápagos birds were new species—unique to the islands, yet unmistakably South American in affinity. Historians largely agree that Gould's analysis was most likely the final factor convincing Darwin of transmutation (Sulloway 1982b, Browne 2002).

Between the findings of Owen and Gould, then, we have the crucial juxtaposition of temporal patterns of species relationship in the fossil record with spatial (biogeographic) patterns. The idea of transmutation prompted Darwin to consider again the nature of species and varieties. He did so largely in his private diary and notebooks, but in his public writing he said little to reveal the ferment of ideas he was developing. His *Journal of Researches* gives only suggestive comments, for example: "We may infer, that, with the exception of a few wanderers, the organic beings found on [the Galápagos] archipelago are peculiar to it; and yet that their general form strongly partakes of an American character.... This similarity in type, between distant islands and continents, while the species are distinct, has scarcely been sufficiently noticed" (Darwin CR 1839, p. 474).

Darwin reopened the notebook he was working on during the last leg of the *Beagle* voyage (his "Red Notebook") soon after hearing Lyell's presidential address in mid-February 1837 (Sulloway 1982b). His first evolutionary musings in this notebook, probably dating to the time of his meeting with Gould in March 1837, pertain to how species might change, prompted by observations of, for example, the contiguous ranges of the two South American rheas. Here is his first entry, preserving what Mayr (1991) called Darwin's "telegraph style" of notewriting: "Speculate on neutral ground of 2. Ostriches; bigger one encroaches on smaller.—change not progressi[ve]: produced at one blow...Yet new creation affected by Halo of neighboring continent" (Barrett et al. 1987, p. 61). Darwin's idea here is that species might change rapidly, "at one blow." Two pages later he muses again over the rheas, and relates their geographic relationship to the temporal relationship of extinct and living mammals of South America. These patterns suggest rapid transitions to him, "not gradual change or degeneration," he writes; "if one species does change into another it must be per saltum [by sudden transitions]" (Barrett et al. 1987, p. 63). By that summer, Darwin opened a new notebook dedicated to transmutation, designated his "B Notebook": "In July," he recorded in his diary, "opened first note Book on 'transmutation of Species'— Had been greatly struck from about month of previous March—on character of S. American fossils—& species on Galapagos Archipelago. These facts origin (especially latter) of all my views."

Toward an "excellently true theory"

Realizing the reality of transmutation immediately raised a host of pressing questions to Darwin: Does change occur quickly, or slowly? Does it occur according to some fixed law that places limits on how different species can become, or on how many different species can exist at any one time in a given taxonomic group? What is the significance of islands? What are the environmental or geological factors? And, of course, What causes change? It was not until the fall of 1838 that Darwin hit upon the mechanism of natural selection. Darwin long maintained that he was inspired by domestication, and that the Reverend Thomas Robert Malthus's *Essay on the Principle of Population* then provided him with the insight that selection as practiced by breeders could also apply in nature: "All my notions about how species change are derived from long continued study of the works of (and converse with) agriculturists and horticulturalists," he wrote to Harvard botanist Asa Gray in July 1857, "and I believe I see my way pretty clearly on the means used by nature to change her species" (Burkhardt et al., vol. 6, p. 431). Similarly: "I came to conclusion that Selection was the principle of change from study of domesticated productions; and then reading Malthus I saw at once how to apply this principle," he wrote to Wallace in April 1859 (Burkhardt et al., vol. 7, p. 279). Domestication is so compelling an analogy to the natural process of species change that Darwin later seemed to see it as the initial inspiration for his ideas on both transmutation and natural selection. As we shall see, reflections on domesticates may have preceded Darwin's insight from Malthus, but they did not present an analogy in quite the straightforward manner he later imagined.

