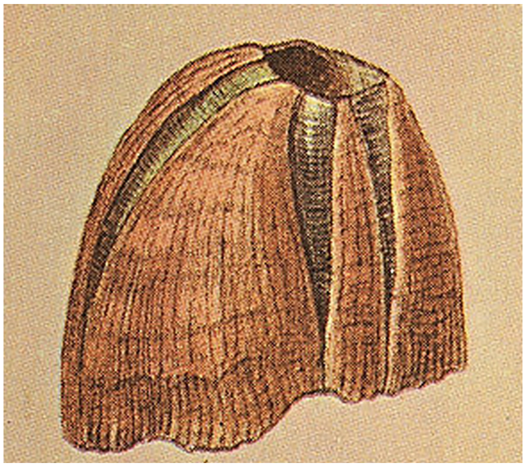

Contributions

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History of Ecological Sciences, Part 40: Darwin's Evolutionary Ecology

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Charles Darwin (1809–1882) was the greatest biological scientist and a major contributor to ecological sciences (Vorzimmer 1965, Acot 1983, Dajoz 1984:46–50, 58–83). Natural history before Darwin had many ingredients of ecology, but was weak in theory. The balance of nature, including Linnaeus' version, economy of nature (Egerton 2007*b*:81–84), was the main example, and it was never developed as a precise theory (Egerton 1973, Kricher 2009). The evolutionary ideas of Erasmus Darwin and Lamarck had ecological relevance (Egerton 2008, 2010*a*) but were not developed into an elaborate theory like Charles Darwin's theory of evolution by natural selection.

What do I mean by evolutionary ecology? A coyote might eat different prey in different parts of its geographic range, so that is not much of an evolved relationship. However, other relationships have evolved. Augustin-Pyramus de Candolle, one of the leading botanists during the first three decades of the 1800s, was uninterested in studies on floral mechanisms that seemed to guide specific species of insects into pollinating a specific species of plants, because he did not believe that one biological species was modified to meet the needs of another species. He was aware of Lamarck's evolutionary speculations about species striving to change, but he was among the majority of botanists and zoologists who did not find Lamarck's teachings convincing. Darwin's first book after publishing the *Origin of Species* was on the mechanisms among orchid species that guide particular insect species to pollinate that orchid species—caused by natural selection, not by Lamarckian striving—one example of evolutionary ecology. Another example is a harmless animal species evolving by natural selection to mimic a dangerous species as a protection from predators. Darwin's *Origin* unleashed this line of thought before ecology became an organized science, and later ecologists readily adopted this intellectual tool (Kolasa 2011:28, 39).

Darwin's *Journal of Researches* (1839) made substantial contributions to ecology (Egerton 2010*b*), and he was as well equipped after his voyage to advance understanding of the economy of nature as to

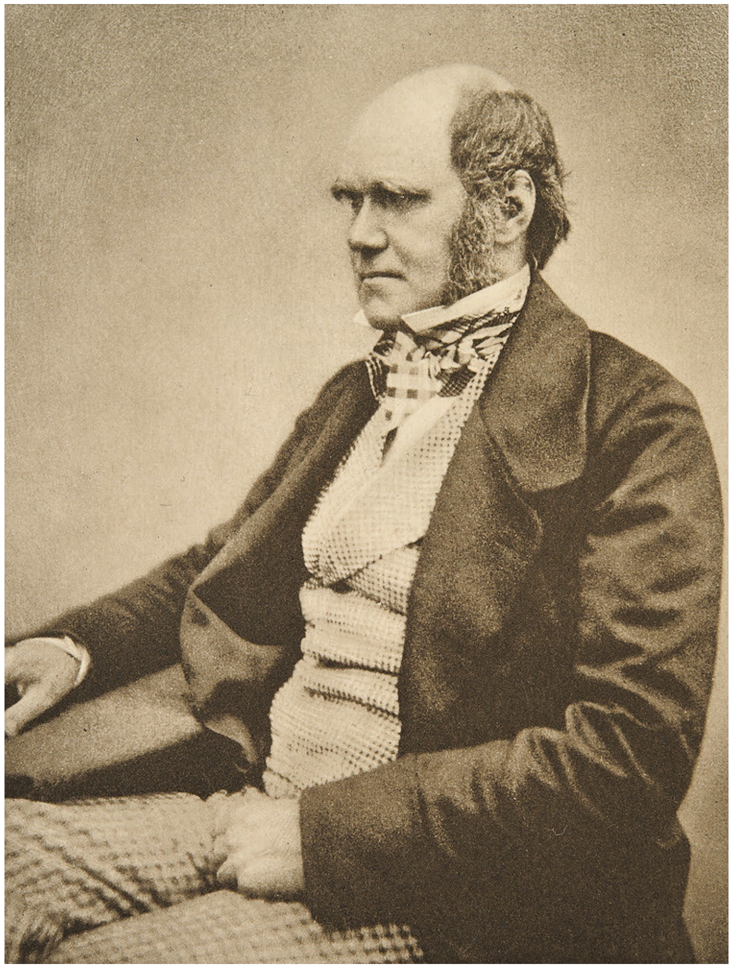


Fig. 1. Charles Darwin, about 1854. Seward 1909:Frontispiece.

advance evolutionary biology. After the *Beagle* publications, Darwin continued being an observational naturalist, but he also became an experimentalist. Darwin followed in the footsteps of three role models: Gilbert White, an observer, Humboldt, an observer–correlationist–experimenter, and Lyell, an observer–theoretician. Darwin commonly investigated several different subjects in a year, and even when our scope is limited to ecological subjects, a strictly chronological presentation is impractical. His post-*Beagle* books (Freeman 1965) usually were preceded by articles in periodicals on the subject. Fortunately, these articles are mostly republished in *The Collected Papers of Charles Darwin* (two volumes, 1977), and more completely in Darwin's *Shorter Publications, 1829–1883* (Darwin 2009). All of Darwin's books are available on the Internet ‹Darwin–online.org.uk›, and are also republished (Darwin 1986–1990). His *Correspondence* has been published by Cambridge University Press since 1985 (18 volumes extend to 1870) and is also online ‹darwinproject.ac.uk›. The present discussion is organized in the chronological order in which he published relevant books, since the *Beagle* volumes covered in part 37 (Egerton 2010*b*). Darwin was one of the world's greatest correspondents, and many of his correspondents were happy to send useful information to him. His publications are also available in a collected set (1986–1990) and at *Darwin online.*

After leaving the Galapagos Islands, Darwin had wondered in 1836 whether mockingbirds from different islands were varieties or species (Egerton 2010*b*:412–414). In March 1837, ornithologist John Gould convinced Darwin that his finch and mockingbird specimens from the Galapagos Islands were different species, and that realization made Darwin an evolutionist (Egerton 2010*b*:416). Darwin then began keeping notebooks in which he recorded his readings and thoughts on transmutation. His eureka moment came on 28 September 1838 (Darwin 1987:375), when he read Thomas Robert Malthus' *Essay on the Principle of Population* (Edition 6, 1826). Why did he read a book that would seem to be peripheral to his quest? He had recently finished his *Journal of Researches* (1839), which he had modeled on Humboldt's *Personal Narrative of Travels*, and Humboldt had praised Malthus' *Essay* (Egerton 1970:331–332). Using information in his notebooks, Darwin wrote two early drafts of his theory, 1842 and 1844 (1909). Those notebooks and drafts provide insights into the literature he read and the progress in his thinking, 1837–1844 (Limoges 1970, Manier 1978, Kohn 1980, 1985, Ospovat 1981, Hodge 2003). Anonymous publication of Robert Chambers' *Vestiges of the Natural History of Creation* (1844), followed by unfavorable reviews from naturalists, inhibited Darwin from publishing his theory at that time.

Instead, he wrote two monographs on living barnacles and two on fossils (1851–1854) that "brought about a new way of thinking about morphological comparisons" (Ghiselin 1969:109), and one cirripedologist (Crisp 1983:73–74) even suggested that these monographs could be considered Darwin's greatest works, even though Darwin had misunderstood aspects of female anatomy! The interest he developed in invertebrates at Edinburgh continued throughout the voyage of the *Beagle*, and he had wanted to include a volume on invertebrates to *Zoology of the Voyage of H. M. S. Beagle*, but had not managed to do so (Love 2002:266–269). His specific interest in barnacles had been piqued in January 1835 when he discovered in the Chonos Archipelago, off the mainland of Chile, the smallest known barnacle (seen with his microscope), which he named *Cryptophialus minutus* (Darwin 1854:23, 566–586, 2000:274–276, Richmond 1988, Keynes 2003:264–265, Stott 2003:xx–xxi, 62–63). *C. minutus* was a parasite that bored through the shell of a conch *Concholepas peruviana* and lived in its body.

While overseeing the volumes describing his vast collections from his voyage and also writing his *Journal of Researches*, he did not pause to explore this oddity, but after those *Beagle* volumes appeared, he returned to this species and was soon studying all of the barnacles. His monographs mostly contain systematic descriptions and classifications of species (Winsor 1969*a*, *b*, Ghiselin and Jaffe 1973, Southward 1983, Richmond 1988); however their introductions are relevant. Barnacles ate "infusoria" (plankton), minute spiral univalves (snails), and crustacea, including larvae of other barnacles (Darwin 1851:45–46). Pedunculated barnacles (Fig. 2) extend over the whole world, and most species have large ranges, especially those that attach to floating objects. Of those species that attach to fixed objects or to littoral animals, one rarely finds more than three or four species in any locality (Darwin 1851:65–66). Cirripedes are usually bisexual, differing from all other crustacean; when sexes are separate, males are minute and permanently epizoic on females (Darwin 1854:15). Sessil barnacles (Fig. 3) live from latitude 74° 18′ North, south to Cape Horn.

The area between the north Philippine Archipelago and south Australia, extending to New Zealand on the right and Sumatra on the left, has a greater number of species than the rest of the world. Probably this is mainly due to the broken nature of the land, providing diversified habitats and due to much of the coast being rocky. There are more species on the rocky coast of western South America than on its sandy or muddy eastern coast. Coral reefs are unfavorable for all barnacles except *Pyrgoma*, and few barnacles are known from Pacific islands. Where they can live, species are few and individuals are infinite. No genus with more than one species is confined to the torrid zone. *Pyrgoma* species are confined to the torrid zone except for one species that is found from the Cape Verde Islands to England and Ireland (1854:159–160).

