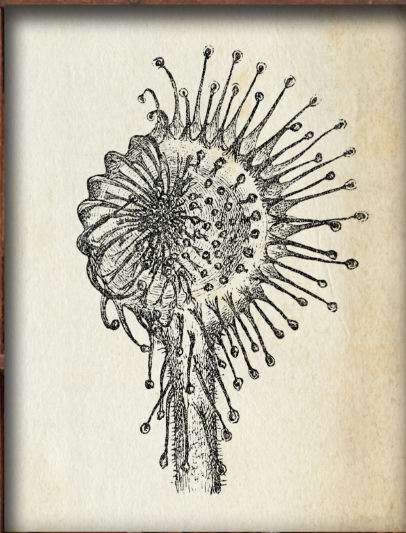
INCLUDING DO-IT-YOURSELF EXPERIMENTS

DARWIN'S BACKYARD



HOW SMALL EXPERIMENTS LED TO A BIG THEORY

JAMES T. COSTA

PREFACE

We can only imagine that Emma Darwin had the patience of Job. At one point in the 1850s, sheets of damp paper stuccoed with frog eggs lined the hallway of her house, pigeons cooed boisterously in a dovecote in the yard, row upon row of glass jars with saltwater and floating seeds filled the cellar, and malodorous pigeon skeleton preparations permeated the air. And that was only the beginning: there was a terrarium of snails with suspended duck feet, heaps of dissected flowers, and

Down House, Darwin's home of 40 years in Kent, south of London. Photograph by the author.

the fenced-off plots in the lawn where the grass was carefully scraped away to study struggling seedlings. Of course, being married to Charles Darwin over a dozen years by then, she was undoubtedly used to it. Charles, she might have said to friends, was *experimentising* again.

Darwin's experimentising, which appeared to some as merely the odd pursuit of an eccentric Victorian naturalist, turned out to push the envelope on his—and our—understanding of the biological world and our place within it. Darwin was laying the empirical groundwork for key elements of his revolutionary ideas on evolution.

This book introduces a Charles Darwin that few people know. His evolutionary ideas were not pulled out of thin air. He was an observer and experimentalist, and his clever and quirky investigations were not the schemes of some solitary eccentric sequestered in a lab. No, Darwin's home was his laboratory, and his and Emma's large family of seven surviving children often worked with him as his able field assistants. Darwin even published with his kids, in a fashion: the very year *On the Origin of Species* was published, a notice on rare beetles appeared in the *Entomologist's Weekly Intelligencer* by Darwin, Darwin, and Darwin—the authors being sons Franky, Lenny, and Horace, ages 10, 8, and 7, written with a wink by their proud dad on their behalf. He also had a talent for roping the butler and governess into his field studies, along with his cousins and nieces. He signed up legions of friends and strangers alike to make observations, try experiments, send him specimens, and serve as sounding boards. Yet, while Darwin may be a household name and his work equally well known, most are unfamiliar with Darwin the scientist, let alone the person.

His landmark books are appreciated as astonishing compendia of information, yet even many Darwin enthusiasts have little sense of Darwin the inveterate observer and correspondent, ingenious synthesizer and experimentalist, or family man. The rich array of experimental projects carried out by Darwin and his family reveal a very different—very *human*—side of a person too often seen as a cardboard icon. Whether enthusiastically taking up one son's suggestion to test the viability of seeds in the crops of dead birds, staking out and chasing oddly buzzing bumblebees in the garden, or venting his frustration to friends over uncooperative fish spitting out the seeds he was trying to feed them, Darwin's experiments are often humorous and always instructive. They may have been "fools' experiments," as he liked to call them, but as a Darwin friend pointed out, "fools' experiments conducted by a genius often prove to be leaps through the dark into great discoveries."

Through his experiments and other investigations Darwin systematically gathered data testing his evolutionary ideas. Beginning with his geological works of the 1840s, his experimentising and other pursuits provided invaluable material that bolstered his arguments. His pace picked up considerably in the 1850s, when his experiments became behind-the-scenes efforts to look into nature as no one had before, through the lens of evolution and natural selection. Darwin referred to the *Origin of Species* as "one long argument," but we should step back and consider his entire post-*Origin* opus in precisely the same way: one *longer* argument. After the *Origin*, he published myriad papers and some 10 books: on orchids, domestication, human evolution, climbing plants, animal behavior, carnivorous plants, flower structure, and earthworms. The topics are far-ranging yet all of a piece in support of a grand vision, many involving a prodigious number of homespun experiments and other projects.

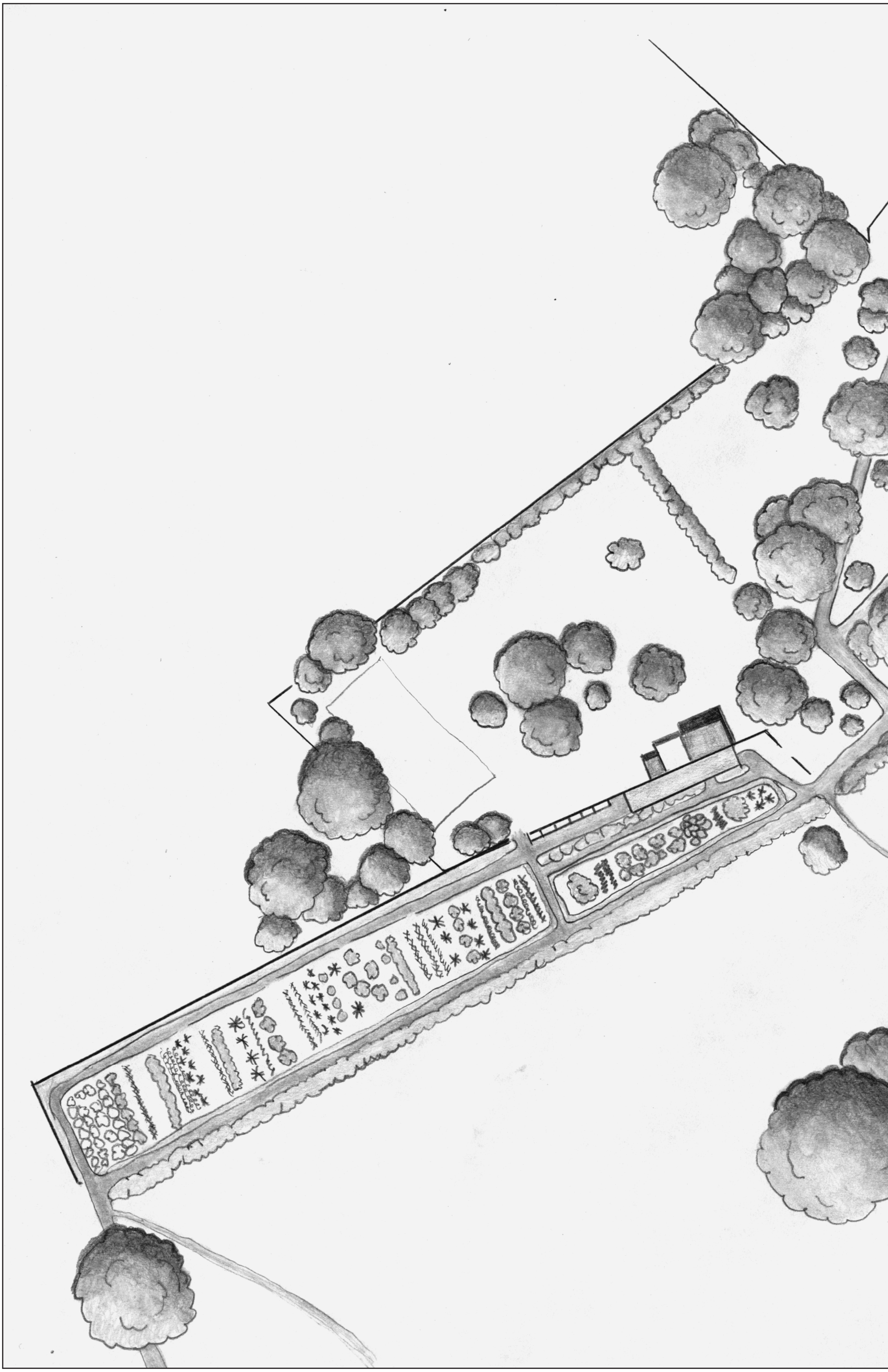
Beyond the fun of coming to know Darwin as worm whisperer, chaser of bees, and flytrap fancier, this book too has a serious point to make. Darwin's experiments instruct as well as entertain. Novel, amusing, at times hilarious, yes,—but they also shine a spotlight on science as a process. Darwin was a prototypical MacGyver figure: sleuth of the sandwalk—his gravelly thinking path at Down House—he shows how real insights into nature can be gained with simple tools at hand in yard, garden, or woodland. Modern visitors to Down House, ably managed by English Heritage, can see several of these experiments replicated in the meticulously restored gardens, greenhouses, and grounds. The deeper message here is that Darwin's experiments provide object lessons and blueprints for how science works. By and large these exper-

A view of Darwin's gravel thinking path, the sandwalk. Photograph by the author.

iments can be done here and now, in any schoolyard, backyard, classroom, or kitchen.

Anyone can become an experimentiser like Darwin and learn how to look a bit more closely at the natural world. In this regard, Darwin's experiments are an untapped resource that has been staring us in the face for a century and a half. At a time of much hand wringing over the teaching of evolution and critical thinking in science, one invaluable resource for helping communicate the essence of scientific inquiry has been all but overlooked. It is none other than the field's founder: Darwin himself. In *Darwin's Backyard,* I show how we can draw upon Darwin in exploring nature and better understanding evolution and how science works. Taking a thematic approach, this book thus has dual goals. First, I aim to take readers on a journey to see Darwin and his remarkable insights through the lens of his family life: his expansive curiosity at work and how family, friends, and a wider circle of naturalists were an integral part of this process. This very human Darwin with his homespun experiments is not the Darwin that most people are familiar with. Yet without appreciating this side of him, neither the man nor his achievements are to be fully understood. Second, I aim to show how Darwin's method has relevance today: how his backyard experiments can be *your* backyard experiments. To this end I offer up a menu of Darwin-inspired experiments, using that term inclusive of Darwin's observational projects as well as those more experimental in method.