Arguing from domestication to a natural process of species change was more problematic for Darwin than one might assume. One reason for this was the widespread notion that domesticated organisms varied only within limits, and that variations amounted to "monstrosities"—occasional novelties, great in magnitude. A related view held that these organisms were unnatural and impermanent, readily "reverting" back to some generic type in a state of nature and so teaching us nothing about natural species (Lyell held this view, and the argument also resonated with Wallace, who opened his 1858 transmutation paper with this very point). Nonetheless, production of domestic varieties assumed great importance to Darwin. Although scholars are not in agreement as to precisely how or to what extent domestication served as an analogy for a natural process of species change for Darwin (e.g., Herbert 1971, Ruse 1975, Kohn 1980, Evans 1984, Sterrett 2002, Gildenhuys 2004), it is clear that he drew inspiration from astronomer John Herschel's philosophy of science, which advocated analogy as a way to discover "true causes" (*vera causae*) in nature. It is clear, too, that domestication played a role in the derivation of his general concept of selection as an agent of change applicable to both domestication and nature (Gildenhuys 2004).

Darwin's C Notebook (dated from about March through June 1838) bears entries pertaining to domestic varieties that most likely reflect Darwin's reading of key agricultural breeding tracts. The power of selection, or "picking," in creating varieties was extensively discussed by leading agricultural breeders of the day (e.g., John Saunders Sebright, Robert Bakewell, and John Wilkinson), in publications that Darwin owned and annotated (Evans 1984). Most striking is a case made by Sebright against the then widely held notion that new varieties are made simply by crossing: "The alteration which may be made in any breed of animals by selection, can hardly be conceived by those who have not paid some attention to this subject; they attribute every improvement to a cross, when it is merely the effect of judicious selection" (Sebright 1809, quoted in Ruse 1975). Darwin began to scrutinize Sebright's work and other publications on breeding in around March 1838, around the time he opened the C Notebook. His reading of the agriculturists may have prompted him to seek out a mechanism of change in nature parallel or equivalent to the process employed by breeders, ultimately showing that the same process operates in both contexts (e.g., Evans 1984, Gildenhuys 2004). In this view, while an appreciation of the production of domestic varieties precedes Darwin's reading of Malthus, domestication as an analogical process became fully apparent to Darwin over a period of time. This is supported by notebook entries pertaining to domestic varieties in the months between March and September 1838 (bracketed by his reading of Sebright and other breeders in March and his crucial reading of Malthus in September), as well as in the months after reading Malthus. Some of these entries are worth examining.

Early in the C Notebook Darwin uses the term "picking" several times in the context of producing domestic varieties (e.g., C17, C34, C106), and in C133 he cites Sebright and Wilkinson, declaring: "Whole art of making varieties may be inferred from facts stated." A key insight appears to be the breeders' assertion that "picking" over a period of time is sufficient to create new varieties—crossing, or hybridization, is unnecessary. Darwin's Malthusian insight comes about three-quarters of the way through the D Notebook, in passages dating to September 1838. The "energetic language" of Malthus suddenly crystallized for him the epic scale of struggle and checks on population growth in natural populations. "Until the one sentence of Malthus no one clearly perceived the great check amongst men," Darwin writes. He then gives examples of struggle in nature, concluding with the now-famous metaphor of the wedges (later appearing in chapter 4 of the *Origin*): "One might say there is a force like a hundred thousand wedges trying to force every kind of adapted structure into the gaps in the economy of Nature, or rather forming gaps by thrusting out weaker ones" (D135).

It is not until we are well into the E Notebook that domesticated varieties are discussed together with natural species: "It is a beautiful part of my theory, that domesticated races...are made by precisely the same means as species—but latter far more perfectly and infinitely slower" (E71). Kohn (1980) suggests that before this point, Darwin saw domesticated varieties as analogous to natural species in a broad sense, but not produced by analogous causes per se. Then, by the time of this entry, Darwin sees them as causally analogous, and subsequently inverts the presentation of his argument to proceed from the compelling domestication analogy. In entry E118, for example, he comments that domestic varieties have been produced "by training, & crossing, & keeping breed pure." He continues: "[And] so in plants, *effectually* the offspring are picked & not allowed to cross" (emphasis in original). Darwin next rhetorically asks, "Has nature any process analogous...if so she can produce great ends—But how." And finally: "Make the difficulty apparent by cross-questioning... even if placed on Island—if &c. &c.—Then give my theory.—excellently true theory." Here, then, were the beginnings of a blueprint for the logical exposition of his theory: Open with the production of domesticated varieties as analogy, followed by a presentation of "my theory." Domestication and artificial selection became the opening observation, setting the stage for his argument for transmutation in nature by the analogous process of natural selection, followed by evidence for transmutation from fields like biogeography and paleontology. Note that this represents an inversion of the order of his actual insights.