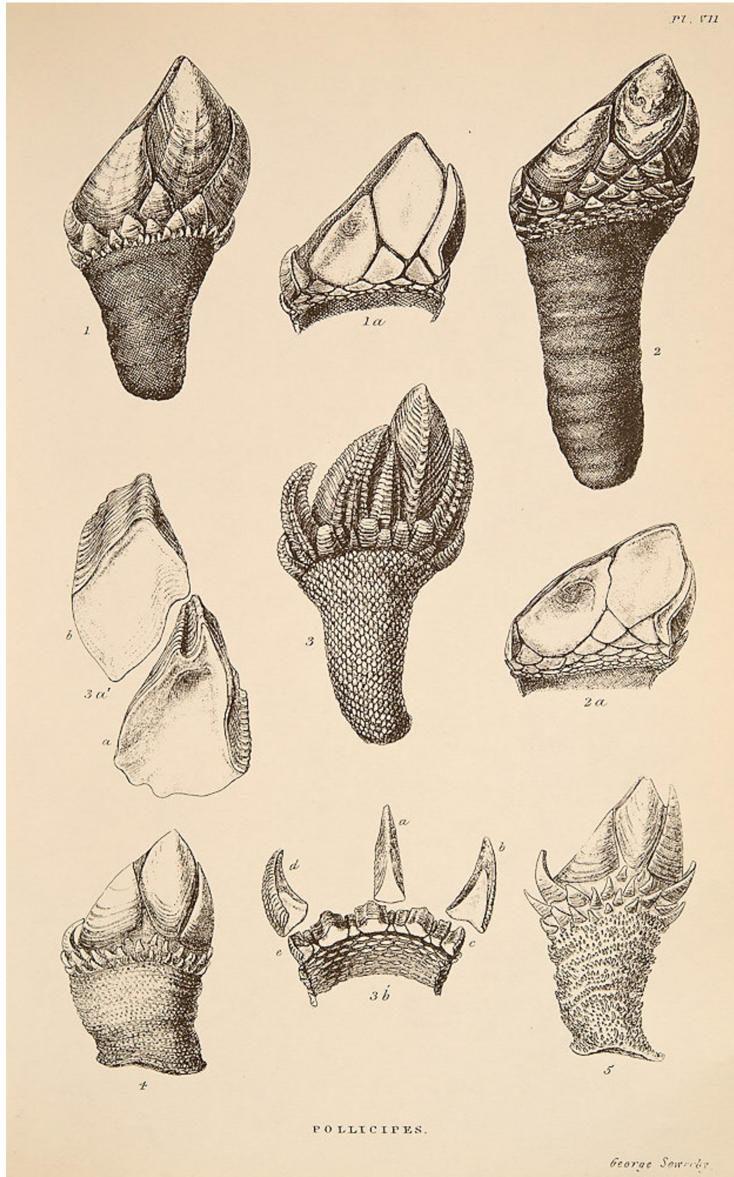
James Dana's great work, *Crustacea* (1852–1855), has an excellent chart with isocrymal lines, showing mean temperature of waters along their course for the coldest 30 consecutive days in any season. He showed that these lines are most influential for the distribution of marine animals. These measurements were a further elaboration on the isothermal lines that Humboldt introduced into environmental studies (Egerton 2011:158). Dana divided the torrid and sub-torrid zones from the temperate zones at isocryme 68°, and the temperate zones from the sub-frigid and frigid zones at 44°.

Darwin found no barnacles confined to frigid zones. Darwin knew 147 species, seven of doubtful habitat. Of the remaining 140, 37 inhabited both torrid and temperate zones, 46 were exclusively in torrid, and 57 were exclusively in temperate zones. The temperate zones, though smaller in area with considerably less lengthy coastlines, had the most species. There are two temperate zones, separated by torrid zones, and the number of species in any zone seems to depend on the isolation of sub-zones. *Balanus* was the largest known genus, with 36 species of known habitats: 9 in the torrid zone, 15 in temperate zones, and 12 in both zones (Darwin 1854:160–162). Darwin divided the oceans with barnacles into five provinces and listed the species in each province (Darwin 1854:164–171). His two volumes on living and two on fossil barnacles won the Royal Society Medal in 1854. D. T. Anderson, *Barnacles: Structure, Function, Development and Evolution* (1994), provides a modern perspective on Darwin's work.

After publishing on barnacles, at Lyell's urging, Darwin returned to his natural selection project and was in the midst of writing a huge monograph, when he was interrupted by arrival in his mail of Alfred Russel Wallace's manuscript, "On the Tendency of Varieties to Depart Indefinitely from the Original Type," in 1858. Wallace became a co-discoverer of evolution by natural selection, and Lyell and Joseph Hooker arranged for extracts of Darwin's work, along with Wallace's article, to be read on 1 July and published in 1859 by the Linnean Society of London (Darwin and Wallace 1859). Darwin then abandoned his large manuscript and wrote a more readable abridgment, *On the Origin of Species* (1859). His longer manuscript was partly used in later books, but those parts not so used are now published (Darwin 1975) and provide many citations to his sources not included in *Origin*.

Darwin presented his theory in the first four chapters, followed by nine chapters on diverse supporting evidence. *Origin* chapters 1–2 presented noncontroversial evidence that variation occurs in both domestic and wild populations of species.

Fig. 2. Pedunculated Pollicipes. By George Sowerby. Darwin 1851: from Plate 7, 1964.



Chapter 3, “Struggle for Existence,” was based on his Malthusian insight plus supporting natural history data from Linnaeus, de Candolle, Lyell, and others. One of his examples was the elephant, which was the slowest breeding animal. In this case, he made the hypothetical calculation himself, assuming that all offspring reproduce (1859:64, 1964)

> *...it breeds when thirty years old, and goes on breeding till ninety years old, bringing forth three pair of young in this interval; if this be so, at the end of the fifth century there would be alive fifteen million elephants, descended from the first pair.*

There would be six editions of *Origin* during Darwin’s lifetime, with each new edition corrected

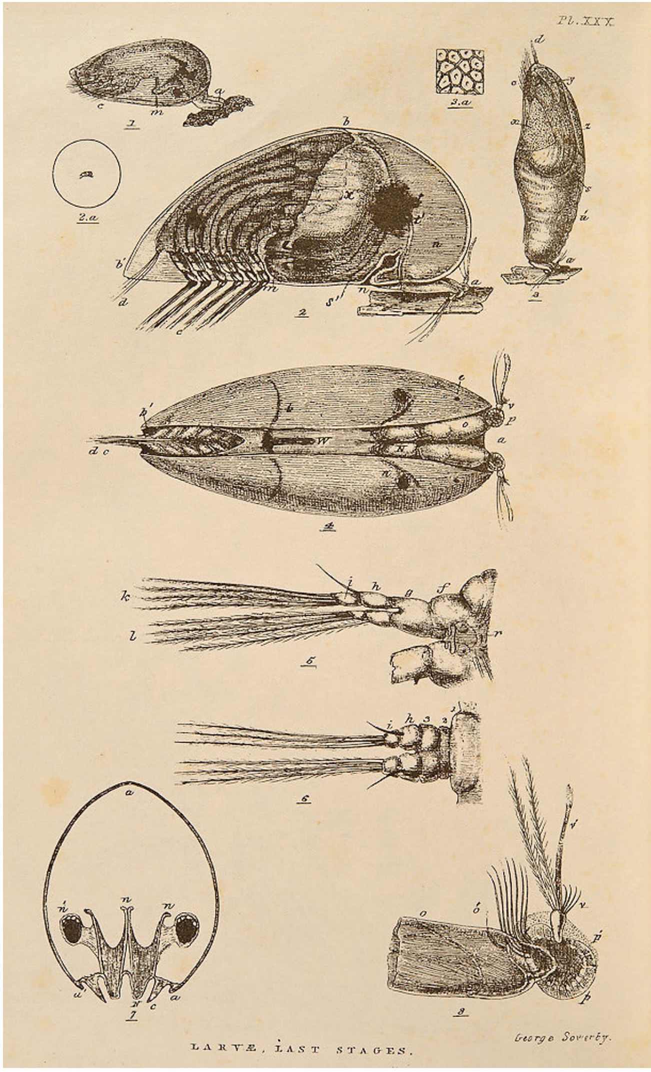


Fig. 3. Sessile barnacle: larvae of *Lepus australis*. By George Sowerby. Darwin 1854: from Plate 30, 1964.

and updated. There were only minor changes in this quoted passage for the first five editions, the fifth appearing in 1869 (Peckham 1959:24). However, two readers independently calculated the hypothetical rate of elephant increase that differed from Darwin's, which prompted him to publish two responses in the *Athenaeum* (Darwin 1869*a*, *b*), and then published this modified statement in the sixth edition of 1872 (Peckham 1959:148)

> *…it breeds when thirty years old, and goes on breeding till ninety years old, bringing forth six young in the interval, and surviving till one hundred years old; if this be so, after a period of from 740 to 750 years there would be nearly nineteen million elephants alive, descended from the first pair.*

But since there would never be nineteen million elephants, descended from one pair, alive at the same time, there must be checks on the growth of populations of all species. To illustrate the complexity