Where did Darwin's penchant for experimentising come from? Though his no-nonsense father once despaired that his bug-collecting, horse-riding son would never amount to much, Charles Darwin clearly came by his philosophical turn of mind honestly—after all, his grandfather Erasmus Darwin was a famed physician and poet, with an inventive mind so fertile that the poet Samuel Taylor Coleridge coined the term "darwinizing" to describe his brand of wild speculation. Coleridge considered Erasmus to be "the most inventive of philosophical men," and his grandson was certainly cut from the same cloth. To understand the evolution of this experimentiser, we will start with his first forays into science as a kid, in league with his beloved older brother Erasmus, his grandfather's namesake, and their sometimes disastrous chemistry experiments. We'll meet, too, Darwin as a college student, making sense of the natural world from Edinburgh to Cambridge, and the exhilarating experience of the *Beagle* voyage. Here we see a working method born, inspired by Charles Lyell's landmark *Principles of Geology*. Within months of his return from his formative voyage around the world, Darwin was convinced of the reality of evolution and became



Down House and grounds, site of many of Darwin's investigations. Drawing by Leslie C. Costa.

the Lyell of biology. Over time his curiosity grew and his experimental eye was cast further and further afield, ferreting out the secrets of barnacles and bees, primroses and pigeons, weeds and worms. And yet in a sense he didn't look further than the gardens, woodlands, and meadows of his beloved home, morphed into a kind of *Beagle*, a ship on the Downs with family and friends his dedicated crew. Marcel Proust once wrote that "the real voyage of discovery consists not in seeking new landscapes but in having new eyes." Darwin did travel to new landscapes, but for most of his life he simply learned to see what was before him, with new eyes. In getting to know Darwin the experimentiser, we, too, can learn to discover the unfamiliar in the familiar.

Cullowhee & Highlands, North Carolina

2

Barnacles to Barbs

January 1835 found the 26-year-old Darwin and his *Beagle* comrades along the west coast of South America, amid the splendid desolation of the endless rugged and densely forested islands, looming snow-capped mountains, and deep bays and channels of the submerged Chilean Coast Range. Despite being high summer the weather was far from balmy: it was a place where "it rained as if rain was a novelty," he commented ruefully in his diary; where the rain "never seems to grow tired of pouring down." A week in the Chonos Archipelago, January 8th through the 14th, "passed rather heavily," he wrote; "the climate is so very bad & the country so very uniform in its character."[1] Between downpours he managed to get out on shore and collect, though, and it was there that, poking around a windswept gravelly beach, a number of thick Chilean abalone shells of the genus *Concholepas* caught his eye. They were riddled with tiny holes, like shot; holes he recognized were caused by the drilling of a minute organism. Intrigued, he collected some.

Back onboard the *Beagle*, snug in his cabin-cum-lab, Darwin duly recorded his find as specimen no. 2495 and, under the microscope, carefully dissected adults and several early stages of what turned out to be an odd parasitic barnacle. Yellowish in color and upside-down in their holes, they were unlike any barnacle he had ever seen. "Who would recognize a young Balanus [barnacle] in this illformed little monster," he asked in his specimen notebook, concluding that "it is manifest this curious little animal forms new genus."[2] Darwin didn't know it then, but he had found the smallest barnacle species in the world and was to bestow, years later, the name *Cryptophialus minutus* upon it. He also didn't realize that there was far more to this barnacle than met the eye; a decade later the by-then confirmed but closeted evolutionist would take another look at these specimens and make an astounding discovery, one that he believed had profound implications for his secret evolutionary ideas. As if somehow auguring his incendiary views to come, a few days after collecting his burrowing barnacle, on the night of January 19th, the towering Volcán Osorno erupted. Plainly visible to the astonished crew of the *Beagle* despite a distance of over 70 miles, Darwin recorded the spectacle in his diary, "a very magnificent sight."[3]

The destructive power of the eruption and the earthquake that followed was awful, but at the same time Darwin could not help but notice the astonishing geological effects of the event: the beach was uplifted some 10 feet, stranding hapless nearshore marine life high and dry and gasping, a palpable demonstration of Lyellian processes at work. Two weeks later, along the same coast, he trekked inland to see oyster beds deep in a forest at an elevation of 350 feet: evidence of uplift past that resonated deeply with the newly raised shoreline. At this point he was not many years away from applying gradual Lyellian geological and landscape change to equally gradual change in species, and would come to appreciate a profound correspondence between his mystery barnacle and the mysteries of geological change.

But quite a lot was to happen before then. For one thing, nearly 2 years yet remained of his *Beagle* voyage; 2 more years of strikingly beautiful landscapes and endless, featureless ocean, fascinating peoples, intriguing collecting, and near-constant seasickness. "I hate every wave of the ocean, with a fervor, which you, who have only seen the green waters of the shore, can never understand" he wrote from Tasmania to his cousin William Darwin Fox a year later.[4] Yet there is no question that the voyage was a turning point. Darwin would declare in his diary that "nothing can be more improving to a young naturalist, than a journey in distant countries . . . the habit of comparison leads to generalization."[5] *Generalization*, the opportunity to see the big picture, connect disparate dots, inductively puzzle out the laws of nature. The collections and observations made at a given time and place on this or that species, fossil, or geological formation had great value, and collectively they yielded insights greater than the sum of the parts. So it was that organisms as seemingly dissimilar as cirripedes and domestic pigeons would eventually be united under a common explanatory framework: methodical analysis of structure and development within each of these groups, with all of their attendant oddities, would yield mutually reinforcing evidence for evolution by natural selection. Much later, discoveries of *Hox* genes would confirm the deep structural bond of invertebrates and vertebrates—of organisms as dissimilar as barnacles and barbs, the fancy pigeons of Barbary descent—in spectacular fashion that surely would have thrilled Darwin. The stage was set for this in South America, on a remote and windswept Patagonian beach.

In that same letter to Fox, Darwin commented how he looked forward "with a comical mixture of dread & satisfaction" to the scientific work awaiting him at home. "I suppose," he mused, "my chief place of residence will at first be Cambridge & then London"—scientific centers of choice for organizing and working up his extensive collections and notes, their museums and scientific societies lately displaying a "rapidly growing zeal for Natural History" that would be immensely useful, he was sure. That would come to pass, but as a transitional stage between his wide-ranging travels and settling down permanently at Down House—not unlike the barnacles that would come to captivate him. As Charles Kingsley, the clergyman-naturalist-historian and prolific author, wrote of them in his 1855 book on seashore life:

> This creature, rooted to one spot through life and death, was in its infancy a free swimming animal, hovering from place to place upon delicate ciliae, till, having sown its wild oats, it settled down

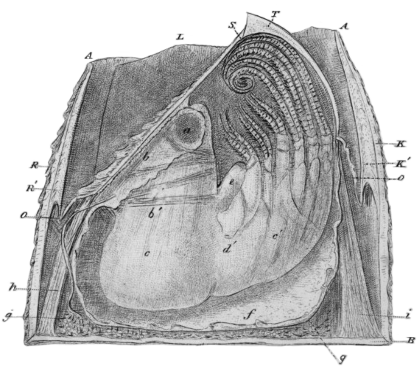
> in life, built itself a good stone house, and became a landowner, or rather a *glebae adscriptus*, for ever and a day. Mysterious destiny![6]

Mysterious indeed, these barnacles—so like diminutive *glebae adscriptus,* the medieval laboring "adscripts of the soil" permanently attached to the land. But a deeper mystery was how the identity of these humble organisms eluded naturalists until just a few years before Darwin's walk on that beach in southern Chile: before the 1830s they had been classified as mollusks.

Barnacles are arthropods, classified today in the infraclass Cirripedia of the subphylum Crustacea, meaning their closest relatives are crabs, shrimp, lobsters, and their ilk. They take their name from their elongated, slender and gracefully curved legs, or cirri ("cirripede" is derived from the Latin *cirrus*, "curled" or "tufted," like cirrus clouds, and *pede*, "foot"), tipped with fine hairs for sweeping food particles from the water column. The shell-like armor and two-part valves of common encrusting barnacles, together with the erroneous belief that they did not undergo metamorphosis, may well have misled naturalists since time immemorial into thinking that they were odd relatives of limpets or clams. It was not until 1830 that John Vaughan Thompson (1779–1847), a British army surgeon accomplished in zoology and botany, revealed their remarkable structure and metamorphosis in a memoir published in his collection *Zoological Researches, and Illustrations; or Natural History of Nondescript Or Imperfectly Known Animals*. Seen through a good microscope, these organisms were far from nondescript, but they certainly were imperfectly known. Thompson worked out the surprising life history of barnacles, and how their anatomical structure pointed to a relationship with arthropod crustaceans. Piquing the interest of other naturalists, studies confirming and extending Thompson's findings appeared in due time, but so too did studies arguing against Thompson's findings. The matter was not fully settled until the early 1840s, but most naturalists acknowledged the organisms' true identity well before then.

Thompson showed that barnacles start out as a free-swimming oneeyed larva he called the *nauplius*, compact with odd projecting structures for swimming, resembling a menacing alien spacecraft of the kind you might see in a *Star Trek* movie. After six months or so these mature into an adult affixed to one spot. In between is a short-lived transitional stage of the barnacle, mobile but nonfeeding, which Thompson called the *cyprid*, which plays the role of scout, feeling out potential real estate for permanent settling using specialized antennae. Once a suitable spot is found, the cyprid attaches itself headfirst by producing a glue-like substance from the antennae. The head-standing critter soon metamorphoses into an adult, and an even stronger substance cements the deal, literally, as the adult is permanently bound to the substrate by its head. It also begins to secrete protective calcareous plates—a fortified cell.

Now the barnacle takes on its familiar form: little cones or volcano-shaped structures stuccoing rocks, boats, shells, even whales and turtles. At least, that's the form of the common sessile or "acorn" barnacles; a whole other group of them are "pedunculate," or goosenecked, perched atop a flexible stalk attached to the substrate. The adults can continue to grow for a time, molting within the safety of their shelter as all good arthropods do, and expanding the protective plates as they get larger.



The sessile (acorn) barnacle *Balanus tintinnabulum* encased in its protective shell. Note the modified legs, or cirri, which serve as the food-gathering structures of these suspension-feeders. From Darwin (1854), vol. 2, plate 25.

Thompson's well-thumbed memoir on barnacles was among the many books in the *Beagle*'s reference library (which was at Darwin's fingertips, lodged in the same cozy 10 × 11-foot poop cabin where he worked by day and slung his hammock by night).[7] With Thompson's book at hand and his keen marine zoology interests, inspired by his Edinburgh mentor (and evolutionist) Robert Grant, Darwin was familiar with barnacles and their habits. Yet none that he knew of drilled holes. His cataloging and dissecting done, however, he packed the shot-through *Concholepas* shells away and moved on to the next intriguing collections as the *Beagle* made its way northward along the coast.