A theory by which to work

After formulating the principle of natural selection, Darwin continued to struggle with issues such as crossing, heritability, reversion, and the extent and cause of variability. He voraciously read scientific treatises and journals (Vorzimmer 1977), sent lists of questions to contacts in the agricultural community, and even distributed a questionnaire to breeders in the spring of 1839. A major milestone had been reached: Malthus had given him "a theory by which to work," as he expressed it in his autobiography. "But I was so anxious to avoid prejudice, that I determined not for some time to write even the briefest sketch of it" (Darwin CR 1958, p. 20). That first brief sketch of 35 pages was written in 1842, followed by a detailed 230-page essay in 1844 (see Darwin F 1909). In both of these preliminary works, a basic, three-part presentation is evident, following an outline that is thought to date to about 1842 (Vorzimmer 1975, Hodge 1977):

> I. The Principles of Var. in domestic organism[s].
>
> II. The possible and probable application of these same principles to wild animals and consequently the possible and probable production of wild races, analogous to the domestic ones of plants and animals.
>
> III. The reasons for and against believing that such races really have been produced, forming what are called species.

Darwin may have structured the exposition of his theory in this way as a conscious effort to present a philosophical argument. In this regard, the influence of John Herschel and, to a perhaps lesser extent, that of philosopher William Whewell is evident (Ruse 1988, Snyder 2006). Darwin personally knew these philosophers and read their works, and was familiar with their ideas on the nature of the scientific enterprise—notably, their thoughts on identifying *verae causae* in nature. In Herschelian logic, the case for a *vera causa* is best made by demonstrating (or arguing plausibly for) the existence of a mechanism, the causal adequacy or competence of that mechanism, and the responsibility of the mechanism in explaining observed phenomena (Hodge 1992, Hull 2003, Waters 2003). The responsibility case resonates with Whewell's concept of consilience of inductions, which holds that a *vera causa* can be demonstrated through the concordance of otherwise disparate observations. Snyder (2006) noted that the consilience aspect of Darwin's theory was especially potent: Beyond merely explaining facts, his theory tied together many classes of facts with a single causal explanation.

The philosophical roadmap provided by the existence, adequacy, and responsibility or consilience argument model sheds light on the three-part outline Darwin used in the 1842 and 1844 *Sketch* and *Essay,* as well as in the *Origin* itself: the creation of domestic varieties by artificial selection as an analog to divergence of natural varieties and species, arguing for the existence and adequacy of transmutation by natural selection. Selection, the causal agent of change under domestication, must also occur in nature as a logical result of abundant variability and severe struggle, the outcome of which depends in large part on that variability. Accordingly, chapter 1 of the *Origin* presents the domestication analogy, and chapters 2–4 set forth the logical argument for selection in nature being based on abundant, heritable natural variation, with differential survival and reproduction linked to that variation. These comprise the existence and adequacy cases. Darwin then turns to disciplines as diverse as hybridism, the fossil record, instinct, biogeography, morphology, and embryology to argue that his model of transmutation by natural selection is consistent with the observed facts, underscoring the responsibility of natural selection as causal mechanism. The remaining chapters thus largely make a case for the wide applicability of the theory, though this running "responsibility case" argument is prefaced with a set of chapters devoted to frankly acknowledged problems and difficulties (chapters 5–8).

Darwin's evolutionary ideas continued to develop as he read, experimented, sent endless queries to naturalists the world over, and pondered. The 1844 publication of the metaphysical evolutionary work *Vestiges of the Natural History of Creation,* and its wholesale rejection by the scientific establishment, may have reinforced Darwin's conviction that he needed to continue to amass data and observations for a complete and well-substantiated theory. Though he came to the essential components and logical structure of the theory by the early 1840s, other elements came to him over his years of study and experimentation. The most important of these later insights was undoubtedly the principle of divergence, which became the centerpiece of his grand vision for not just transmutation but also diversification. This principle lies at the heart of the only illustration found in the *Origin*: the divergence of character diagram of chapter 4.