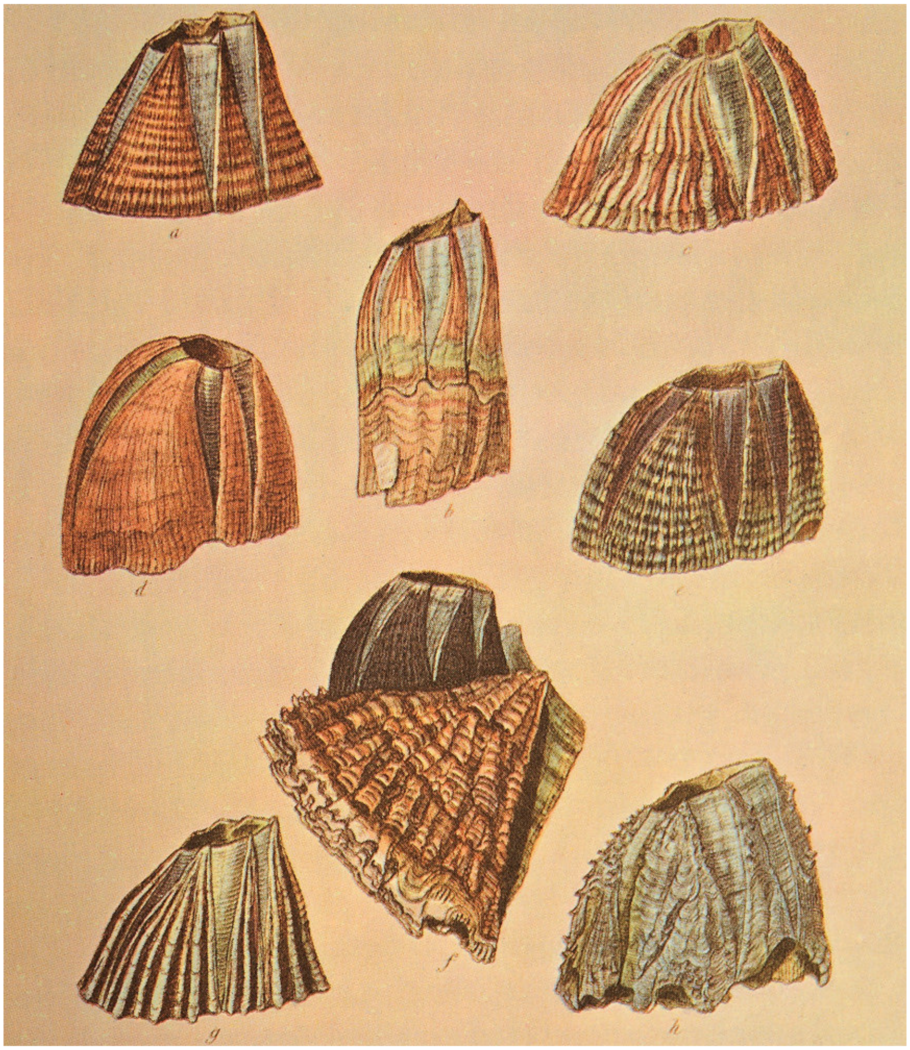


Fig. 4. Sessile acorn barnacles *Balanus*. By George Sowerby. Darwin 1854: from Plate 1, 1964.

of such checks, Darwin explained the interrelationships of red clover, humble bees, mice, and cats: only humble bees pollinate red clover, but field mice eat humble bees, and cats eat mice. Therefore, the success of red clover fields might depend on the local population of cats (1859:73–74). Although we now know that this food chain is more complex than Darwin realized (Egerton 2007*a*:52–53), his conclusion is still valid: if we speculate on those checks and their magnitudes, "It will convince us of our ignorance on the mutual relations of all organic beings…" (1859:78). Revolutionary paradigms, such as *Origin*, reorient sciences and uncover new problems to study (Kuhn 1970).

In chapter 4, Darwin theorized that the outcomes of struggles for existence would be natural selection, the controversial subject of chapter four. He again warned, "Let it be borne in mind how infinitely complex and close-fitting are the mutual relations of all organic beings to each other and to their physical conditions of life" (1859:80). Yet, we can detect the effects of natural selection (1859:84).

Fig. 5. Darwin's study and laboratory, Down House. Photo, John Webb. Karp 1968:6.

> *When we see leaf-eating insects green, and bark-feeders mottled-grey; the alpine ptarmigan white in winter, the red-grouse the colour of heather, and the black-grouse that of peaty earth, we must believe that these tints are of service to these birds and insects in preserving them from danger. Grouse, if not destroyed at some period of their lives, would increase in countless numbers; they are known to suffer largely from birds of prey; and hawks are guided by eyesight to their prey—so much so, that on parts of the Continent persons are warned not to keep white pigeons, as being the most liable to destruction. Hence I can see no reason to doubt that natural selection might be most effective in giving the proper colour to each kind of grouse, and in keeping that colour, when once acquired, true and constant.*

He is speaking here of protective coloration, though without naming it.

Nine chapters of supporting evidence include 11–12 on geographical distributions, which included his discoveries on the voyage of the *Beagle* and "marked the end of the purely descriptive era, and the

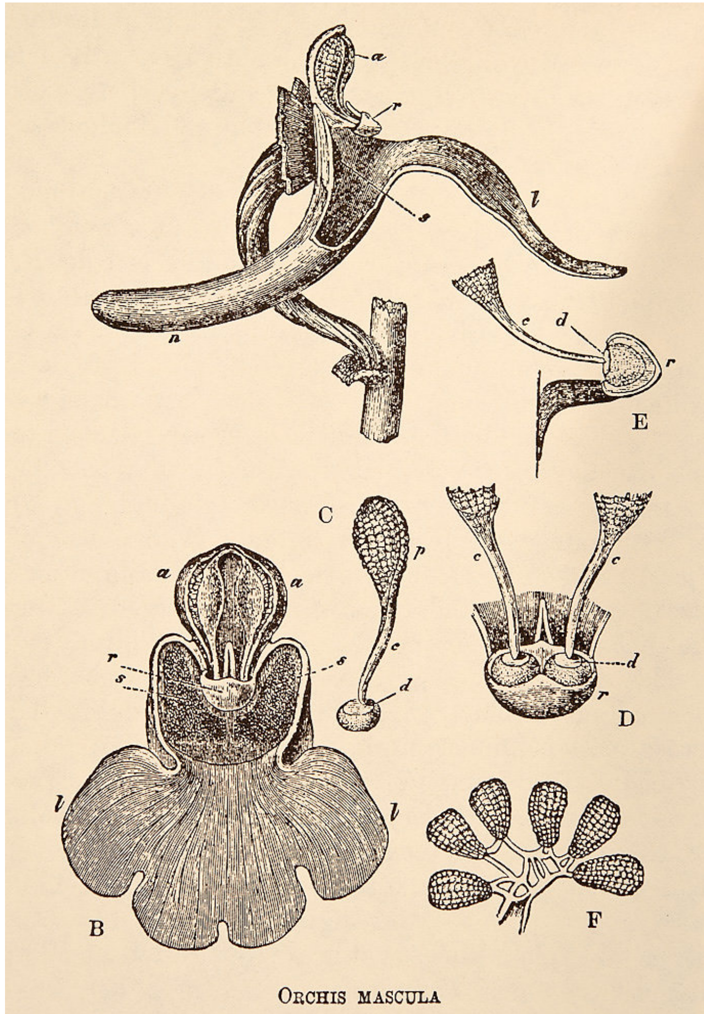


Fig. 6. Dissected flower of early orchis *Orchis mascula*. Drawn by G. B. Sowerby. Darwin 1862: Fig. 1. An explanation of all these figures accompanied this illustration.

beginning of a period of interpretation and speculation and re-examination of the phenomena in the field of geographic distribution of plant and animal life…" (Schmidt 1955:767; also Hofsten 1916:327–329, Richardson 1981, Browne 1983:195–224). His biogeography was also indebted to his post-*Beagle* consultations with Hooker and Asa Gray (Porter 1993). Numerous other examples of what we call ecological observations occur in the *Origin*, most famously the last paragraph (1859:489)

> *It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us.*

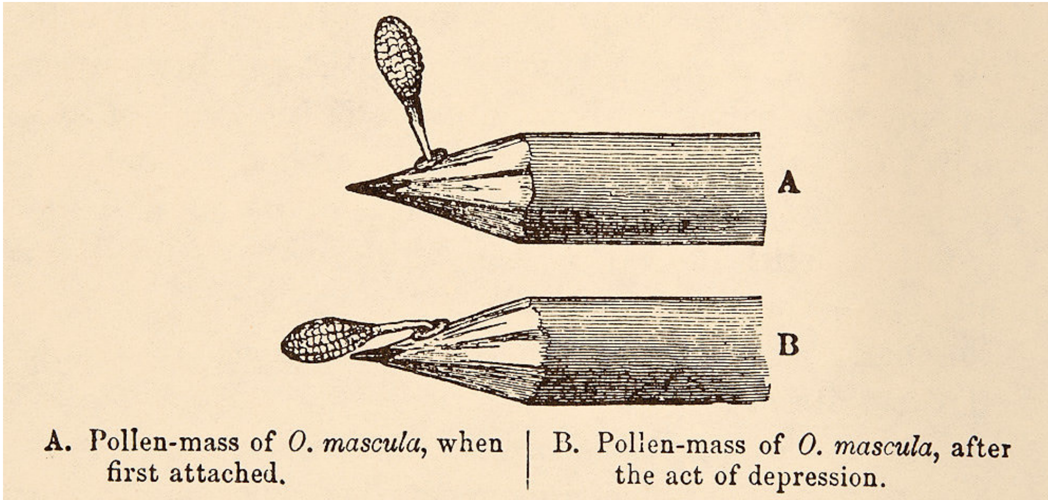


Fig. 7. Darwin substituted a sharpened pencil for a bee and poked it into an *Orchis mascula* flower and found that the pollinium attached to it (A), then bent at a right angle to be in position to pollinate the next orchid the bee entered. Drawn by G. B. Sowerby. Darwin 1862: Fig. 2.

Darwin's theory might have undermined the related concepts of the economy of nature and the balance of nature, but this last quotation shows why it did not (Egerton 1973:341–342, Pearce 2010).

"The theory of evolution by natural selection is an ecological theory—founded on the ecological observations by perhaps the greatest of all ecologists" (Harper 1967:247).

It is no wonder, then, that one of Darwin's most fervent disciples, Ernst Haeckel (1834–1919), realized the need not only for a new science of evolutionary biology, but also for a new science of ecology, which he named and defined in his *Generelle Morphologie der Organismen* (two volumes, 1866). Haeckel dedicated *Generelle Morphologie* to Goethe, Lamarck, and Darwin, and sent a copy to Darwin. Although Darwin had spent some time teaching himself German, he found Haeckel's writings difficult to understand (Desmond and Moore 1991:541–542, Browne 2003:269–270), and might not have read Haeckel's discussions of "oecologie."