Cuidado

Barnacles were on Darwin's mind again in March 1837, the month that saw him turn into a transmutationist. He had just moved to London, renting a place on Great Marlborough Street in Bloomsbury for easy access to the British Museum, and conveniently just up the street from his brother 'Ras. The parallel Darwin perceived between geography and geology—the geographical distribution of related species and its uncanny correspondence with the relationship between living and extinct species of an area—got his adrenalin pumping, as he realized this correspondence spoke of species changing. The epiphany fired his imagination, sending him seeking more information, new observations, to test his hunch. Questions abounded, but among Darwin's earliest notebook entries as a transmutationist we find him especially concerned with reproduction, metamorphosis, and the unity of life, all somehow bearing, he was sure, on the nature of species, varieties, variation, and change—and barnacles were front and center.

In March 1837 he pulled out his old marine zoology notebook from Edinburgh, flipped it over, and commenced a series of notes from the back. The first of these, under the heading "Zoology," referenced the recent debate over barnacle metamorphosis.[8] John Obadiah Westwood, the Oxford arthropod specialist, challenged Thompson's interpretation of barnacle structure and development, and therefore their classification. His critique was based on the prevailing view of relationships between animal classes and phyla, which held that crustaceans are more closely related to vertebrates than to insects. Westwood reasoned that since many insects and no vertebrates exhibited metamorphosis—no vertebrate experienced anything at all like the radical transformation of caterpillar to butterfly, say—by analogy crustaceans should not be so insect-like as to metamorphose either. Westwood was not alone in this belief—odd as it may seem today, notable naturalists of the day could not see the evidence for metamorphosis that Thompson pointed out; such is the power of preconceived ideas, perhaps. Westwood concluded that the weight of evidence pointed to barnacles as some sort of anomalous mollusk, somewhere between the "articulates" (arthropods) and vertebrates. Thompson and Westwood read dueling papers at the Royal Society, published back-to-back in the Society's *Philosophical Transactions* in 1835. It was these papers that Darwin referenced in his notebook.

Darwin's money was on Thompson's interpretation, maybe owing to the stock he put in the argument based on the clear segmentation and other arthropod-like features of the barnacle's early stages. This may be the earliest indication of Darwin's interest in the value of development to inform relationships. In this case early stages were used to make decisions about classification, but later he would see how early stages, especially embryos, could give clues to evolutionary diversification. That idea, too, was in its infancy in the 1830s, and Darwin was abreast of the latest discussions. Richard Owen (1804–1892) would have impressed the utility of early stages upon the younger naturalist in the many conversations they had in his post-*Beagle* years. Darwin might have even heard Owen, a rising star and first permanent Hunterian Professor at the Royal College of Surgeons, hold forth on the subject in his acclaimed Hunterian Lectures in the spring of 1837. On May 9th of that year Owen declared to a rapt 400-plus audience that studying the structure of fully developed animals is inadequate for diagnosing true relationships. Early developmental stages were key: just as entomologists now gain insight into insect relationships by studying their immature stages, "What should we know of the zoological relations of the Barnacle, if we were acquainted only with its organization in the last fixed stage of existence?"[9] In this very same lecture, however, Owen took a dim view of such discreditable ideas as transmutation—a public condemnation that would have reinforced Darwin's resolve to keep his evolutionary speculating to himself had he been present.

Reproduction became as central to Darwin's transmutational musings as geography and geology. In July 1837, during a visit to the family home in Shrewsbury, he started a fresh notebook with copious notes on his transmutationist grandfather's work *Zoonomia*. In it he speculated on the nature of species relationships over time: a branching pattern captures the essential idea of change within lineages as well as links between lineages, and he showed that he understood the dynamic of lineages diverging over time, as in one comment pointing out that gaps between groups like arthropods and vertebrates will grow over time, as extant species become more divergent from their common ancestor. "Heaven know[s] whether this agree[s] with Nature," he wrote, literally ending on an underscored cautionary note: "Cuidado"—*caution*.[10]

And proceed with caution he did, at least publicly—that was only prudent, as he was becoming something of a rising star. But in the privacy of his notebooks his speculations and questions ran rampant as he immersed himself in literature of all kinds, from hard-core geology, botany, and zoology to practical agricultural improvement and breeding, with philosophy, religion, and literature thrown in. He boned up on the prevailing arguments against transmutation, clarifying the key issues but also arming himself. Darwin knew only too well Lyell's extensive anti-transmutation arguments in the watershed *Principles*. The fifth edition came out in 1837, the very year of Darwin's conversion to transmutation; reviewing Lyell's arguments he wrote in the margin of his copy: "If this were true, adios theory."[11]

Another Volcano Erupts

From time immemorial those inclined to see transmutational change cited links throughout the organic world as evidence: species or their taxonomic groupings can be arranged in something of a sequence, it was thought, generally in order of increasing "complexity" (however that was defined). Schemes varied, but their common denominator was *continuity*, the idea that all forms could be linked through a chain of intermediates—versions of the ancient Greek Scale of Nature idea that became codified in some strains of Christian thought. With increased knowledge of geological strata and the fossil record in the eighteenth and especially nineteenth centuries came the realization that to a large extent this chain seemed to map onto a temporal sequence. The Chain of Being and its development over geological ages were thus easily interpreted in terms of an unfolding divine plan marked by successive bouts of creation (and extinction), a teleological view that inevitably had as its aim the arrival of humanity, the pinnacle of creation made in the very image of the Creator. But such chains of relationship are just as easily interpreted in transmutational terms, as Lamarck (and later Darwin) came to believe.

One of the most serious arguments *against* transmutation, in contrast, was based on supposed *dis*continuities, morphological gaps between major animal groups. If there were such gaps, the rug was pulled out from under any possibility of transmutation. Thus was born the concept of *embranchements*, distinct, separate, decidedly unlinkable taxonomic groups reflecting distinct body plans, an idea introduced by the illustrious and formidable Georges Cuvier in Paris. Cuvier (1769–1832) recognized four basic body plans—*Radiata* (sea stars, jellies, and relatives), *Mollusca* (bivalves, slugs, cephalopods . . . and barnacles), *Articulata* (arthropods and relatives), and *Vertebrata* (all animals with backbones: fish, reptiles, amphibians, birds, and mammals)—each fully independent of the others. Sure, recognizing the diversity of forms within these categories, certain taxa in one *embranchement* could "approach" others in another *embranchement,* but there was no possibility of a real relationship or link between *embranchements*, let alone a passage—barnacles might have some traits that apparently "approach" insects among the articulates, for example, but they were essentially mollusks no matter how much "articulateness" they may exhibit, and one was certainly not derived from the other.

Cuvier's system was devised in explicit refutation of his (unfairly) reviled colleague Lamarck, with his notorious transmutational ideas. No linkage between the fundamental taxonomic groups, no possibility of some kind of "passage," no transmutation. *Why* transmutation was seen as such an affront is a bigger issue than we have space for here; suffice it to say that this became a signal issue for a larger battle over materialism and natural law versus divine providence, and thus over atheism versus received religion. In important respects this was a false dichotomy, not least because then, as now, some simply saw transmutation by natural law as *itself* a divinely ordained process. But the readiness with which the anticlerical revolutionaries of France and their hopeful counterparts in Britain in the late eighteenth and early nineteenth centuries brandished the banner of change, transmutation in all things—from societies to species—and the ensuing horrors this unleashed in the Terror would only harden the position of conservatives defending the social order through the central authority of church and state. Thus it was that transmutation was itself transmogrified into a byword for atheism and even sedition by Darwin's day.

That was certainly the way that Richard Owen saw it. He embraced Cuvier's system of *embranchements* with gusto, and his later term *archetype* (ideal generalized form of a given species or group) was inspired by Cuvier. Fervently opposed to Lamarck and transmutationism, Owen was determined to stamp out such heresy in England. Lyell's polemic against Lamarck and transmutation in the *Principles* was written in the same conviction, though not the same mean-spiritedness. Owen's antipathy and Lyell's disapproval would have been abundantly clear to Darwin, and concerns over the social implications of his theory were behind his note of *cuidado*.

Transformation was thus very much on Darwin's mind in the late 1830s—not least his own transformation as his thinking developed. In the fall of 1837, not long after his brief notes on the Thompson-Westwood debate over crustacean metamorphosis, he delved into another and more famous debate, one that took place back in 1830 and had implications that struck at the very heart of his transmutation theory. That was the year that Georges Cuvier squared off against his younger colleague and sometime protégé, Étienne Geoffroy Saint-Hilaire at the Académie Royale des Sciences in Paris. The issue was no less than the unity of life. For years Cuvier and Geoffroy argued, mostly in private, over the fundamental question of relationship between Cuvier's four *embranchements*. Geoffroy (1772–1844) was as brilliant an anatomist as Cuvier, and while not an out-and-out transmutationist, he was a friend and supporter of Lamarck, who had died the year before the debate. Geoffroy subscribed to an idea that might be described as a zoological uber-plan: he saw a single generalized body plan uniting all animals, all four *embranchements*, allowing that some creative force had fashioned each from the same basic starting point. Perhaps some had even been derived from others, rather than being created *de novo*. Geoffroy's evidence was anatomical structures that he traced through development—essentially what we call homologies today. Through a series of acclaimed studies he had built up a body of work establishing not only unity of the animal body plan, but also principles of connection between seemingly disparate forms, the significance of rudimentary structures, and his "law of balancement of organs." It was Geoffroy who discovered that the mammalian skull could be understood in terms of fusion of various bones, separate in so-called "lower" vertebrate forms and, significantly, early embryological stages of "higher" forms. "Nature constantly uses the same materials," Geoffroy maintained, "and is ingenious only in varying their forms." Early on Cuvier applauded his younger colleague's discoveries, but when Geoffroy sought to derive from them a visionary new philosophy of morphology proclaiming the unity of all animal forms, Cuvier balked.

The trigger of the great debate was a paper Geoffroy encouraged, read by a pair of younger naturalists presenting anatomical evidence that cephalopods form a linking group between mollusks and vertebrates. Cuvier did not take it well. The senior naturalist's vehement rejection of the paper provoked Geoffroy to enter the fray. The argument soon became public as the savants presented dueling papers at the Académie Royale through the spring and summer of 1830. This all unfolded against the backdrop of another drama developing in Paris at the same time: the political upheaval that culminated in *le trois glorieuses*, the Three Glorious Days in late July 1830 when the people rose up and, manning the barricades, forced the abdication of the repressive King Charles X. It was a matter of perspective which was the more significant battle: one Frédéric Soret, of Geneva, had occasion to visit the aging polymath Johann Wolfgang von Goethe in Weimar, Germany, just as news of the Paris uprising reached the city, setting "everyone in a commotion," as Soret recalled. He recounted his meeting with the German savant:

> "Now," [Goethe] exclaimed as I entered, "what do you think of this great event? The volcano has come to an eruption; everything is in flames, and we no longer have a transaction behind closed doors!" "A frightful story," I replied. "But what else could be expected under such notorious circumstances and with such a ministry, than that matters would end with the expulsion of the royal family?" "We do not appear to understand each other, my good friend," replied Goethe. "I am not speaking of those people at all, but of something entirely different. I am speaking of the contest, of the highest importance for science, between Cuvier and Geoffroy Saint-Hilaire, which has come to an open rupture in the Académie."[12]

Soret was at a loss for words. There is no question whom Goethe was rooting for: a visionary in the same mold as Geoffroy, Goethe himself had made fundamental contributions to comparative anatomy, and even advanced a theory of unity of form in botany that paralleled Geoffroy's work in zoology.