Divergence of character is a process, Darwin envisioned, by which natural selection acts on varieties of a species to enhance their competitiveness, an important outcome of which is the differential survival and reproduction of the most divergent varieties on average (insofar as the most divergent varieties compete least). This leads to a de facto ecological division of labor—niche partitioning, in modern terms—yielding an ever-ramifying divergence pattern when iterated over time: the tree of life (Tammone 1995). Browne (1980) showed that Darwin's divergence principle was fully formulated as late as spring 1857, whereupon he inserted it into his already-complete chapter on natural selection in the summer of 1858. (As we shall see, Darwin finally initiated a book on descent with modification in 1856; see Stauffer [1975].) Its genesis was far earlier, however, with roots that trace to Darwin's extensive barnacle studies, which resulted in four monographs published between 1851 and 1854.

Among other insights, his studies of fossil and extant barnacles helped to impress upon Darwin the abundance of natural variation in virtually all points of structure, and to clarify the difficulties inherent in delineating species and varieties. It was the nature of variation and patterns of its occurrence in species and varieties that next led Darwin to undertake a statistical study of varieties in species of different sized plant genera—a form of statistical plant geography dating back to the early 1800s, pioneered by Humboldt and dubbed "botanical arithmetic" by him in 1815.

Humboldtian botanical arithmetic was undertaken to help delineate patterns of "creative activity" on the globe, with an eye toward identifying centers of creation. Darwin's version of botanical arithmetic looked at the creative activity of natural selection on a more local level, in a process of species splitting that at once explained ever-increasing competitiveness as well as species diversification, extinction, coexistence, and, by extension, the hierarchical classification system (Browne 1980).

The scope of Darwin's botanical arithmetic study was considerable. He first tallied from some dozen botanical tomes such data as whether genera with many varieties or with wide ranges also boasted many species—to him, a gauge of active generation of new species. But then his friend and neighbor John Lubbock showed him that this approach was simplistic, suggesting a far better one that used proportional ratios to calculate observed and expected numbers of varieties associated with species of precisely defined large and small genera. "You have done me the greatest possible service in helping me to clarify my Brains," Darwin wrote to Lubbock. "What a disgraceful blunder you have saved me from. I heartily thank you" (Burkhardt et al., vol. 6, p. 430). Darwin then scrambled to redo all of his calculations of the previous 20 months. To his amazement and delight, he found that species in small genera (having one to three species) consistently exhibited fewer varieties than expected, compared with those in larger genera (with four or more species). This new approach crystallized for him the way in which natural selection drives diversification and grows the tree of life. "These facts are of plain signification," Darwin later wrote in the *Origin*. On the basis of his botanical arithmetic, he maintained that "where...the manufactory of species has been active, we ought generally to find the manufactory still in action" (Darwin CR 1859, p. 56).

It is often unappreciated just how central these botanical studies, and the divergence principle they inspired, were to the development of Darwin's overall theory. He mentioned the importance of his principle of divergence in a letter to a friend, the botanist Joseph Dalton Hooker, in August 1857, and described it in some detail the following month in a letter to another confidante, the American botanist Asa Gray:

> One other principle, which may be called the principle of divergence plays, I believe, an important part in the origin of species. The same spot will support more life if occupied by very diverse forms: we see this in the many generic forms in a square yard of turf...or in the plants and insects, on any little uniform islet, belonging almost to as many genera and families as to species.... We know that it has been experimentally shown that a plot of land will yield a greater weight, if cropped with several species of grasses than with 2 or 3 species. Now every single organic being, by propagating so rapidly, may be said to be striving its utmost to increase in numbers. So it will be with the offspring of any species after it has broken into varieties or sub-species or true species. And it follows, I think, from the foregoing facts that the varying offspring of each species will try (only few will succeed) to seize on as many and as diverse places in the economy of nature, as possible. Each new variety or species, when formed will generally take the places of and so exterminate its less well-fitted parent. This, I believe, to be the origin of the classification or arrangement of all organic beings at all times. These always seem to branch and sub-branch like a tree from a common trunk; the flourishing twigs destroying the less vigorous—the dead and lost branches rudely representing extinct genera and families. (Burkhardt et al., vol. 6, p. 445)