In the 23 years after publishing *Origin*, Darwin published 10 more books and numerous articles. His subjects were diverse, but they all had the same objective of expanding and elaborating proofs for his theory. As we saw in part 37 (Egerton 2010*b*), despite having made a diligent collection of plants on the Galapagos Islands and elsewhere, Darwin thought of himself as a zoologist and geologist during and immediately after his voyage on the *Beagle*, and his new book-length publications after his *Beagle* volumes were on barnacles. Nevertheless, his post-*Origin* research and publications were as much or more on plants as on animals (Allan 1977, Morton 1981:413–419 , Ornduff 1984, Magnin-Gonze 2004:188–192). He was usually assisted by his son Francis (1848–1925), a trained botanist (Desmond 1977:173–174, Browne 2003:434–435, 465–469, 2004, Junker 2004), and sometimes by his

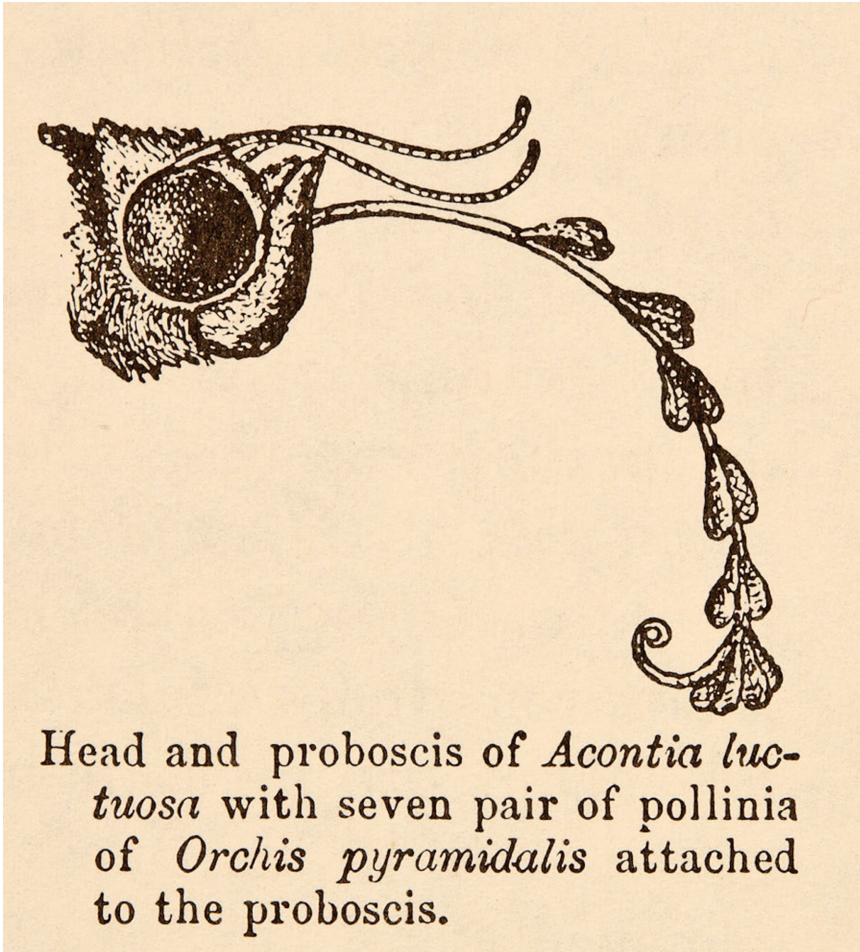


Fig. 8. Head and proboscis of *Acontia luctuosa* with seven pair of pollinia of *Orchis pyramidalis* attached to its proboscis. Darwin 1877*b*:31.

son George (1845–1912), who also had scientific interests (Browne 2003:434–436). However, Darwin's close relationship and correspondence with botanist Joseph Dalton Hooker (1817–1911) after 1843 was a most valuable source of information and judgment (Browne 1978, 1983:197, 215–216, 1995:518–521, 2003:see index).

Darwin's next book after the *Origin* was *On the Various Contrivances by which British and Foreign Orchids are Fertilized by Insects, and on the Good Effects of Intercrossing* (Darwin 1862, second edition 1877). It benefited from his extensive knowledge of insects (Clark 2009:106–109) and was a step toward Darwin becoming a botanist. In 1841, Robert Brown, botanist at the British Museum, had recommended that Darwin read Christian Konrad Sprengel, *Das entdeckte Geheimniss der Natur, im Bau und in der Befruchtung der Blumen* (1793). Darwin obtained a copy of this "wonderful book" (Darwin 1958:127), and his annotations indicate that he did read this German book (Ghiselin 1977:xvii). Darwin began

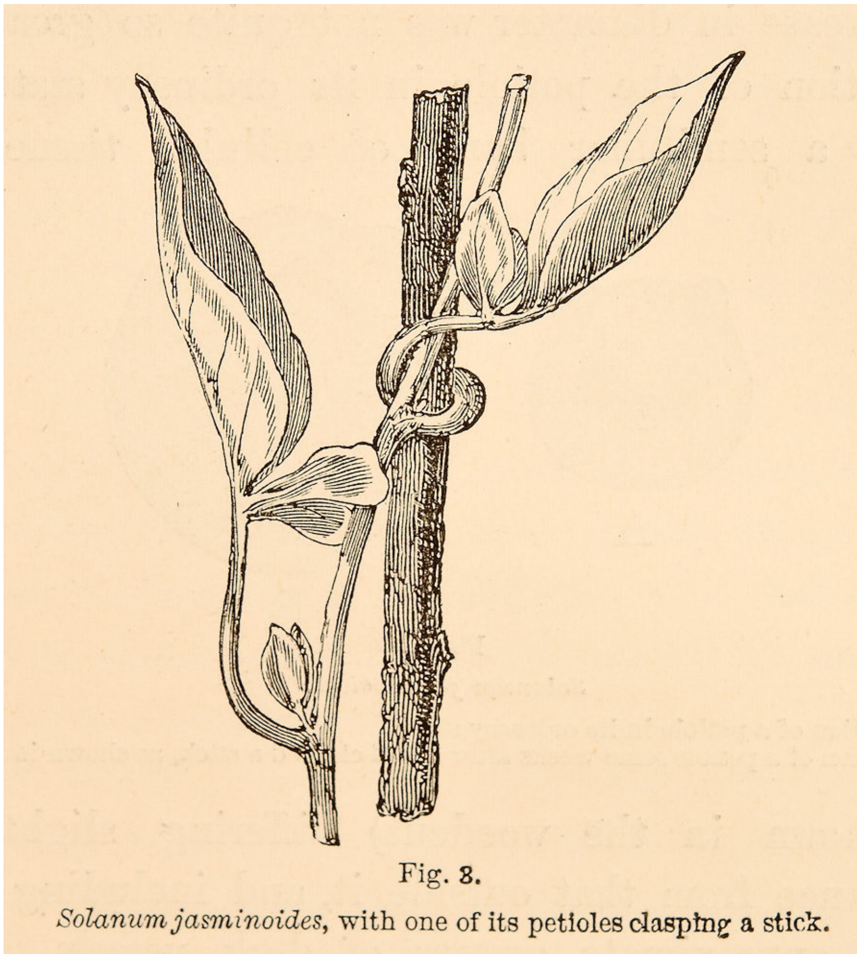


Fig. 9. A leaf climber, *Solanum jasminoides*, with petiole clasping a twig. By George Darwin. Darwin 1875*a*:73.

studying the pollination of kidney beans (Darwin 1857, 1858), then learned that orchids have an enormous range of floral mechanisms that interact with pollinating insects (Darwin 1860, 1861). Francis Darwin reported (F. Darwin 1899:xiv) that this book amplified a sentence in the *Origin* (1859:92), but did not indicate which sentence. Most likely it was one of these

> *Those individual flowers which had the largest glands or nectarines, and which excreted most nectar, would be oftenest visited by insects, and would be oftenest crossed; and so in the long-run would gain the upper hand. Those flowers, also, which had their stamens and pistils placed, in relation to the size and habits of the particular insects which visited them, so as to favour in any degree the transportal of their pollen from flower to flower, would likewise be favoured or selected.*

It was Darwin's chance to show that the unusual structures of many orchid flowers were not a result of nature's whim or God's design, but of natural selection (Basalla 1962). His orchid book first determined how specific species were fertilized and then attempted to explain how the mechanism evolved between orchids and insect pollinators to ensure cross–pollination between flowers rather than self-pollination. Native orchids grew within walking distance of his house, and "no British county excels Kent in the number of its orchids" (quoted in Browne 2003:170). Before his book, there was no scientific explanation for the bizarre or spectacular shape and color of some orchids. Darwin explained how both shape and color were oriented toward the insect pollinator. Eight chapters describe and illustrate different kinds of orchids and explain their pollination mechanisms.

He began with a native, early orchis, *Orchis mascula*, and took eight pages to explain its parts and their functions. Despite the amount of detail to which he subjected readers, this was a popular book. Many people grew orchids, and this book was a case history of Darwin's theory. It was welcomed by his supporters but convinced few of his opponents (Basalla 1962). Darwin admitted that biology had not yet collected enough information on the interactions between flowers and pollinators, but sometimes he could test his hypotheses himself, as he did with *Orchis mascula*. Using a pencil point as a "bee," (Darwin 1862: Fig. 2), he showed that the pollinium firmly attaches to the bee-head substitute, then within 30 seconds bends at a right angle, which positions it to fertilize the stigma of the next orchid the bee enters.

Comparative studies led him to generalize (Darwin 1877*b*:30) that orchids with short nectaries were pollinated by either bees or flies, and those with long nectaries by butterflies or moths. Mr. F. Bond sent Darwin 23 species of Lepidoptera that he had caught fertilizing *Orchis pyramidalis*, having pollinia stuck to their proboscises.

After Darwin published his orchid book, Asa Gray suggested that lady's-slipper, *Cypripedium,* was fertilized: "by small insects entering the labellum through the large opening on the upper surface, and crawling out by one of the two small orifices close to the anthers and stigma" (Darwin 1877*b*:230). Darwin tested this by dropping flies into the labellum of *C. pubescens* without positive results, but when he dropped a small bee, *Andrena parvula,* into the labellum, it behaved as Gray predicted. The Madagascar star orchid, *Angraecum sesquipedale,* has a nectary up to 12 inches deep, and Darwin predicted that there must be a sphinx moth with a proboscis long enough to reach its nectar (Darwin 1877*b*:162–163). In 1873, Fritz Müller found a Brazilian Sphingid moth with a proboscis 10–11 inches (0.25 m) long (Riley 1882:76). Later, a Madagascan moth, *Xanthopan morganii praedicta*, was discovered and has been photographed sipping *A. sesquipedale* nectar (Samper 2007).

Compared to the blockbuster *Origin* (500 pages), *Orchids* is much narrower in scope and briefer (300 pages), but it is not a minor work (Ghiselin 1977:xi).

> *The book evoked a major revolution in botany and in biology as a whole. It completely changed our conception of sexuality and gave rise to enormous literature on pollination ecology. Everything that has subsequently been done on the broad topic of coevolution and related areas has been influenced, directly or indirectly, by this book.*

Evolutionist John Alcock calls it "one of the most adaptationist books of all time" (Alcock 2006:16). Darwin listed in the second edition of *Orchids* (Darwin 1877*b*) 3.3 pages of publications that had appeared since he published the first edition—testimony to this book's influence.