The Cuvier-Geoffroy debate is directly relevant to Darwin's development as an experimentiser, though it took time for him to feel the aftershocks of the seismic events of 1830 at the Académie. There is no evidence that he knew about the debate at the time, his letters and diary filled instead with excited talk of beetle collecting, fishing, hunting, and horses. *Le trois glorieuses* found him preparing for a trip to north Wales. Geoffroy had published an account of the debate in his *Principles of Zoology* (1830), including his and Cuvier's papers read at the Académie. Darwin laboriously made his way through Geoffroy's book in late 1837, filling four notebook pages with comments: "[Geoffroy] states there is but one animal: one set of organs—the other animals created with endless differences," reads one entry—note the word "created" underscored. He saw the transmutational significance, continuing: "does not say propagated, but must have concluded so."[13] Several passages are marked in Darwin's copy of the book, the margins littered with exclamation marks, comments, and notes to extract quotations. It is telling which passages got him excited: explaining about the "natural development" of animal bodies (a phrase underlined by Darwin), Geoffroy stated that "man, considered in his embryonic state, in the womb of his mother, passes successively through all the degrees of evolution of the lower animal species: his organization, in its successive phases, approaches the organization of the worm, the fish, the bird."[14]

Geoffroy, familiar with the embryological work of Karl Ernst von Baer, was convinced that modifications at various stages of embryological development were key to his idea of unity of all animal forms—an idea with clear evolutionary implications. Cuvier, dismissive of Geoffroy's "unity of composition" talk as "contrary to the simplest testimony of the senses," maintained that the resemblances that Geoffroy pointed to merely reflect how the "agreement of parts" simply follow from their "coordination for the role that the animal has to play in nature." Form follows function, in Cuvier's view, not the other way around. Darwin excitedly scored this passage, too. But where Cuvier asserted that "conditions of existence"—adaptation to environment, say—explained resemblances, Darwin disagreed: resemblance may also follow from common ancestry. As for the "unity of composition" that Cuvier so emphatically dismissed, it's clear from Darwin's marginal comment that it was a given: "The unity of course due to inheritance." Common ancestry was common sense to Darwin.

Darwin's interest here resonated with his interest in Thompson's barnacle work. He noted how Geoffroy acknowledged a wide gap between insects and mollusks, but also the variation within each group, certain organ systems being more or less developed in each and forming something of a series. "This explains the large hiatus that has been noticed between the families," the Frenchman asserted, "especially with regard to the beings at the center of each series, and also the very numerous relations that they exhibit at their extremes." Referencing this in his notebook that fall of 1837, Darwin noted that barnacles were just such a group at the extreme of the series, and wondered whether Geoffroy thought that such a series was linear or could be branched.

The Whole Art of Making Varieties

But in the late 1830s barnacles were filed away in Darwin's mind—or maybe mentally shelved is more like it, similar to his tagged *Beagle* specimens shut up in sturdy glass-doored museum cabinets. As we'll see, he returned to them nearly a decade later, but now he increasingly looked at the puzzle of reproduction, inheritance, and variation through the lens of domestic breeds—a knotty issue that would shed light on the species question. It was knotty because common sense and the prevailing view held that little could be learned from domesticated breeds. If anything they were evidence that species could *not* change, as Lyell so eloquently expounded in the *Principles*: domestic varieties were changeable only to a degree, it was claimed, and as soon as they run wild they revert back to their generic form. Patently unnatural, domestic animals couldn't survive in a state of nature; only a Gary Larson could imagine wild packs of fancy poodles. Darwin's first hunch was that the environment somehow interacted with individuals to engender variation and species change, and if kept separate from other individuals undergoing their own changes, wholesale transmutation would eventually be achieved.

Thinking along these lines, his initial interest in domestication had more to do with how people affect variation by controlling the environment of farmed plants and animals. But by summer of 1838 he began to have second thoughts: maybe there was more to domestic breeds than met the eye? Immersing himself in the breeders' craft, he pressed friends and acquaintances for information and struck up conversations with anyone and everyone having practical experience with one kind of domestic group or another: beekeepers and horticulturists, pigeon fanciers and husbandrymen, poultry aficionados and dog breeders. There was plenty of expertise close at hand, too, between the coachmen and gardeners who worked for his father and Uncle Josiah. And, of course, he pored over the writings of the likes of Bakewell, Yarrell, Youatt, Wilkinson, Sebright, and other pioneering breeders behind Britain's first agricultural revolution. The problem was that there was often conflicting information on phenomena like hybridization and heritability. Soon their pamphlets yielded an unexpected insight.

Darwin was primed to appreciate the basic idea of selection applied by people to improve animal breeds months before his reading of Malthus catalyzed his insight into selection in nature. It's hard to say *when* he became conscious of the concept, but unmistakably it first appears in entry 17 of transmutation notebook C, dating to February 1838: "The changes in species must be very slow owing to physical changes [being] slow and offspring not picked as man [does] when making varieties," he wrote in his usual shorthand.[15] This is a revealing comparison: believing that physical changes in the environment induce changes in species, and aware that "picking" offspring, *selecting* those that will or will not be bred, is the way that people create new varieties, he is suggesting here that the rate of species change in nature is slower in part because there's no one to do the picking and accelerate the process. His thinking along these lines is evident in a number of other entries; he was beginning to appreciate more and more the analogy between domestic breeds and species and varieties in nature. It all had to do with the power of picking.

"Picking" becomes methodical selection in his thinking through the influence of two agricultural improvement pamphlets: Sir John Saunders Sebright's *The Art of Improving the Breeds of Domestic Animals* (1809), and John Wilkinson's *Remarks on the Improvement of Cattle* (1820). These works, which Darwin heavily annotated in March 1838, drove home the power of selective breeding. In fact, the word "selection" in this very context is used repeatedly by Sebright and Wilkinson, in passages that Darwin underscored. Consider, for example, Sebright's assertion that the art of breeding consists "in the selection of males and females, intended to breed together, in reference to each other's merits and defects," or that traits like "the fineness of fleece, like every other property in animals of all kinds, may be improved by selection in breeding." Yes, climate, soil, and other environmental factors have some effect on wool quality, he acknowledged, "but not so much as is generally supposed."[16] Sebright's use of the word "selection" meant selective breeding, with some individuals chosen for breeding and others for the pot. He shook his head at the widespread misapprehension that improvements are achieved and new varieties made by hybridizing existing breeds: "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," he declared. "They attribute every improvement to a cross," when the actual cause was simple: "it is merely the effect of judicious selection."[17] The power of selection is what it's all about, a point underscored by Wilkinson:

> The worst must unquestionably be rejected, while the rest, and especially the best of these, are carefully to be preserved for future stock. . . . By such procedure [i.e., selection], animals have at length been produced, so different from the generality of the stock from whence they were originally taken, that none but such as are well acquainted with these matters, could have an idea, that there existed between them the least affinity. The distinction indeed between some, and their own particular variety, has scarcely been less than the distinction between that variety and the whole species.[18]

Darwin gave this passage an excited double score in the margin, as he did another passage where Wilkinson emphasized that such changes "are in general gradual," proceeding "but slowly through several generations." This was all electrifying. In his C notebook, he declared, "Sir J Sebright pamphlet most important," and that the "Whole art of making varieties may be inferred from facts stated."[19] He saw clearly a parallel between domestic and wild animals, and the power of selection to diversify. His ungrammatical notebooks make for difficult reading, but their almost stream-of-consciousness shorthand also conveys a sense of the energy and excitement of discovery Darwin must have been feeling.

In mid July, he opened a fresh notebook. About 25 percent of the entries pertain to domestication and record his ups and downs in relating what he learned from Sebright, Wilkinson, and others to species and varieties in nature. "The varieties of the domesticated animals must be most complicated," he lamented at one point. In selective breeding only a few individuals are picked out to reproduce, but how does that happen in nature? And he still sensed that separation played a role in the formation of new breeds by preventing intermixing: "The very many breeds of animals in Britain shows, with the aid of seclusion in breeding how easy races or varieties are made," he wrote a few pages later (emphasis Darwin's).[20] Always alert to observations or data bearing on species and varieties, he was amazed by the sheer number of rose varieties when he visited the famous botanic garden and arboretum of George Loddiges in Hackney, just north of London: "Loddiges garden 1279 varieties of roses!!! Proof of capability of variation," he recorded on 23 September 1838.[21] Variation enough to permit the cultivation of so many rose varieties suggested an inexhaustible supply—so much for Lyell's insistence that variation was limited! And unlimited variation meant an unlimited capacity for change.

That visit to Loddiges' garden came just a week before Darwin's re-reading of Malthus provided the spark that led him to natural selection—suddenly grasping nature's version of the picking and choosing process going on in farmyards and fields for centuries. The key was superfecundity. This was a vision of reproductive output on a staggering scale. Picture each bit of confetti in a ticker-tape parade as so many lottery tickets. There are scant few winners; the vast majority in the confetti blizzard are destined to be swept away. What determines winning or losing in the farmyard is the breeder calling the shots; in nature it is the demands of the immediate environment determining which of those hopeful propagules makes it. Variations—ubiquitous, abundant, small, and (very importantly) random—provide the raw material, with Malthusian population pressure the crucible for selection to act, slowly, inexorably changing species according to the demands of their environment.

In another notebook Darwin sketched out how he might explain the process to others, an outline for an argument if you will, building on domestication as an analogy. First, he noted to himself, point out that new varieties are made in two ways: one is by environmental change, while the other is by picking offspring and preventing free intercrossing. Next ask: "Has nature any process analogous?—if so she can produce great ends." Rhetorically asking "But how?" he instructs himself to "make the difficulty apparent by cross-questioning." Finally, he says, "Here give my theory—excellently true theory."[22] An excellently true theory it was, but there were so many details yet to work out. What causes all that variation? To what extent is it heritable, and how? What role does environment play? How common is hybridization, and what are its effects? Why do parental traits sometimes blend in offspring and sometimes seem unequally expressed? Some of these issues weren't resolved until the twentieth century, with the revelations of Mendel and the later insights into DNA structure and gene expression. Darwin could only grasp at straws.