By the time he had reformulated his botanical analysis, Darwin had made considerable progress on what he called his "species book." Darwin began this book in 1856 in response to urging by Lyell. Alfred Russel Wallace's lucid "Sarawak Law" paper of 1855 had indicated to Lyell that Wallace was converging on Darwin's idea, though Darwin did not agree; indeed, Wallace was already a committed evolutionist, and was seeking a mechanism for species change. This insight soon came, and Darwin had completed only some 10 chapters when he was forestalled by the arrival of Wallace's brilliant Ternate essay of 1858 (Stauffer 1975). The first of July, 1858, marked the presentation of both Wallace's essay and extracts of Darwin's writings on the subject to the Linnean Society, but this was only the beginning. Compelled to work rapidly to edit down the two-thirds of the book he had written and to draft abbreviated versions of the final third of the chapters, Darwin was abjectly apologetic for the "abstract" nature of the volume that he produced in November 1859. *On the Origin of Species* may have lacked the extensive footnoted references, tables of supporting data, and numerous argument-buttressing examples and observations that his longer, more traditional, scientific treatise would have had, but it perhaps reads better as a narrative unburdened by the distractions of footnotes and tables.

One longer argument

Darwin felt that his "abstracted" presentation would leave him open to criticism—his desire to present thorough evidence in a lengthier tome was most likely the key reason he held off publishing his theory earlier, despite its extensive development by 1844 (van Wyhe 2007). In the *Origin*'s introduction, he declared his intention to give a more detailed treatment in the future: "No one can feel more sensible than I do of the necessity of hereafter publishing in detail all the facts, with references, on which my conclusions have been grounded; and I hope in a future work to do this" (Darwin CR 1859, p. 2). Significantly, Darwin planned to follow the *Origin* with three works dedicated to a fuller exposition of his theory, one for each component of his three-part logical argument. "You have hit on exact plan," he wrote to Thomas Henry Huxley shortly after the *Origin* was published, "which on advice of Lyell, Murray &c I mean to follow, viz bring out separate volumes in detail & I shall begin with domestic productions" (Burkhardt et al., vol. 7, p. 434). Accordingly, what was a 36-page chapter on variation under domestication in the *Origin* became the two-volume *Variation of Animals and Plants under Domestication.* He reiterated in the introduction to *Variation,* too, that he intended to present his theory in three works, of which *Variation* was the first. In the second, he would expand his case for variation in nature, struggle for existence, natural selection, and address various difficulties, and in the third work, "try the principle of natural selection by seeing how far it will give a fair explanation of the several classes of facts just alluded to" (Darwin CR 1868, p. 9). Note that these planned volumes mirror the existence, competence, and responsibility arguments that constitute the logical layout that Darwin had settled on many years earlier for his theory.

Thwarted by illness, the necessity of frequent revisions to the *Origin,* and numerous writing projects, Darwin succeeded in producing only *Variation,* the first of these planned works. Two sizable projects preceded *Variation*: an 1862 volume on orchid pollination and a long article in 1865 on climbing plants. Darwin also published some 60 articles and letters in an astonishing array of journals and magazines between the *Origin*'s appearance in 1859 and the publication of *Variation* in 1868, reflecting an expansive curiosity and Herculean efforts to test and accumulate new evidence for his theory (*http://darwin-online.org.uk/*).

Looking at Darwin's major works as a whole, certain themes are evident. The geological books following the *Beagle* voyage (coral reefs in 1842, volcanic islands in 1844, the geology of South America in 1846) reflect Darwin's Lyellian manner of interpreting geological processes. Darwin's explanation for the formation of coral island atolls (recognized as correct today), which surprised even Lyell, makes for a study in induction, geological uniformity, and the power of inferring process from pattern. Darwin became biology's Lyell by applying to organisms the geologists' way of looking at the world: Species change gradually, by the slow, incessant action of purely natural processes. Darwin undertook his four barnacle monographs of the early 1850s for several reasons: For one, these organisms might reveal much about natural variation and classification, and, for another, the barnacles are a remarkably diverse group with which he could explore the implications of transmutation (Love 2002, Stott 2003).