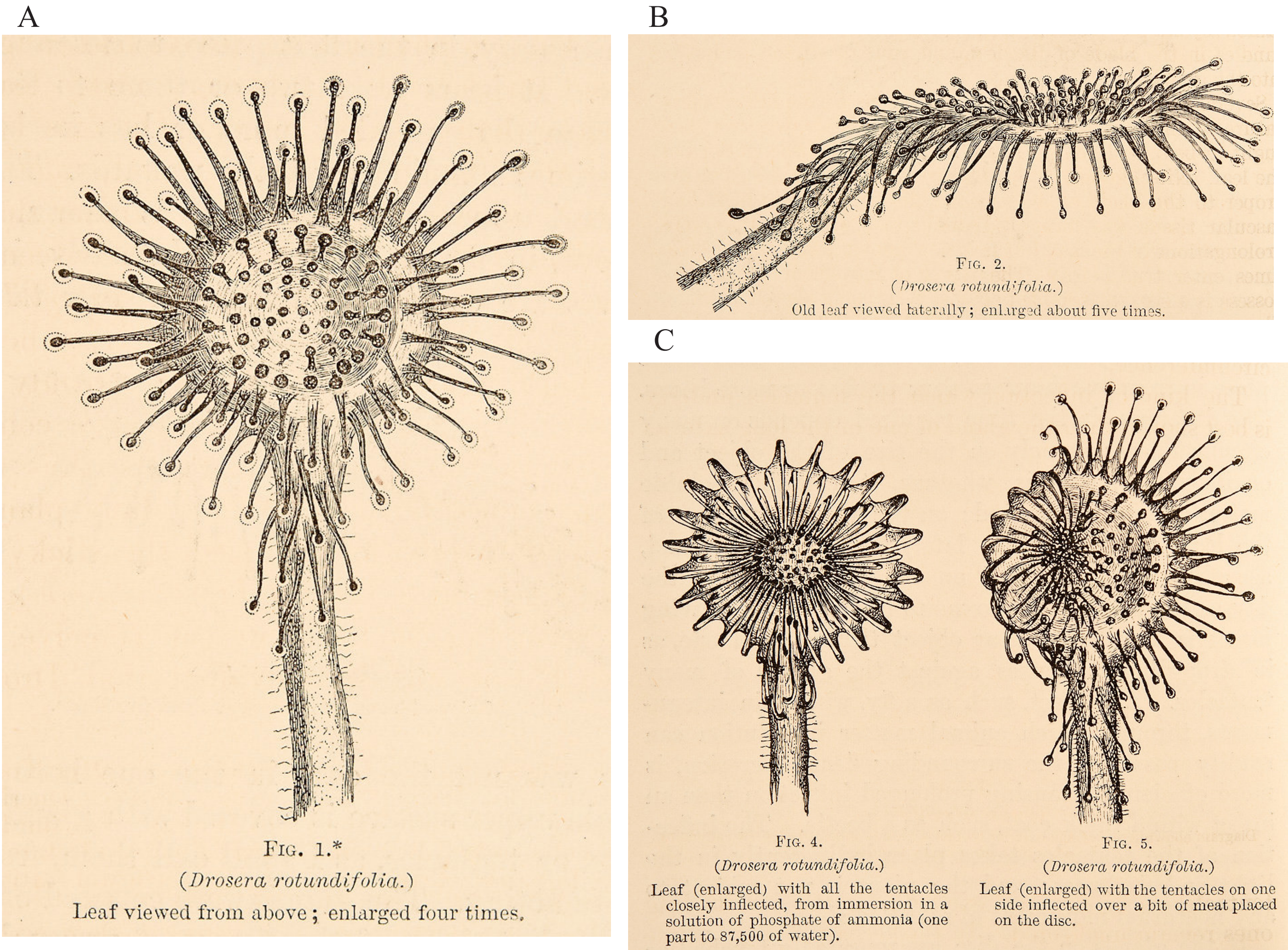
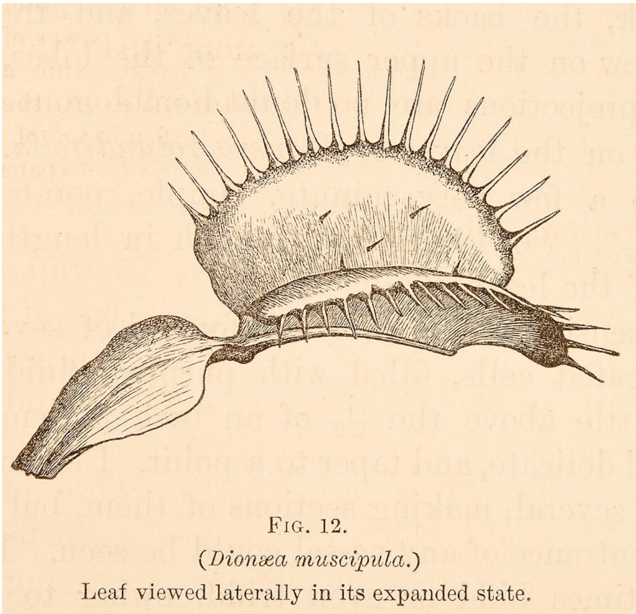


Fig. 10. Sundew leaves (A, B) in repose (Darwin's Figs. 1 and 2), and (C) responding to stimulus (Darwin's Figs. 4 and 5). Darwin 1875*b*:3, 4, 10.

Darwin's next book, *On the Movement and Habits of Climbing Plants* (Darwin 1865, 128 pages), first appeared as parts 33–34 of the *Journal of the Linnean Society of London* (Freeman 1965:50), and only appeared as a book in the second edition (Darwin 1875, 208 pages). He was primarily interested in the evolution of this habit and its advantages for these plants. Climbers include twining plants in which the stem twins around another plant (Chapter 1), leaf climbers (Chapter 2), tendril-bearers (Chapters 3–4), hook climbers and root climbers (Chapter 5).

The tendrils in most species which he studied were derived from leaves or flower peduncles, but he also cited tendrils derived from branches reported by Hugo Mohl and Fritz Müller (Darwin 1875*a*:194–195). Hook climbers included roses, *Galium*, and *Dipladenia* (1875*a*:183–184). Root-climbers, including ivy *Hedera helix* and figs *Ficus repens* and *F. barbatus*, cling to trees or walls with their roots (1875*a*:185). He did not study the impact of climbing plants on their hosts, and he did not mention the tropical strangler fig that eventually kills its host. Botanist Francis Darwin (1848–1925; Browne 2004*b*, A



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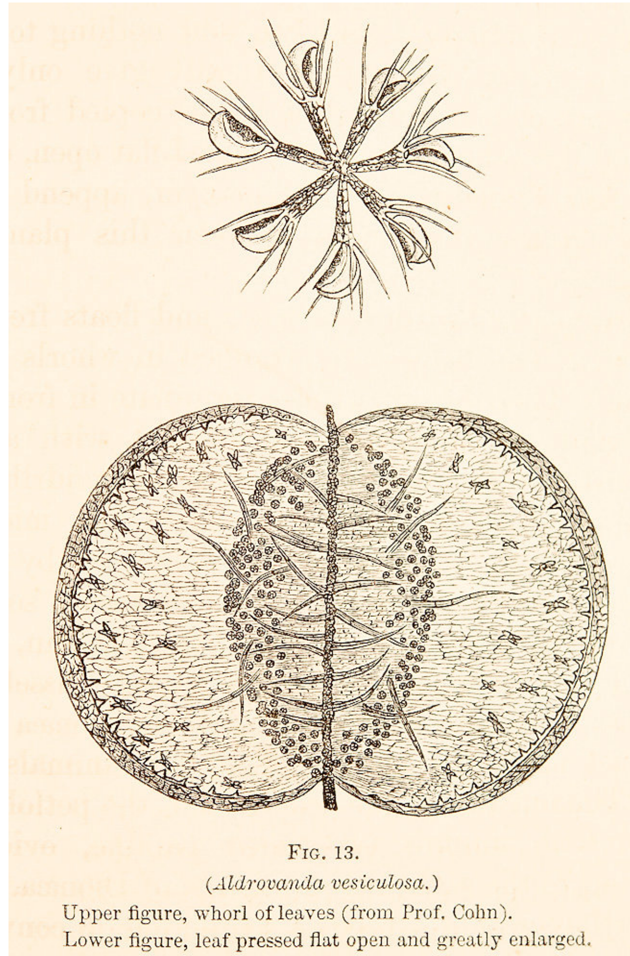

Fig. 11 (A) Venus flytrap *Dionaea muscipula*. (B) *Aldrovanda vesiculosa*, a European aquatic flytrap. Darwin 1875:287, 323.

Junker 2004) later placed his father's book in a broader context of studies on this phenomenon (Darwin 1909:387–392).

Insectivorous Plants (Darwin 1875*b*) appeared in the same year as the second edition of *Climbing Plants*, but it was a more substantial book (462 pages), illustrated by sons Francis and George. Botanist Francis Darwin (1848–1925) was his father's assistant and secretary during the 1870s (Browne 2004*b*, Junker 2004). We saw in part 25 (Egerton 2007*b*:261) that William Bartram had mentioned in 1791 that the American Venus flytrap, pitcher plant, and sundew all captured insects, but he did not explain their methods or why. Darwin had read Bartram's *Travels* in 1839 (Costa 2009). Darwin first took up the subject in the summer of 1860, when he experimented on the movements of the sticky hairs (he called them tentacles) on sundew (*Drosera rotundifolia*) leaves, but he had failed to understand how the hairs responded to stimuli and had moved on to other subjects by February 1861 (Browne 2003:146–151). He returned to the subject on 23 August 1872 (Darwin 1959:19) and bought a bigger and better microscope for this research (Browne 2003:409). Darwin picked up where he had left off in 1861, with his "beloved Drosera" (Allan 1977:235).