Just as Darwin was entering his own new domestic life—he and Emma were married in the chapel at her home, Maer Hall, in January 1839, and soon happily residing on Upper Gower Street, London—he pondered domestic breeds ever more deeply. He pestered friends, family, and colleagues with questions at every opportunity, and gathered all manner of information bearing on domestic varieties and breeding, even starting a separate notebook on questions and experiments. A slender notebook of about 40 pages, it's divided into sections that tell us something about his working method between about 1839 and 1844: "Experiments in crossing &c. Plants," "Questions Regarding Plants," Questions Regarding Breeding of Animals," "Experiments in crossing animals," are some of the general headings for lists of questions directed to botanists and horticulturists like his Cambridge mentor

Henslow and the gardeners at Maer and Shrewsbury, medical men like his father and Henry Holland (Darwin's doctor in London), zoologists and museum men like John Gould and Edward Gray, breeders like William Yarrell, and others.[23]

As he wrote in his autobiography, with natural selection he had "at last got a theory by which to work." But although he was bursting with questions and did manage experiments and other investigations (see especially Chapter 6 for Darwin's work on crossing and pollination at this juncture), he was able to direct frustratingly little of his efforts to his species theory in the next several years. He was overwhelmed as a new husband, parent, and ambitious young scientist determined to make a name for himself. After William Erasmus ("Doddy," later Willy) was born in 1840, Emma was in a nearly continuous state of pregnancy for the next decade or more. On the scientific front he was in demand as an active participant in the learned societies, and there was the seemingly unending task of writing up his *Beagle* material. His output was prodigious, with three volumes on geology (coral reefs in 1842, volcanoes in 1844, and the geology of South America in 1846), plus his travel memoir (first out in 1839), introductions to the *Beagle* voyage's zoological volumes (fish, reptiles, birds, and more), and last but not least, various geological and zoological papers.

With a mysterious illness beginning to manifest itself on top of (maybe because of?) the work load, soon after their second child, Anne Elizabeth, was born in 1841 he resigned from the secretaryship at the Geological Society and stepped down from the council of the Royal Geographical Society. This illness was to worsen and plague him for the rest of his life, with periods of violent gastrointestinal distress and severe headaches that came and went. The precise nature of the malady is still debated today—was it the lingering effects of a parasite picked up on the *Beagle* voyage? A psychosomatic reaction to the stress and strain of harboring ideas he knew would be fiercely repudiated by society and threaten to estrange his devout wife? Overwork, or an allergy or metabolic condition like lactose or gluten intolerance? Perhaps some inherited disorder? We may never know.[24] What is certain is that he responded to what would be considered quack treatments today: the "water cure" (dousing in chill water and lying motionless for hours wrapped in wet towels) together with strict regulation of his exertions, mental and physical. The enforced idleness was maddening to Darwin, but it seemed to have a positive effect, at least for a time.

Prior to the worst manifestations of his illness the family got away to Maer for a month's respite each summer, and it was there, in 1842, that he finally managed to gather his thoughts and write out a brief sketch of his theory to date. He opened this brief account with the analogy from domestic breeds, entitling the first section "On variation under domestication, and on the principle of selection." It was a format he stuck with: from the expanded 230-odd page *Essay* version of this sketch written out 2 years later to his "big species book" manuscript *Natural Selection* to *On the Origin of Species* itself, he consistently set up his case for evolution by natural selection with domestication as a strong analogy with variation, selection, and slow, steady change in nature.[25] It was a philosophical and rhetorical approach that was likely inspired by the renowned John Herschel, whom we met in Chapter 1. In his *Preliminary Discourse on the Study of Natural Philosophy* (1830), the much-admired astronomer, mathematician, and philosopher pointed to the power of analogy as one way to gain insight into *vera causae*—true causes—in nature. This was a book that Darwin studied closely, one of just two cited in his autobiography many years later: the other was Humboldt, and together they fired up his zeal for science. He recalled, "No one or a dozen other books influenced me nearly so much as these two."[26]

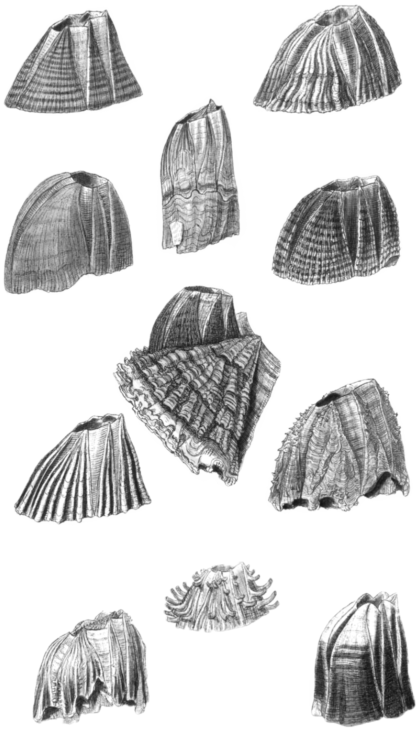
By the time Darwin penned his lengthy *Essay* in 1844 he had a largely complete theory—there were some key details missing yet, as we will see in the next chapter, but in structure and content the *Essay* very much has the look of a condensed version of the *Origin* that appeared 15 years later. Darwin thought it was sufficiently complete at that stage that he hired the local schoolteacher to write out a fair copy (his own handwriting anything but fair), sealing it in an envelope with a poignant letter asking Emma to publish the essay without delay in the event of his untimely death. But if it was *that* complete, and he had that much faith in its essential correctness, why not just go ahead and publish it? That is a question that scholars have debated and discussed for over a century. Some have claimed that Darwin delayed publishing out of fear of the repercussions, or out of respect for the deep religious convictions of his wife. There may be something to the repercussions idea—it may not be coincidental that the scandalous *Vestiges of the Natural History of Creation* came out that same year, thrusting the idea of transmutation into the limelight in 1844 and provoking venomous condemnation by the leading lights among naturalists—many of them Darwin's scientific friends, mentors, and professors. But it's also true that he simply wasn't ready to publish: he had more work to do, probably more than he realized then—not least a return to barnacles, which Hooker had something to do with.

Darwin had struck up a correspondence with botanist Joseph Dalton Hooker (1817–1911) soon after Hooker's return in the fall of 1843 from a 4-year southern voyage under James Clark Ross, on which he served as both assistant surgeon and naturalist. (That was the acclaimed voyage that confirmed the existence of a vast new continent—Antarctica.) Knowing that Hooker was going to work on a flora of the southern lands, Darwin asked Henslow to forward his Galápagos plant collection to him in case they proved useful. Hooker thanked him warmly, and they started corresponding on points of common interest as scientists and travelers. Their friendship grew to the point where, in January of 1844, the year he penned the *Essay*, Darwin ventured to take Hooker into his confidence. "I have been now ever since my return engaged in a very presumptuous work & which I know no one individual who would not say a very foolish one," Darwin ventured. He explained how he had been struck by the Galápagos species he observed, and the fossil mammals of South America, and how he resolved to collect any and all facts that might bear on the question of the nature of species. "I have read heaps of agricultural & horticultural books, & have never ceased collecting facts," he continued. "At last gleams of light have come, & I am almost convinced (quite contrary to opinion I started with) that species are not (it is like confessing a murder) immutable." Darwin hastily added a reassuring line distancing himself from the unpalatable ideas of Lamarck: "Heaven forfend me from Lamarck nonsense of a 'tendency to progression' 'adaptations from the slow willing of animals' &c."—yet, he had to acknowledge, the conclusion he had come to was not so very different from the Frenchman's, though the mechanism of change is very different. "I think I have found out (here's presumption!) the simple way by which species become exquisitely adapted to various ends." How would Hooker take this? Darwin was a bit worried: "You will now groan," he wrote, "& think to yourself 'on what a man have I been wasting my time in writing to.'"[27] Far from contemptuous or dismissive, Hooker was intrigued and invited his new friend to tell him more.

The Barnacle Returneth

While Hooker was not dismissive of Darwin's species theory, he wasn't an instant convert either. His skepticism proved invaluable to Darwin: the botanist was a font of information and a fierce (but friendly) critic, constantly challenging Darwin to sharpen his arguments and defend his evidence. He helped Darwin recognize where the weaknesses of his theory lay. They exchanged long letters in which Darwin peppered Hooker with questions seeking data, observations, and Hooker's judgment on matters relating to geographical distribution, variation, classification, structure, and species relationships. Darwin pored over botanical manuals and turned to Hooker for assessment of this or that observation, ever on the lookout for facts that would bear on his theory. It was in this vein that Darwin wrote Hooker expressing interest in an article on species and their variation by Frédéric Gérard, in the newly published *Dictionnaire universel d'histoire naturelle*. Darwin picked up on intriguing language used by Gérard, such as how species can *develop* certain traits (sounding like thinly veiled transmutationism), and how the Frenchman questioned whether "species" per se even existed on the basis of their often unclear boundaries. Darwin's innocent query provoked a contemptuous reply from Hooker: Gérard was "evidently no Botanist," he sniffed, but one of those "narrow-minded studiers of overwrought local floras." He had little patience for armchair naturalists who make a big deal out of variable characters and questionable delineations of species that were, after all, issues discussed in cautious terms by careful and methodical botanists, yet "taken up by such men as Gerard, who have no idea what thousands of good species there are in the world." Hooker declared that he was "not inclined to take much for granted from any one [who] treats the subject in his way & who does not know what it is to be a specific Naturalist himself."[28]

Reading between the lines, Darwin realized that Hooker was indirectly referring to him and his grandiose theorizing, going on about species and varieties but really having little idea what these are like in nature. "How painfully . . . true is your remark that no one has hardly a right to examine the question of species who has not minutely described many," he acknowledged. But, he continued, defensively: "I was, however, pleased to hear from Owen (who is vehemently opposed to any mutability in species) that he thought it was a very fair subject & that there was a mass of facts to be brought to bear on the question, not hitherto collected." Darwin would take comfort in the fact that he had "dabbled in several branches of natural history and geology," he said, and although he would get "more kicks than half-pennies," he would pursue his species theory. At least he would improve upon Lamarck,



Some of the acorn barnacles studied by Darwin. Courtesy of Richard Milner.

he ventured: "Lamarck is the only exception, that I can think of, of an accurate describer of species at least in the Invertebrate kingdom, who has disbelieved in permanent species, but he in his absurd though clever work has done the subject harm, as has Mr Vestiges, and, as (some future loose naturalist attempting the same speculations will perhaps say) has Mr D."[29]

Hooker was quick to say that he wasn't insinuating that *Darwin* was one of those armchair naturalists. Rather, he wrote, smoothing things over, "what I meant I still maintain, that to be able to handle the subject at all, one must have handled hundreds of species with a view to distinguishing them & that over a great part—or brought from a great many parts—of the globe." But Darwin felt the truth of Hooker's criticism. "All which you so kindly say about my species work," he replied, "does not alter one iota my long self-acknowledged presumption in accumulating facts & speculating on the subject of variation, without having worked out my due share of species." This exchange of letters took place in September 1845.[30] Within a year Darwin was deep into a systematic study of barnacles, an undertaking that he first thought might take up to a year but in fact ballooned to 8 years. By the end of it he had "minutely described" many species, earning "the right to examine the question of species."