At first glance, his first post-*Origin* book, on the pollination of orchids, might seem like more of the same. This treatise, an exploration of the rich diversity of pollination-associated structural adaptations found in different orchid groups, is also an argument for the gradual coevolution of flower and pollinator, a case study in the kind of tinkering Darwin says we should expect from a process like natural selection. Orchids are variations on a theme, with different structures used to the same or similar ends in different groups (Beatty 2006). Darwin concluded the book discussing the significance of this observation, and he was especially keen to hear what Asa Gray, a theistically minded friend and supporter, thought of his orchid analysis. Gray immediately saw Darwin's strategy in the book, as revealed by Darwin's comment: "No one else has perceived that my chief interest in my orchid book, has been that it was a 'flank movement' on the enemy.... It bears on design, that endless question" (Burkhardt et al., vol. 10, p. 330).

Plants became increasingly important study subjects for Darwin, and he treated various aspects of botany in four subsequent books (insectivorous plants in 1875, crossing and selfing in 1876, forms of flowers in dioecious plants in 1877, and movement and sense perception in climbing plants in 1880). Think of these as applications and implications of his theory: His interest in carnivorous and climbing plants lay in their animal-like qualities of movement and perception, suggesting fundamental physiological links between plants and animals that are to be expected if these divergent groups share common ancestry. At the same time, Darwin's analysis of the effects of crossing and selfing shares much with his study of the evolution of dioecy: Early on he became convinced that outcrossing is important for health and vigor, and that the evolution of sex, and sexes, results from the action of selection to encourage, if not enforce, outcrossing. The diverse reproductive strategies of plants make them ideally suited for comparative analysis, for which Darwin expanded his Down House greenhouse and procured many botanical specimens for study from Hooker, by then director of the Royal Botanic Gardens at Kew (Browne 2002).

There were later zoological books as well. *Descent of Man* (1871) and *Expression of the Emotions in Man and Animals* (1872) constitute Darwin's statements on human evolution and the fundamental relationship between humans and other animals—the touchiest of evolutionary topics, which he had long avoided in his public writings. Darwin realized the philosophical implications of his theory for humans from the beginning. Consider the passion of entries like this one from the C notebook: "But Man— — wonderful Man. 'divino ore versus coelum attentus' [with divine face turned toward heaven]...he is Mammalian.—his origin has not been indefinite—he is not a deity." Or, from the M notebook: "Origin of man now proved.... He who understands baboons will do more towards metaphysics than Locke" (Barrett et al. 1987, pp. 263, 539). But Darwin was coy about extending his thinking to humans in the *Origin,* going merely so far as to declare, near the end of the book, that "light will be thrown on the origin of man and his history" (Darwin CR 1859, p. 488)—intensified only slightly by the minor change to "much light" by the final edition of 1872. The 1860s and 1870s saw much discussion of the bearing of Darwin's theories on human origins. Huxley and Lyell both published books on the subject in 1863, and German zoologist Ernst Haeckel argued forcefully for human evolution in *Anthropogenie* (Engelmann, 1874). Darwin had his own ideas about humans; beyond merely arguing for descent from other primates, he believed the mechanism behind the diversification of human races was sexual selection (which is why the second half of *Descent* is dedicated to a survey of sexual selection in the animal kingdom). *Descent* and *Expression* represent yet another important demonstration of his theory's wide applicability.

Even Darwin's final work, *The Formation of Vegetable Mould, through the Action of Worms* (1882), also relates to his theory, albeit in a more general philosophical manner. His case for how diminutive earthworms gradually shape the very landscape through slow but incessant activity is a uniformitarian argument for the long-term effects of small mundane processes, a vision that links the geological and biological worlds.