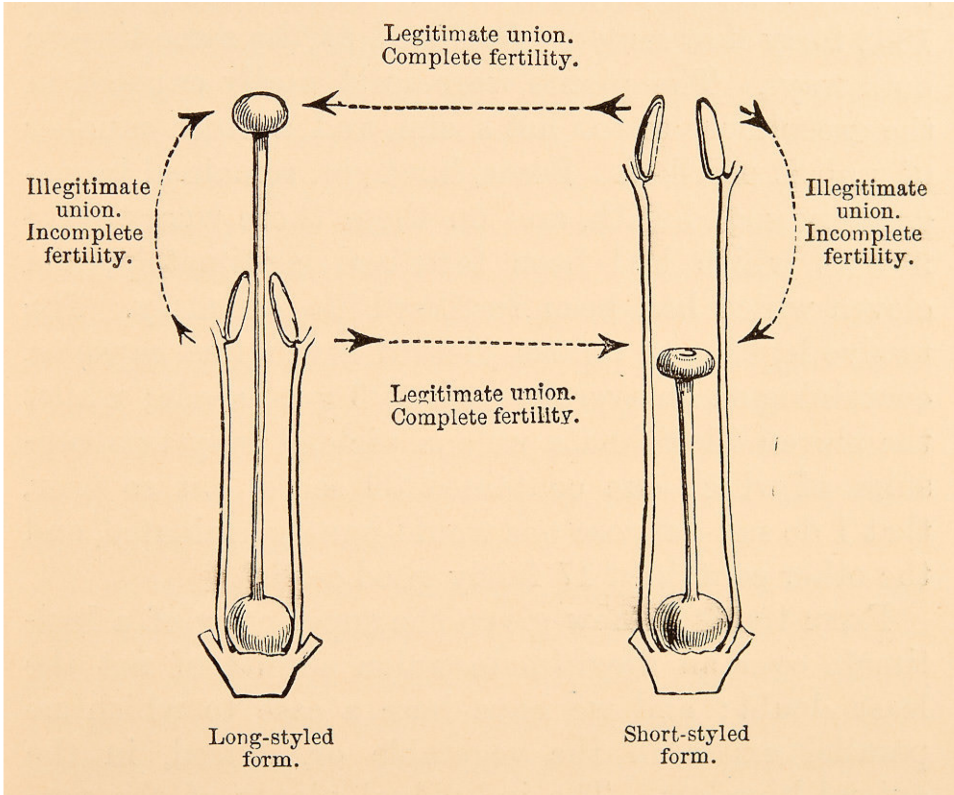

Fig. 12. Diagram of the two forms of *Primula veris* flower showing the mechanism to avoid self-fertilization. Darwin 1877*a*:27.

Sixty percent of the book discussed sundew leaves. He and son Francis subjected leaves to various physical and chemical experiments to learn what caused the hairs to close, and also the plant's ability to digest various substances. They did not discuss the fact that insectivorous plants live in acidic bogs where bacteria do not decompose dead vegetation, releasing nutrients for further use. The remaining chapters describe the mechanisms of the Venus flytrap, *Aldrovanda, Pinguicula, Utricularia,* and a few others.

M. A. Curtis of Wilmington, North Carolina, had reported (1834:123) his discovery of glands inside the folding leaf of Venus flytraps that secrete digestive juices, and Kirby and Spence had reported (Kirby and Spence 1818, I:295) that a leaf fed fine filaments of raw beef grew better than leaves not fed (Darwin 1875:301, note). Carnivorous plants continue to fascinate both botanists and amateurs, and modern literature describes growing and observing these species (such as Lloyd 1942, Pietropaolo and Pietropaolo 1986, Ellison et al. 2003, Tucker 2010, Zimmer 2010).

Darwin's books, *The Effects of Cross and Self Fertilization in the Vegetable Kingdom* (1876) and *The Different Forms of Flowers on Plants of the Same Species* (1877*a*) are relevant to ecology since insects

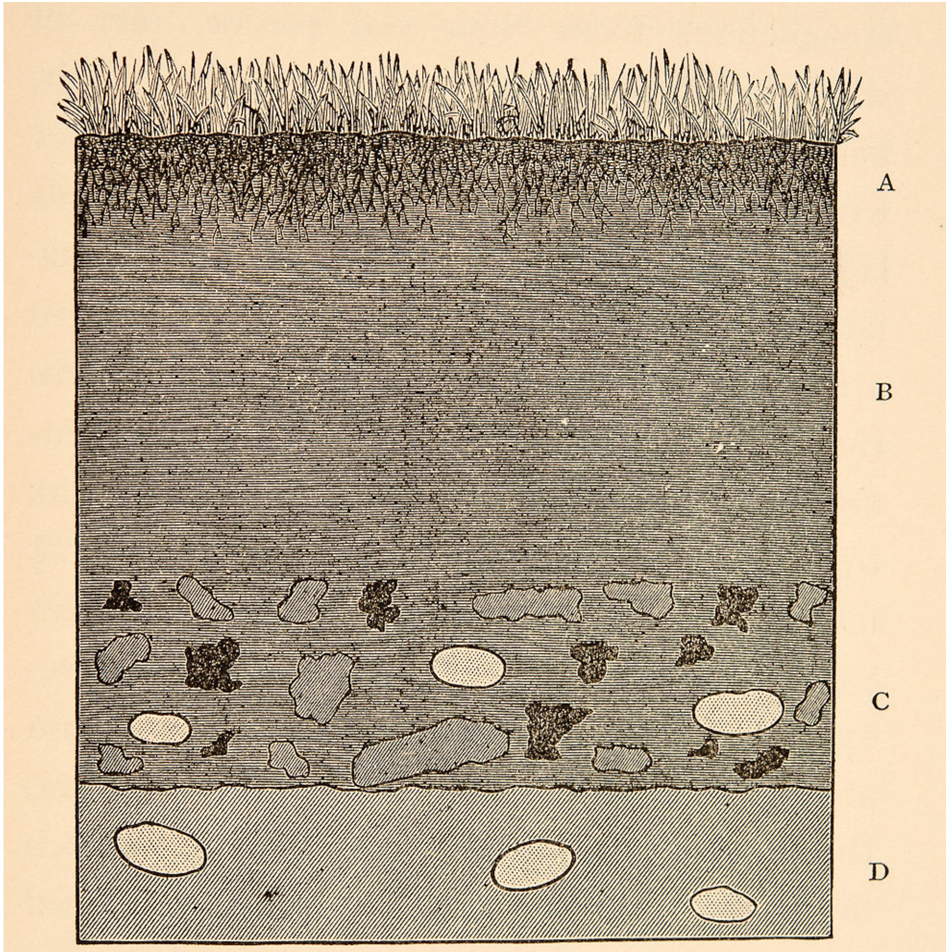

Fig. 13. Cross-section of Josiah Wedgwood's field on which burnt marl and cinders had been spread about 15 years before, after it had been plowed and harrowed, and left undisturbed since. Darwin 1840, reprinted 1881.

were the usual pollinators (Allan 1977:249–276). Cross-fertilization had been a theme in his *Orchids*, and in this new book he extended those investigations more broadly (Drouin 2008:144–146). Darwin emphasized the importance of cross-fertilization for fertility and vigor, and he illustrated the mechanism that had evolved in *Primula veris* to insure cross-fertilization: some flowers had long styles and others short styles, so that the anthers were separated from the stigmas and did not fertilize them. Darwin over-generalized to some extent and was challenged by other botanists (Baker 1965).

Peter Ayres (Ayres 2008:11) considered *The Power of Movement in Plants* (1880) Darwin's greatest botanical work. Darwin acknowledged the assistance of his son Francis on its title page. Emphasis was on circumnutating movements, and there were experiments and monitoring of plant growth. It depended upon what Francis had learned in the laboratory of Julius von Sachs (1832–1897), though it corrected some of Sachs' comments (see Sachs in Ayres 2008:Index). Sachs felt that he had been attacked by amateurs and dismissed Francis Darwin's attempt at reconciliation (James 1969:64, De Chadarevian 1996). Francis Darwin later (1909:392–400) revisited the subject of this book, but not the controversy

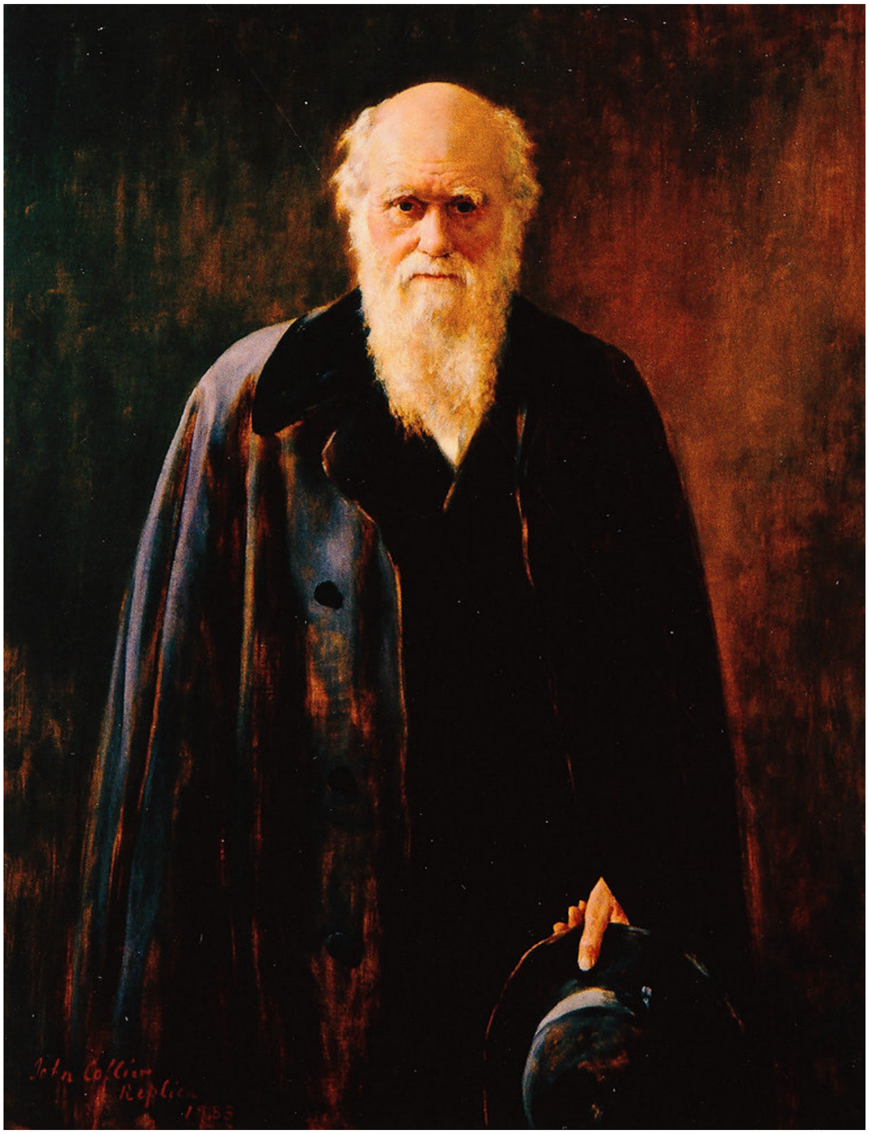

Fig. 14. Charles Darwin in 1881. By John Collier, Huxley's son-in-law, for the Linnean Society of London. A copy is also in the National Portrait Gallery, London.

with Sachs. He briefly discussed the break with Sachs in his memoirs (Darwin 1920:68–69).