Darwin's barnacle work snowballed in part because other naturalists cheered him on: Hooker, certainly, but also Richard Owen at the Royal College of Surgeons, and the famed zoologist Louis Agassiz at Harvard, who called the world of barnacles a "great desideratum" desperately in need of study. The real coup came when the zoological keeper at the British Museum, Edward Gray, agreed to lend Darwin the Museum's entire cirripede collection, much of it uncataloged. Imagine that: the whole national collection at his fingertips! But the other reason the project exploded was the unexpected discoveries he made—discoveries with profound implications for his species theory. As Janet Browne aptly put in her monumental Darwin biography, the barnacle studies would prove to be another of Darwin's "explorations into the reproductive unknown."[31]

Darwin's barnacle odyssey began with the curious specimen he found on the windswept beach in the Chonos Archipelago. He showed it to Hooker, who had come to Down House in the fall of 1846 to meet Darwin's old *Beagle* shipmate Bartholomew Sulivan. Just back from South America, Sulivan had completed a detailed survey of the Falkland Islands, among other accomplishments, as commander of his own ship. Back in 1835 when Darwin first found his burrowing barnacle, he commented in his notes that "it is manifest this curious little animal forms new genus." Now he asked Hooker to help him name it, and they came up with *Arthrobalanus*—or "Mr. Arthrobalanus" in their frequent discussions of the odd crustacean. In fact this creature seemed doubly odd: besides its burrowing habit, Darwin thought he could discern *two* penises. It took a while, but he eventually realized that the Mr. was in fact a Ms. The "penises" were the cirri, filament-like feeding appendages, of female specimens. He wasn't to discover the male of this species for several years yet—it turned out to be the smallest barnacle male known. In the meantime his skills at dissection got steadily better, helped by Hooker's recommendations for improving the optics of his microscope. In one letter he thanked Hooker thrice over: for helping with the microscope, for suggesting he use porcupine quills instead of glass tubes in dissection, and for the gift of "capital" chutney. Between the three, "I have many daily memorials of you," he joked, and proudly reported that he devised a set of wood blocks to support his wrists while dissecting, "a splendid invention." He was excited with his new cirripede hobbyhorse. "As you say," he wrote to Hooker, "there is an extraordinary pleasure in pure observation . . . After having been so many years employed in writing my old geological observations it is delightful to use one's eyes & fingers again."[32]

This was November of 1846, and the Darwin household was growing in more ways than one: he and Emma enlarged the house over the past year to include a schoolroom and two bedrooms, as their family had grown to four children (1-year-old Georgy, 3-year-old Etty, 5-year-old Annie, and 7-year-old Willy)—and counting, with baby Bessy joining the family in July of 1847. By this time Darwin was deep into his barnacle work, and although he took some time to attend scientific meetings in London and Oxford now and then what he loved best was the "absolute rurality" of Down. His friends loved it too, and he regularly invited them for scientific respites from London. It was an idyll compared to the noise, smoke, and grit of the city, though at times it must have seemed almost as crowded: besides growing family and domestic staff there was a near-constant procession of visiting scientific friends (often with their wives and children) and relatives such as Charles's brother 'Ras (despite professing to hate country life) and other siblings and their families. Their Aunt Sarah Wedgwood also made frequent appearances, having moved to the village of Downe to be close to Charles and Emma. Darwin loved the conviviality of family and friends, but it was also understood that he had to often retreat to his study, where he would "do his barnacles" in peace.

The following year, 1848, brought joy, sadness, and excitement: Franky, the latest addition to the family, came along in August, but just a few months later Darwin's father, Dr. Robert Darwin, died in Shrewsbury. The excitement came from his most startling barnacle discoveries yet: while most barnacle species were hermaphrodites bearing both male and female sexual organs, he came across one (*Ibla cumingii*) that was not only single-sex, but had males reduced to tiny nubs adhering to the carapace of the comparatively gigantic females. The males were mere rudiments, eyeless, limbless, near-microscopic bags of sperm. This was astonishing: having separate sexes was strange enough, but there was practically nothing to compare with the radical difference in size and development of the two sexes in this species—rather as if human males were reduced to tiny testes adhering to women like ticks. He wrote excitedly to Henslow in April 1848 about the "microscopically minute" males:

> *But here comes the odd fact . . . [the males] become parasitic within the sack of the female, & thus fixed & half embedded in the flesh of their wives they pass their whole lives & can never move again.*

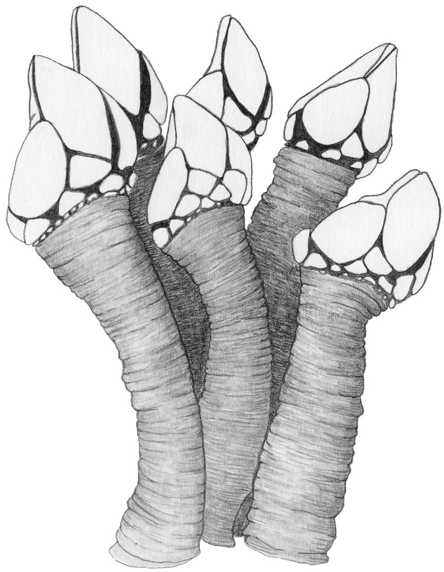
"Is it not strange," he mused, "that nature should have made this one genus unisexual [sexes separate], & yet have fixed the males on the outside of the females—the male organs in fact being thus external instead of internal."[33] It was strange, and things got even stranger when he realized that another barnacle, *Scalpellum*, was both hermaphroditic *and* had tiny "parasitic" males. Now why have these extra, or *complemental* males, as Darwin called them, when male equipment was already built-in, as it were? He wrote excitedly to Hooker: "I had observed some minute parasites adhering to [*Scalpellum*], & these parasites, I now can show, are supplemental males . . . so we have almost a polygamous animal, simple females alone being wanting."[34] He went back and scrutinized earlier specimens, rightly thinking he may have mistaken diminutive males for the odd parasite, and indeed found several new cases of complemental males. Recall how he had been mistaken about the double penis of what turned out to be Arthrobalanus females. Now he actually found Arthrobalanus males, which turn out to be the minutest of minute complementals but equipped with a penis nearly nine times the length of the male's body.

It dawned on him that the sexual strategies of these barnacles were of tremendous significance: no less than evidence of an evolutionary differentiation from hermaphrodites into males and females. Animals and plants were initially hermaphroditic, he began to think, then slowly differentiated over eons into the two-sex arrangement so common today. *Why* was another matter, but this explained anomalous features of anatomy like the nonfunctional nipples of male mammals or rudimentary stamens of female flowers, and it dovetailed with a growing insight from his studies of reproduction and pollination (see Chapters 6 and 7); namely, that nature abhors perpetual self-fertilization. How and why the sexes formed was yet another exciting line of investigation. Something like a grand unified theory of life's evolution driven by natural selection was taking shape in his mind. "I never [should] have made this out," he exclaimed to Hooker, "had not my species theory convinced me, that an hermaphrodite species must pass into a bisexual species by insensibly small stages, & here we have it, for the male organs in the hermaphrodite are beginning to fail, & independent males ready formed." This was the kind of evidence he needed. The odd sex lives of his barnacles may not be a smoking gun for transmutation, but they were not far from it: how else to explain such strange arrangements? It certainly wasn't consistent with the conventional view of perfect design in nature. He half-joked in the same letter that Hooker would "perhaps wish my Barnacles & Species theory al Diabolo [to the devil] together. But I don't care what you say, my species theory is all gospel."[35]

And so it went as he was drawn in deeper and deeper, studying barnacles from every corner of the world. He traced homologies and reconstructed what he thought was the "archetypal" barnacle, showing how its 17 body parts derived from the 21-body-part archetype that the French zoologist Henri Milne-Edwards had identified for Crustacea as a whole. He was astounded by the variation he found, at multiple levels: abundant individual variation, but also unexpected structural and life history variations on a theme, from those puzzling complemental males to groups with elaborate cirri to yet others lacking appendages altogether. Those he classified in their own suborder: "Apoda," the footless barnacles. An "apodal cirripede" may be a contradiction in terms, but as he marveled to Lyell, when it came to barnacles "truly the schemes & wonders of nature are illimitable."[36]

By the time he was through, Darwin had produced the most comprehensive treatment of living and fossil cirripedes yet, culminating in a four-volume set of monographs, two published in 1851 and two in 1854.[37] It was a huge accomplishment, earning him the Royal Society's highest honor, the Royal Medal, in 1853, before the study was even fully published. Some of his interpretations of barnacle anatomy and development did not stand the test of time, but they give us insight into Darwin's early evolutionary thinking and working method. Janet Browne pointed out that the barnacle period marked a sea change in Darwin's awareness of the ubiquity of individual variation. Prior to poring over barnacles he seemed to have had a conception of variation mainly induced by environmental change and other factors acting on the reproductive system. As a result of scrutinizing not just individuals, but *populations* of individuals of many species (albeit populations occupying museum drawers and jars), Darwin gained a new appreciation for the sheer abundance of variability in virtually all traits, great and small. "You ask what effect studying species has had on my variation theories," he wrote Hooker from Malvern, where he was trying to combat his latest bout of illness with the water cure. "I have been struck . . . with the variability of every part in some slight degree of every species: when the same organ is rigorously compared in many individuals I always find some slight variability."[38] He joked that working on systematics would be easy were it not for "this confounded variation," but acknowledged it was a boon for his species theory. It was, after all, the very raw material that selection acted upon, and for selection to shape species as completely as he envisioned, variation must abound in even the most trivial of traits.

In this period, too, Darwin refined a research method that stood him well through all of his subsequent investigations: first, systematic and thorough study, sometimes more experimental and sometimes more observational, but always marked by noticing unnoticed phenomena, asking unasked questions, and connecting dots where others could not see the patterns. Crucially, his method included immersion in the available literature and cultivation of a worldwide network of correspondents: academics and amateurs, aristocrats and humble museum men, ship's captains and army officers—anyone and everyone expert in an area of interest to Darwin or otherwise able to help him was approached to bounce ideas off of and to ask for specimens, observations, and information.