On these grounds I drop my anchor

Darwin's *On the Origin of Species* went through six editions between 1859 and 1872, over the course of which he refined some points, answered critics, and cited new discoveries supporting his arguments (e.g., Kottler 1978, Sulloway 1979, Rhodes 1987). Natural selection had its ups and downs, and for many decades after the *Origin*'s publication, the idea was more down than up—Darwin was far more successful in convincing readers of the reality of transmutation than of his proposed mechanism driving the process. The essence of Darwin's vision for common descent by natural selection, gradually and over immense time periods resulting in marvelous adaptations and the ever-branching "tree of life," remains very much intact today; by the end of his century, however, many subscribed instead to neo-Lamarckian processes, concepts of evolution as an unfolding plan of organic progression, and "hopeful monsters" and other models of saltational evolution (Bowler 1983).

Darwin's belief in the primacy of natural selection wavered little in his later years, and he pointed out that he never argued that it was the sole agent of transmutation, despite claims to the contrary. He asserts in the *Origin*'s final edition that while "it has been stated that I attribute the modification of species exclusively to natural selection, I may be permitted to remark that in the first edition of this work, and subsequently, I placed in a most conspicuous position—namely, at the close of the Introduction—the following words: 'I am convinced that natural selection has been the main but not the exclusive means of modification.' This has been of no avail," he lamented; "Great is the power of steady misrepresentation."

Although there was debate over the process of evolution, evolution itself quickly became the cornerstone of biology that it is today. Darwin was steadfast in his belief in the scientific process that led him to his insights, a commitment to natural law reflected in the epigraphs (Bacon and Whewell) he selected for the *Origin*. Ultimately, it was the astonishing range of observations and phenomena explicable once a process of transmutation is posited that convinced most of his readers of evolutionary change, just as it had convinced him years earlier. "I fully admit there are very many difficulties," he wrote to Asa Gray shortly after the *Origin* was published, "but I cannot possibly believe that a false theory would explain so many classes of facts as I think it certainly does explain. On these grounds I drop my anchor, and believe that the difficulties will slowly disappear" (Burkhardt et al., vol. 7, p. 369).

The light shed by evolutionary theory today on even more "classes of facts" than Darwin could have imagined is an excellent starting point in educating students and the general public about this remarkable science. In doing so, we might profitably take a page from Darwin's playbook and teach Darwin with Darwin himself (Costa 2003). The most readily appreciated argument in support of the reality of species change is the very one that convinced the young Darwin: the expansive explanatory power of the concept, tying together seemingly disparate fields. Most of Darwin's contemporaries saw how compellingly his theory unified biogeography, paleontology, embryology, instinct, and other fields. Modern students are in a position to appreciate a far more expansive unification, encompassing new disciplines unknown to Darwin—the fruits of more than a century of research since the *Origin*'s final edition.

Drawing on Darwin's own intellectual odyssey and the way in which he argued for his theory, we can at once highlight the creative process of scientific discovery, illuminate the rich interplay of induction and deduction in formulating hypotheses, and show how predictions can be framed and tested on the basis of those hypotheses. My approach in the classroom is to draw on the rich literature of Darwin and

This narrative also reveals the woefully misguided dismissal of Darwin's ideas as "only a theory" or merely an offhand notion that Darwin cooked up in a day, for the pernicious misconceptions that they are.

Darwiniana, from diaries and notebooks to letters, books, and articles, a stunning corpus that, together with more contemporary scholarly works, traces the arc of Darwin's life and thought for my students, much as I have tried to do here. This narrative also reveals the woefully misguided dismissal of Darwin's ideas as "only a theory," or merely an offhand notion that Darwin cooked up in a day, for the pernicious misconceptions that they are. That such views remain pervasive in our culture is symptomatic of a persistent misunderstanding of the nature of science, a misunderstanding that threatens to undermine American scientific leadership and global competitiveness if left unaddressed (NAS 2008).

The happy occasion of the dual Darwin anniversary of 2009 presents an opportunity to do more than celebrate the achievements of Darwin, Wallace, and their successors, and the exciting state of evolutionary biology today. It is also an occasion to reflect on how we can best teach our subject. For starters, I would look to Darwin. Let us also drop our anchor on his philosophical grounds, and follow his lead from there.

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