Darwin's last book was *The Formation of Vegetable Mould, through the Action of Worms, with Observations on Their Habits* (1881). He had briefly dealt with this subject before; on 12 November 1836, he had visited his Wedgwood relatives for four days, and his uncle Josiah Wedgwood (whose daughter, Emma, Darwin later married) showed him fields that had been covered with lime or with marl and cinders some years before, but at the time they were there, those surface deposits were buried, even though the fields had not been plowed since the deposits. His uncle thought that the castings of earthworms had buried those deposits. Darwin had seen in tropical regions that tiny coral polyps could produce gigantic reefs, so he could believe that the actions of earthworms might also have an extensive impact on land. He dug holes, studied the strata, and wrote a talk for the Geological Society of London, which he read on 1 November 1837, and which was published in 1840. In the book he pointed out that earthworms are active at night, and so people do not see them at work, but if one looks closely, one can find their castings of dirt around their holes.

He pointed out rocks, coins, even buildings, that were once on the surface had sunk due to both the worm tunnels below them and the earthworm castings that were deposited around them. He argued that "The vegetable mould which covers, as with a mantle, the surface of the land, has all passed many times through their bodies" (Darwin 1881:239). The worms pull leaves or half-decayed leaves into their burrows to a depth of 2 or 3 inches (Darwin 1881:242), but their burrows can penetrate down to 5 or 6 inches or more (Darwin 1881:247). The book abounds in measurements and calculations, such as "on Leith Hill Common, dry earth weighing at least 7.453 lbs. was brought up by worms to the surface on a square yard in the course of a year" (Darwin 1881:270). Besides their general impact on the land, "Worms prepare the ground in an excellent manner for the growth of fibrous-rooted plants and for seedlings of all kinds" (Darwin 1881:312). And therefore, "It may be doubted whether there are many other animals which have played so important a part in the history of the world, as have these lowly organized creatures" (1881:316).

Soil scientists judge this book as "an astounding precursor in the field of the earth sciences, in such varied subjects as erosion, matter transfer at the scale of the bigger watersheds, alteration and pedogenetic processes, ecology, soil bio-functioning and pedo-archaeology" (Feller et al. 2006:96). Earthworm ecologists also have a high regard for Darwin's book (Tomlin et al. 1995:160, Edwards 1998:v)

In 1866, Darwin's German disciple, Ernst Haeckel, sent him a copy of his *Generelle Morphologie der Organismen* (two volumes), which named and defined a new science of "oecologie." Darwin's copy has passages marked or annotated, though not the ecology discussion (Di Gregorio and Gill 1990:355–357). Yet, Darwin's own writings are full of ecological observations and comments. His *Journal of Researches* (1839) and other *Beagle* writings were important beginnings (Egerton 2010*b*); the climax of his ecological contribution was in the *Origin*, with modest contributions in other works discussed above. Linnaeus had first invented an ecological science in 1749, the economy of nature (Egerton 2007*b*:81–82), but since he believed species were unchanging, so was his economy of nature. In the first half of the 1800s, naturalists developed a changing economy of nature concept (Egerton 2010a), without it becoming the basis of an important science. Something more was needed before that happened, and Darwin's evolutionary ecology became a foundation on which ecological sciences would be built two decades after his death.

Literature cited

Acot, P. 1983. Darwin et l'écologie. Revue d'Histoire des Sciences **36**:33–48.
Alcock, J. 2006. An enthusiasm for orchids: sex and deception in plant evolution. Oxford University Press, Oxford, UK.
Allan, M. 1977. Darwin and his flowers: the key to natural selection. Faber and Faber, London, UK.

Anderson, D. T. 1994. Barnacles: structure, function, development, and evolution. Chapman and Hall, London, UK.
Ayres, P. 2008. The aliveness of plants: the Darwins at the dawn of plant science. Pickering and Chatto, London, UK.
Baker, H. G. 1965. Charles Darwin and the perennial flax—a controversy. Huntia 2:141–161.
Basalla, G. 1962. Darwin's orchid book. Actes du dixième congrès international d'histoire des sciences 2:971–974.
Bohlin, I. 2000. Charles Darwin, 1809–82, British naturalist. Pages 163–165 *in* A. Hessenbruch, editor. Reader's guide to the history of science. Fitzroy Dearborn, London, UK.
Browne, J. 1978. The Charles Darwin-Joseph Hooker correspondence: an analysis of manuscript resources and their use in biography. Society for the Bibliography of Natural History Journal 8:351–366.
Browne, J. 1983. The secular ark: studies in the history of biogeography. Yale University Press, New Haven, Connecticut, USA.
Browne, J. 2003. Charles Darwin: the power of place. Knopf, New York, New York, USA.
Browne, J. 2004*a*. Charles Robert Darwin (1809–1982). Dictionary of Nineteenth-Century British Scientists 2:531–538.
Browne, J. 2004*b*. Francis Darwin (1848–1925). Dictionary of Nineteenth-Century British Scientists 2:538–540.
Clark, J. F. M. 2009. Bugs and the Victorians. Yale University Press, New Haven, Connecticut, USA.
Costa, J. T. On Charles Darwin's reading of William Bartram's *Travels*. Chinquapin 17, number 3:1, 4–7.
Crisp, D. J. 1983. Expanding Darwin's investigations on the barnacle life-history. Linnean Society of London Biological Journal 20:73–83.
Curtis, M. A. 1834. Enumeration of plants growing spontaneously around Wilmington, N. C., with remarks on some new and obscure species. Boston Society of Natural History Journal 1:82–141.
Dajoz, R. 1984. Eléments pour une histoire de l'écologie: la naissance de l'écologie modern au XIX[e] siècle. Histoire et Nature 24–25:5–111 + 7 plates.
Darwin, C. R. 1840. On the formation of mould. Geological Society of London Transactions 5:505–509. Reprinted in C. R. Darwin. 1977. Volume I, pages 49–53 *in* P. H. Barrett, editor. The collected papers. University of Chicago Press, Chicago, Illinois, USA.
Darwin, C. R. 1851*a*. A monograph of the sub-class Cirripedia, with figures of all the species: the Lepadidae, or pedunculated Cirripedes. Ray Society, London, UK. Reprinted in C. R. Darwin. 1964. A monograph on the sub-class Cirripedia. J. Cramer, Weinheim, Germany.
Darwin, C. R. 1851*b*. A monograph of the fossil Lepadidae, or, pedunculated Cirripedes of Great Britain. Paleontological Society, London, UK.
Darwin, C. R. 1854*a*. A monograph of the sub-class Cirripedia, with figures of all the species: the Balanidae (or sessil Cirripedes), the Verrucidae. Ray Society, London, UK. Reprinted in C. R. Darwin. 1964. A monograph on the sub-class Cirripedia. J. Cramer, Weinheim, Germany.
Darwin, C. R. 1854*b*. A monograph on the fossil Balanidae and Verrucidae of Great Britain. Palæontographical Society, London, UK.
Darwin, C. R. 24 October 1857. Bees and fertilization of kidney beans. Gardeners' Chronicle, number 43:725. Reprinted in C. R. Darwin. 1977. Volume I, pages 275–277 *in* P. H. Barrett, editor. The collected papers. University of Chicago Press, Chicago, Illinois, USA.
Darwin, C. R. 1858. On the agency of bees in the fertilization of Papilionaceous flowers and the crossing

of kidney beans. Annals and Magazine of Natural History, series 3, 2:459–465. Reprinted in C. R. Darwin. 1977. Volume II, pages 19–25 *in* P. H. Barrett, editor. The collected papers. University of Chicago Press, Chicago, Illinois, USA.

Darwin, C. R. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London, UK. Reprinted 1964. Harvard University Press, Cambridge, Massachusetts, USA.

Darwin, C. R. 9 June 1860. Fertilization of British orchids by insect agency. Gardners' Chronicle number 29:528. Reprinted in C. R. Darwin. 1977. Volume II, pages 32–35 *in* P. H. Barrett, editor. The collected papers. University of Chicago Press, Chicago, Illinois, USA.

Darwin, C. R. 9 February 1861. Fertilization of British orchids by insect agency. Gardners' Chronicle, number 6:122. Reprinted in C. R. Darwin. 1977. Volume II, pages 38–39 *in* P. H. Barrett, editor. The collected papers. University of Chicago Press, Chicago, Illinois, USA.

Darwin, C. R. 1862. On the various contrivances by which British and foreign orchids are fertilized by insects, and on the good effects of intercrossing. John Murray, London, UK.

Darwin, C. R. 1869*a*. Origin of species. Athenaeum number 2174:861. Reprinted in C. R. Darwin. 1977. Volume II, pages 156–157 *in* P. H. Barrett, editor. The collected papers. University of Chicago Press, Chicago, Illinois, USA.

Darwin, C. R. 1869*b*. Origin of species. Athenaeum number 2177:82. Reprinted in C. R. Darwin. 1977. Volume II, pages 157–158 *in* P. H. Barrett, editor. The collected papers. University of Chicago Press, Chicago, Illinois, USA.

Darwin, C. R. 1875*a*. The movements and habits of climbing plants. Second edition. John Murray, London, UK.

Darwin, C. R. 1875*b*. Insectivorous plants. John Murray, London, UK.

Darwin, C. R. 1876. The effects of cross and self fertilization in the vegetable kingdom. John Murray, London, UK.

Darwin, C. R. 1877*a*. The different forms of flowers on plants of the same species. John Murray, London, UK.

Darwin, C. R. 1877*b*. The various contrivances by which orchids are fertilized by insects. Second edition. John Murray, London, UK. Reprinted 1984. University of Chicago Press, Chicago, Illinois, USA.

Darwin, C. R., assisted by F. Darwin. 1880. The power of movement in plants. John Murray, London, UK.

Darwin, C. R. 1881. The formation of vegetable mould, through the actions of worms and observations on their habits. John Murray, London, UK.

Darwin, C. R. 1909. The foundations of *The origin of species*: two essays written 1842 and 1844. F. Darwin, editor. Cambridge University Press, Cambridge, UK. Reprinted 1969. Kraus Reprint Company, New York, New York, USA.

Darwin, C. R. 1959. The autobiography of Charles Darwin, 1809–1882: with original omissions restored. N. Barlow, editor. Harcourt Brace, New York, New York, USA. 1958. Collins, London, UK.

Darwin, C. R. 1959. Darwin's journal. G. de Beer, editor. British Museum (Natural History) Bulletin, Historical Series 2:1–21.