Gooseneck or pedunculated barnacles. Drawing by Leslie C. Costa.

By the time Darwin finished his 8-year barnacle study, his children had gotten used to his scientific work at home. He had seven kids ranging from a teenager of 15 years to a toddler of 3 (there had been eight, but the couple suffered the devastating loss of their eldest daughter, Annie, in 1851). His barnacle work was going on for most to all of the children's lives, depending on the child. Sir John Lubbock, a family friend and neighbor, told an anecdote about this period: when visiting a friend who lived nearby, one of the Darwin boys looked around and, seeing no microscope or dissecting equipment, asked of his friend's dad, "Then where does he do his barnacles?" For all the kids knew, *everyone's* dad worked on barnacles.[39]

Message by Pigeon

Throughout his cirripede odyssey Darwin kept up a number of parallel investigations bearing on his species theory from different angles, "to see how far they favour or are opposed to the notion that wild species are mutable or immutable," he explained to his cousin Fox in March 1855. Central to his researches were, he said, "a number of people helping me in every way & giving me most valuable assistance."[40] Barnacles packed away, he now hoped that Fox would be among the first to assist with his newly rekindled interest in pigeons.

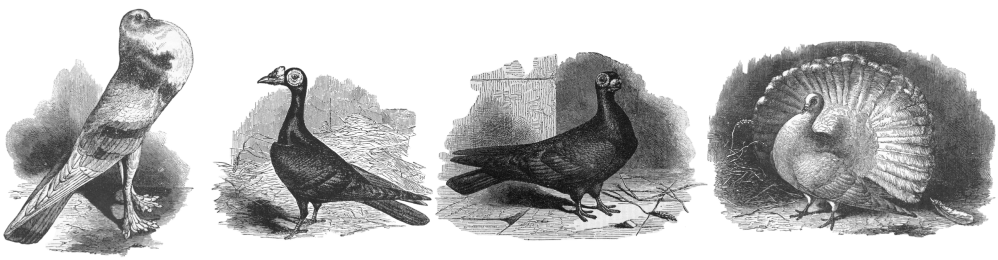
Darwin had long recognized the significance of domestic pigeons for his theory. Back in the late 1830s he even commented in one of his notebooks that pigeons are proof that variation in animals is not limited or constrained: "Analogy will certainly allow variation as much as the difference between species—for instance pidgeons [*sic*]," he wrote.[41] Barnacles may have taken center stage as a diverse and little studied *natural* group of species that he could use to document variation and trace adaptation and descent, but those studies set the stage for the study of a complementary group, one that would serve as an *artificial* case study with its own expression of variation and demonstrated the power of selection. But what to study? Dogs or barnyard animals would not do: too big, and their development too long. His friend William

Yarrell urged him to give pigeons a go. Of course! A group with diverse breeds, yet smallish animals easily kept inexpensively and in quantity, pigeons also grew fairly quickly and had the added bonus of being edible. And when I say diverse breeds, I mean *diverse*: breeds so divergent from one another that they would be easily placed in separate genera, let alone species, were they to be collected and classified by some alien naturalist. There were barbs and fantails, pouters and runts, trumpeters and carriers: pigeons with absurdly, sometimes grotesquely, modified heads, beaks, tail feathers, crops, feet—even behavioral variants like tumblers, with their neurological loose wire that makes them suddenly somersault in midair. Why were these strange breeds developed? Some, like carriers, are "working" pigeons, but pigeon breeding is called "the fancy" for an obvious reason: breeders take a fancy to this or that odd variant, and work diligently to develop it. Back in the mists of time this was probably not deliberate, but in more recent centuries it surely was. He knew pigeons had something to teach us: the often-absurd varieties and breeds carried a message about the power of selection.

It was conventional wisdom among zoologists that all pigeon breeds descended from just one wild species: *Columba livia*, the ubiquitous rock dove of city parks and country farmyards. Or did they? He was surprised to find that, unlike the zoologists, most fanciers believed that each breed was derived from a distinct wild ancestor. He recognized that this view, if widely held among the general public, would be one of many obstacles he would face in making a convincing case for common descent and the power of selection. But even the zoologists had little concept of *how* breeds were made. They often assumed new varieties appeared more or less fully developed, anomalous sports like the odd yellow rose popping up on a red rose bush. Their view is expressed by the prolific naturalist Daniel Jay Browne in his 1850 book *The American Bird Fancier*: "It is from the wild rock pigeon, (*C. livia*) that all those numerous varieties . . . of the common inhabitants of the dove cot have descended," and that "the greater part of them owe their existence to the interference and art of man; for, by separating them from the wild rock pigeon, such accidental varieties as have occasionally occurred . . . and by assorting and pairing them together, as fancy or caprice suggested, he has, at intervals, generated all the various races."[42] Darwin would have read "variations" for "varieties," variations that are more minute and abundant than Browne might have imagined. Subjected to Sebright's "judicious selection," variation upon variation leads to cumulative change over time.

Darwin was sure that the many breeds did not simply represent the domesticated descendants of a like number of ancestral wild species. Certainly the fossil record did not support a profusion of wild canines, bovines, and equines, for example, but maybe at most a few wild progenitors. (Indeed, recent DNA analysis shows that modern cattle, sheep, pigs, and goats likely descend from only two or a few ancestral species or subspecies each.) Darwin needed to prove this for pigeons. Luckily, by this time the use of embryology and development to inform classification was well appreciated, largely thanks to Henri Milne-Edwards's important *Essay on Classification* of 1844. Darwin studied Milne-Edwards while working on his barnacles. Now he realized that by comparing the anatomy of certain domestic varieties from birth through maturation he should be able to show that breeds were identical in early stages and then diverged from one another at different points in development.

Darwin threw himself into the world of fancy pigeons with charac-



Four of the 16 pigeon breeds kept by Darwin (L to R): the pouter, with enormously inflated crop and foot feathers resembling spats; the English carrier, a sleek and strong-flying homing breed used to carry messages; the barb, with flattened, broad beak and large featherless eye-ring; and the fantail, with permanently fanned tail feathers reminiscent of displaying turkeys. From Darwin (1868), vol. I, figs. 18–21.

teristic enthusiasm, but he didn't go so far as to try to selectively breed them himself. Rather like connoisseurs or knowledgeable critics of fine art who are themselves no artists, Darwin studied and observed and immersed himself in the culture, getting to know fanciers at their meetings and visiting their aviaries and shows. And like art aficionados he became a collector, over the next two years procuring every pigeon breed available in Britain and more from further afield—some 16 breeds in all, over 90 birds cooing away in a veritable pigeon condo erected in the garden at Down House. He joined leading London pigeon clubs—the Philoperisteron and Southwark Columbarian—and gamely reported in a letter to Willy, then age 14 and away at boarding school, his adventures with the "strange set of odd men" that frequented them:

> *I want to attend a meeting of the Columbarian Society . . . I think I shall belong to this Society where, I fancy, I shall meet a strange set of odd men.—Mr Brent was a very queer little fish; but I suppose Mamma told you about him; after dinner he handed me a clay pipe, saying "here is your pipe" as if it was a matter of course that I should smoke. Another odd little man (N.B all Pigeons Fanciers are little men, I begin to think) & he showed me a wretched little Polish Hen, which he said he would not sell for £50 & hoped to make £200 by her, as she had a black top-knot.*[43]

Bernard Brent was a leading pigeon fancier and, odd as he and the other "little men" of the Columbarian were, Darwin respected their expertise and was eager to be coached in the fine points of pigeon breeding.

The following February, 1856, found him as game as ever, writing to William on just having acquired some prize breeds: trumpeters, nuns, and turbits. "I am building a new house for my tumblers," he was excited to report, "so as to fly them in summer."[44] Emma and the four youngest children were away visiting her sisters. It may have been then that Etty's pet cat was quietly dispatched, having developed the habit of eating her father's pigeons—something Etty never quite forgave. At one point Darwin's pigeon mania led to another point of contention: the stench of curing and preparing the skeletons led to his pigeon lab being banished as far from the house as possible. Darwin, with his butler, Parslow, presided over the foul witch's cauldrons of pigeon skeletons until even they couldn't take it any longer, and he resorted to outsourcing the skeleton preparations. Owing (once again) to his network of friends and contacts, in short order he assembled an impressive set of skeletons of nearly every breed available in England and beyond.

Indeed, specimens alive and dead arrived daily at Down House, each of which he examined minutely. William Tegetmeier, sometime London writer, editor, beekeeper (as we shall see in Chapter 4), and pigeon fancier was a big help: "Many thanks for your offers about dead Pigeons," Darwin wrote him. "If Scanderoon dies please remember I should wish carcase [*sic*] sent per coach by enclosed address as soon as possible to arrive fresh."[45] His old college friend Thomas Eyton, who developed a sizable collection of bird skins and skeletons at his family estate, also obliged. Darwin explained to Eyton that he had taken up his pigeon project to compare the structure of pigeons at different stages of development; "I mean to try to get Domestic Pigeons from all parts of the world." It wasn't all one-way, of course: there was a gentlemanly exchange of specimens and information, as when Darwin proffered the preserved head of a Chinese breed of dog for Eyton's study of dog skeletons: "I am delighted to hear that you are at dogs; it will be splendid for my work individually, & I am sure most desirable for Science. I have somewhere, I am almost certain, the head of a Chinese Dog: would you like to have this?" (He wrote a week later that he seemed to have misplaced it: "I have been looking everywhere for the Dog's Head. . . . I am vexed at this.")[46]

A Delightful Commencement

Barely a month before Darwin first expressed his pigeon fancy to Fox back in March 1855, a naturalist little known to Darwin, one Alfred Russel Wallace, was waiting out the rainy season in a small bungalow in Sarawak, in northern Borneo. Wallace passed the time gathering his thoughts on the striking parallel between species relationships geographically, in terms of their distribution on earth, and geologically, in terms of their distribution over time in the fossil record. He dashed out an essay and at the first opportunity mailed it off to London. Published the following September, this essay concluded that "*every species has come into existence coincident both in space and time with a pre-existing closely allied species.*" The principle became known as the Sarawak Law. Its evolutionary implications were clear to nearly all except Darwin: impressed, Lyell urged his friend to make haste and publish his species theory. Darwin was less impressed, maybe because he thought of Wallace as a mere collector. Expanding his interest to poultry, and adding chicken, duck, and turkey breeds to his menagerie, Darwin had evidently written Wallace to ask for specimens from southeast Asia. In late summer 1856 Wallace enclosed instructions with his latest consignment bound for London: "The domestic duck var[iety] is for Mr. Darwin & he would perhaps also like the jungle cock, which is often domesticated here & is doubtless one of the originals of the domestic breed of poultry."[47] Wallace also wrote Darwin directly, and in his reply Darwin alluded to the Sarawak Law paper, praising it in cautious terms and remarking "I can plainly see that we have thought much alike," but he was coy about his own interests in species and varieties. He reiterated his desire to obtain "any curious breed" of poultry, and mentioned that Sir James Brooke, the "White Rajah" of Borneo, had kindly sent him pigeons, fowl, and cat skins.[48]

But Wallace was more than a collector. He was a confirmed transmutationist who collected in order to fund his travels investigating the "species question." Having spent four years in Amazonia, he had just recently embarked on what was to become an 8-year odyssey crisscrossing the vast Malay Archipelago stretching from Singapore and Malaysia in the west to Papua New Guinea in the east. Little did Darwin know that in a short couple of years Wallace would succeed in his quest to find the mechanism of species change, natural selection. In the meantime, Darwin began to work away at his big species book, to be entitled

Natural Selection. He progressed steadily, and by coincidence he just started writing up a section on pigeons in 1858 when a bombshell of a package from Wallace arrived, with a manuscript that laid out a formulation of natural selection. The brevity of Darwin's journal entry speaks volumes: "June 14th Pigeons: (interrupted)."[49] He was devastated.