Darwin, C. R. 1964. A monograph on the sub-class Cirripedia. J. Cramer, Weinheim, Germany.

Darwin, C. R. 1975. Charles Darwin's natural selection: being the second part of his big species book written from 1856 to 1858. R. C. Stauffer, editor. Cambridge University Press, Cambridge, UK.

Darwin, C. R. 1977. The collected papers. P. H. Barrett, editor. Two volumes. University of Chicago

Press, Chicago, Illinois, USA.
Darwin, C. R. 1985–2010. The correspondence. F. H. Burkhardt and S. Smith et al., editors. 18 volumes. Cambridge University Press, Cambridge, UK.
Darwin, C. R. 1986–1990. The works. P. Barnett, editor. 29 volumes. Pickering and Chatto, London, UK.
Darwin, C. R. 1987. Charles Darwin's notebooks, 1836–1844: geology, transmutation of species, metaphysical enquiries. P. H. Barrett, P. J. Gautrey, S. Herbert, D. Kohn, and S. Smith, editors. British Museum (Natural History) and Cornell University Press, Ithaca, New York, USA.
Darwin, C. R. 2000. Zoology notes and specimen lists from *H. M. S. Beagle*. R. Keynes, editor. Cambridge University Press, Cambridge, UK.
Darwin, C. R. 2009. Shorter publications, 1829–1883. J. van Wyhe, editor. Cambridge University Press, Cambridge, UK.
Darwin, C. R., and A. R. Wallace. 1859. On the tendency of species to form varieties; and on perpetuation of varieties and species by means of natural selection. Journal of the Proceedings of the Linnean Society of London (Zoology) 3:45–62.
Darwin, F. 1899. The botanical work of Darwin. Annals of Botany 13:x–xix.
Darwin, F. 1909. Darwin's work on the movements of plants. Pages 385–400 *in* A. C. Seward, editor. Darwin and modern science. Cambridge University Press, Cambridge, UK.
Darwin, F. 1920. Springtime and other essays. John Murray, London, UK.
De Chadarevian, S. 1996. Laboratory science versus country-house experiments: the controversy between Julius Sachs and Charles Darwin. British Journal for the History of Science 29:17–41.
Desmond, A., and J. Moore. 1991. Darwin. Michael Joseph, London, UK.
Desmond, R. 1977. Dictionary of British and Irish botanists and horticulturists, including plant collectors and botanical artists. Taylor and Francis, London, UK.
Drouin, J.-M. 2008. L'herbier des philosophies. Editions du Seuil, Paris, France.
Edwards, C. A. 1998. Preface. Pages v–vi *in* C. A. Edwards, editor. Earthworm ecology. St. Lucie Press, Boca Raton, Florida, USA.
Egerton, F. N. 1968. Studies of animal populations from Lamarck to Darwin. Journal of the History of Biology 1:225–259.
Egerton, F. N. 1970. Humboldt, Darwin, and population. Journal of the History of Biology 3:325–360.
Egerton, F. N. 1973. Changing concepts of the balance of nature. Quarterly Review of Biology 48:322–350.
Egerton, F. N. 2007*a*. Understanding food chains and food webs, 1700–1970. ESA Bulletin 88:50–69.
Egerton, F. N. 2007*b*. History of ecological sciences, part 23: Linnaeus and the economy of nature. ESA Bulletin 88:72–88.
Egerton, F. N. 2009*a*. History of ecological sciences, part 31: Animal population studies during the 1700s. ESA Bulletin 89:407–433.
Egerton, F. N. 2009*b*. History of ecological sciences, part 32: Humboldt, nature's geographer. ESA Bulletin 90:253–282.
Egerton, F. N. 2010*a*. History of ecological sciences, part 34: a changing economy of nature. ESA Bulletin 91:21–41.
Egerton, F. N. 2010*b*. History of ecological sciences, part 37: Charles Darwin's voyage on the *Beagle*. ESA Bulletin 91:398–431.
Egerton, F. N. 2011. History of the ecological sciences, part 38B: Naturalists explore North America, 1838–1850s. ESA Bulletin 92:153–184.

Ellison, A. M., N. J. Gotelli, J. S. Brewer, D. L. Cochran-Stafira, J. M. Knettel, T. E. Miller, A. C. Worley, and R. Zamora. The evolutionary ecology of carnivorous plants. Advances in Ecological Research 33:1–74.

Feller, C., E. Blanchart, and D. H. Yaalon. 2006. Some major scientists (Palissy, Buffon, Thaer, Darwin and Muller) have described soil profiles and developed soil survey techniques before 1883. Pages 85–105 *in* B. P. Warkentin, editor. Footprints in the soil: people and ideas in soil history. Elsevier, London, UK.

Freeman, R. B. 1965. The works of Charles Darwin: an annotated bibliographical handlist. Dawsons of Pall Mall, London, UK.

Ghiselin, M. T. 1969. The triumph of the Darwinian method. University of California Press, Berkeley, California, USA.

Ghiselin, M. T. 1977. Foreword. Volume I, pages xi–xix *in* C. R. Darwin. 1977. The collected papers. P. H. Barrett, editor. University of Chicago Press, Chicago, Illinois, USA.

Ghiselin, M. T., and L. Jaffe. 1973. Phylogenetic classification in Darwin's monograph on the subclass Cirripedia. Systematic Zoology 22:132–140.

Harper, J. L. 1967. A Darwinian approach to plant ecology. Journal of Ecology 55:247–270.

Hodge, J. 2003. The notebook programmes and projects of Darwin's London years. Pages 40–68 *in* J. Hodge and G. Radick, editors. The Cambridge companion to Darwin. Cambridge University Press, Cambridge, UK.

James, W. O. 1969. Julius Sachs and the nineteenth century renaissance of botany. Endeavour 28:60–64.

Junker, T. 2004. Sir Francis Darwin (1848–1925). Oxford Dictionary of National Biography 15:208–210.

Karp, W. 1968. Charles Darwin and the origin of species. American Heritage, New York, New York, USA.

Keynes, R. 2003. Fossils, finches and Fuegians: Darwin's adventures and discoveries on the *Beagle*. Oxford University Press, Oxford, UK.

Kirby, W., and W. Spence. 1818. An introduction to entomology; or, elements of the natural history of insects. Volume 1. Edition 3. Longman, London, UK.

Kohn, D. 1980. Theories to work by: rejected theories, reproduction, and Darwin's path to natural selection. Studies in the History of Biology 4:67–70.

Kohn, D. 1985. The Darwinian heritage: including Proceedings of the Charles Darwin Centenary Conference. Princeton University Press, Princeton, New Jersey, USA.

Kolasa, J. 2011. Theory makes ecology evolve. Pages 21–49 *in* The theory of ecology. S. M. Scheiner and M. R. Willig, editors. University of Chicago Press, Chicago, Illinois, USA.

Kricher, J. 2009. The balance of nature: ecology's enduring myth. Princeton University Press, Princeton, New Jersey, USA.

Kuhn, T. S. 1970. The structure of scientific revolutions. Edition 2. University of Chicago Press, Chicago, Illinois, USA.

Limoges, C. 1970. La selection naturelle: etude sur la première constitution d'un concept (1837–1859). Presses Universitaires de France, Paris, France.

Lloyd, F. E. 1942. The carnivorous plants. Ronald Press, New York, New York, USA.

Love, A. C. 2002. Darwin and *Cirripedia* prior to 1846: exploring the origins of the barnacle research. Journal of the History of Biology 35:251–289.

Magnin-Gonze, J. 2004. Histoire de la botanique. Delachaux et Niestlé, Paris, France.

Manier, E. 1978. The young Darwin and his cultural circle. D. Reidel, Dordrecht, The Netherlands.

Morton, A. G. 1981. History of botanical science: an account of the development of botany from ancient times to the present day. Academic Press, London, UK.
Ornduff, R. 1984. Darwin's botany. Taxon 33:39–47.
Ospovat, D. 1981. The development of Darwin's theory: natural history, natural theology, and natural selection, 1838–1859. Cambridge University Press, Cambridge, UK.
Pearce, T. 2010. "A great complication of circumstances"—Darwin and the economy of nature. Journal of the History of Biology 43:493–528.
Peckham, M. 1959. The origin of species by Charles Darwin: a variorum text. University of Pennsylvania Press, Philadelphia, Pennsylvania, USA.
Pietropaolo, J., and P. Pietropaolo. 1986. Carnivorous plants of the world. Timber Press, Portland, Oregon, USA.
Richardson, R. A. 1981. Biogeography and the genesis of Darwin's ideas on transmutation. Journal of the History of Biology 14:1–41.
Richmond, M. 1988. Darwin's study of the Cirripedia. Volume 4, pages 388–409 *in* C. R. Darwin. 1985–2010. The correspondence. F. H. Burkhardt and S. Smith et al., editors. Cambridge University Press, Cambridge, UK.
Riley, C. V. 1882. Darwin's work in entomology. Biological Society of Washington, DC Proceedings 1:70–80.
Samper, C. December 2007. Co-evolution. Smithsonian 38:28.
Schmidt, K. P. Animal geography. Pages 767–794 *in* A century of progress in the natural sciences. California Academy of Sciences, San Francisco, California, USA.
Seward, A. C., editor. 1909. Darwin and modern science. Cambridge University Press, Cambridge, UK.
Southward, A. J. 1983. A new look at variation in Darwin's species of acorn barnacles. Linnean Society of London Biological Journal 20:59–72.
Stott, R. 2003. Darwin and the barnacle. Faber and Faber, London, UK.
Tomlin, A. D., M. J. Shipitalo, W. M. Edwards, and R. Protz. 1995. Earthworms and their influence on soil structure and infiltration. Pages 159–183 *in* Earthworm ecology and biogeography in North America. Lewis/CRC Press, Boca Raton, Florida, USA.
Tucker, A. Feb. 2010. The Venus flytrap's lethal allure. Smithsonian 40(11):48–55.
Von Hofsten, N. Zur älteren Geschichte des Diskontinuitätsproblems in der Biogeographie. Zoologische Annalen 7:197–353.
Vorzimmer, P. 1965. Darwin's ecology and its influence upon his theory. Isis 56:148–155.
Winsor, M. P. 1969*a*. Starfish, jellyfish, and the order of life: issues in nineteenth-century science. Yale University Press, New Haven, Connecticut, USA.
Winsor, M. P. 1969*b*. Barnacle larvae in the nineteenth century: a case in taxonomic theory. Journal of the History of Medicine and Allied Sciences 24:294–309.

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