The ensuing weeks were an emotional maelstrom as Darwin appealed to his friends Lyell and Hooker for help preserving his priority and honor even as his youngest child, baby Charles Waring Darwin, fell dangerously ill; he felt self-loathing for even caring about theories and priority at such a time. His friends hastily arranged for excerpts of Darwin's unpublished outlines of the theory from the 1844 *Essay* and other sources to be read at the Linnean Society, along with Wallace's paper. The papers were read on July 1st, but neither Wallace nor Darwin were present—Wallace still halfway around the world, and Darwin attending the funeral of his son. Within a few weeks, Darwin had regained enough composure to write Wallace explaining what had transpired. He then buckled down to finish his book and cement his priority. He was relieved to hear back that Wallace was delighted with all Darwin had accomplished thus far. Darwin knew he had to get his book out, but also knew that *Natural Selection* would take too long to complete. By the fall of 1858 Darwin resolved to pare it down. His "abstract," as he called it, would become *On the Origin of Species*. Lyell recommended his own publisher, John Murray of London, and by April 1859 Murray had the manuscript in hand.

He asked a few colleagues to review it. One, the Scottish literary editor Rev. Whitwell Elwin, was singularly unimpressed with all but the section on pigeons. He recommended that Darwin get rid of the rest and produce a work on pigeons instead, smoothing the path for a later book expanding on his more unconventional views. "Even if the larger work were ready it would be the best mode of preparing the way for it. Every body is interested in pigeons," Elwin said to Murray.[50] Darwin was appalled, but was reassured that Murray didn't take the recommendation seriously. Yet Elwin did have a point, in that Darwin *had* deployed his arguments on domestication in the very first chapter as a device to smooth the reception for the ideas of common descent and natural selection in subsequent chapters. Many of Darwin's key arguments about natural selection were more speculative than well supported, and he was painfully aware that the *Origin*, which duly appeared in November of 1859, really *was* an abstract of his aborted big book, lacking the range of examples, data, and citations of authorities intended to make his original book unassailable. The remedy was to come out with more detailed treatments expanding on the main arguments of the *Origin*. In fact, his friend Thomas Henry Huxley encouraged Darwin to do precisely that in the weeks after the *Origin* appeared. Darwin was ahead of the curve: "You have hit on exact plan," he assured Huxley, "which on advice of Lyell, Murray &c I mean to follow, viz bring out separate volumes in detail & I shall begin with domestic productions."[51]

Domestication was the first line of argument in the *Origin*: chapter 1 is all about modification of breeds by artificial selection as an analogy for how natural selection works in nature. He would thus begin with a supporting volume on domestication and follow it with a second volume dedicated to the case for natural selection (corresponding to *Origin* chapters 2–4), and then a third reflecting the rest of the book, tackling difficulties and detailing the empirical patterns evident in nature, from fossils to behavior to geographical distribution to comparative anatomy and more, a galaxy of dots neatly connected and facts explained by descent with modification by natural selection.

Darwin only produced the first of this projected series, and even that took nearly a decade: *The Variation of Animals and Plants Under Domestication* was published under Murray's imprint in 1868. What had been treated in a single chapter in the *Origin* was now two volumes, and Darwin's beloved pigeons, covered in a dozen pages in the *Origin*, now had two chapters of their own. Darwin's strategy in these chapters is worth noting: in the first he detailed the characteristics of breeds, highlighting their diversity and rich variation in characters such as beak and skeleton relative to the rock pigeon as "parent-form." Having made a convincing case for variation on a par with what naturalists would ordinarily associate with different genera, in the second chapter he then argued for a single origin of these breeds in all of their breathtaking diversity, culminating in a long final section entitled "Manner of formation of the chief races"—selection, both unconscious and methodical. It is here, in Darwin's treatment of pigeons, that we find the only evolutionary tree ever produced by Darwin for any group of organisms. If domestic breeds in general represented a case study or microcosm of common descent and the power of selection in nature, for Darwin pigeons were a case study of a case study.

By 1868 Darwin was able to do for pigeons what he could not or would not do for barnacles in the 1850s: namely, trace an explicit evolutionary heritage. Why? It may have been the times; in those pre-*Origin* years of barnacle work he was perhaps simply unwilling to tip his hand and publish something too obviously (and controversially) transmutational before he was ready. But, perhaps, in an important respect, barnacles may have set the stage for this pigeon family tree—and indeed helped set the course for Darwin's subsequent life's work. It is ironic that his barnacle work is sometimes portrayed as a distraction that sidetracked Darwin from publishing his species book. On the contrary it was, first, the study that clued Darwin in to the sheer abundance of variation in all points of anatomy—that all-important ingredient for selection to act upon—and the variation he subsequently sought out in pigeons. Second, barnacles were his first overtly *evolutionary* investigation, one that saw the denouement of a new working method that entailed meticulous study, understanding the oddities of barnacle biology in terms of an evolutionary history, and, very importantly, developing a worldwide network of expert contacts that he could appeal to for assistance of all kinds. Darwin's investigations of barnacles and pigeons may not have been experimental in nature, but illustrate a related working method no less important for us to understand the experimentiser.

Experimentising: Doing Your Barnacles

Of the many lessons that Darwin learned in his studies of barnacles and pigeons, perhaps the most important was gaining an appreciation for variability and how related groups of species represent variations on a theme: relationships can be traced by observing the same parts modified in different ways. To explore this idea in a hands-on way, "do your barnacles" like Darwin with these dissections.

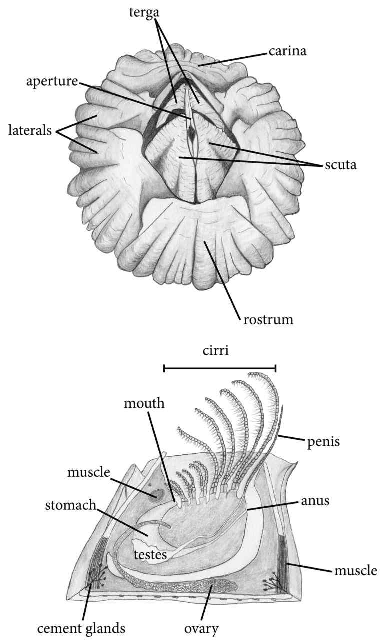
A. Materials

- Notebook and pencil
- Barnacles (acorn and/or gooseneck)
- Limpets (optional, for comparison)
- Dissecting microscope or good hand lens
- Forceps or tweezers
- Pipet or eye dropper
- 2 in. (5 cm) C-clamp
- Shallow pan or tray for dissection (a shallow sardine tin with wax bottom works well; just melt some paraffin wax and pour enough to coat the base of a cleaned sardine can with about 1/10 in. [¼ cm] of wax)
- Glass microscope slides
- Scissors (small and sharp)
- Paper towels

Note on obtaining specimens: If you don't live near the ocean, barnacles and limpets can be obtained through biological supply houses. Ward's Natural Science (www.wardsci.com), www.biologyproducts.com, and www.onlinesciencemall.com sell preserved gooseneck barnacles (generally genera *Pollicipes* or *Lepas*), and Carolina Biological Supply (www.carolina.com) offers the Carolina™ Barnacle Cluster—live acorn barnacles. Limpets, single-shelled grazing snails, can be bought online from saltwater aquarium suppliers (e.g., www.reefcleaners.org and www.liveaquaria.com).

B. Procedure

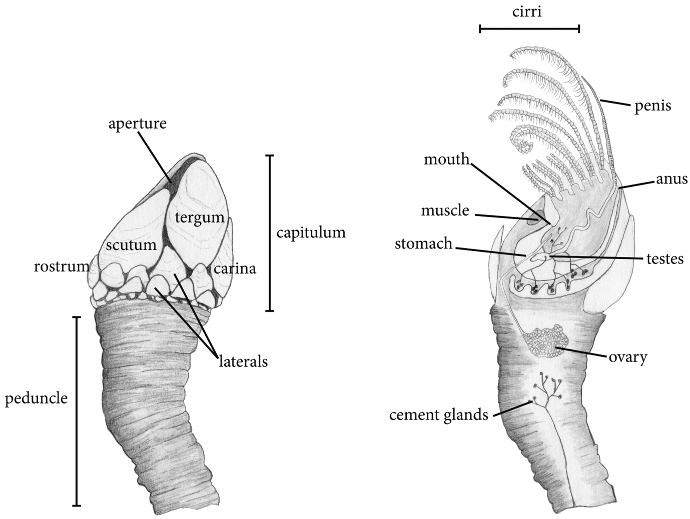
1. Select an **acorn barnacle**. Note that the barnacle's exoskeleton is shaped like a volcano, with a set of six overlapping and rigid calcareous *carinal* or *wall plates* surrounding the barnacle within. Can you identify all six plates?
2. Which way is up? Acorn barnacles are affixed to the substrate on their *dorsal* side, so the "crater" of the barnacle volcano is its *ventral* side.
3. Inside the "crater" are four movable plates called the *opercular plates* (the door is the *operculum*). The two larger kite-shaped plates of the operculum, one on each side, are called *scutal* plates. Adjacent to these are two *tergal* plates, held more or less vertically and so seen edge-on at the top. The opercular plates are opened and closed with muscles.
4. The slit-like opening formed when the operculum is open is the *aperture*. The upside-down barnacle extends its long modified legs (*cirri*), which are feeding organs, through the aperture when feeding.
5. Gently push the operculum open with forceps, and observe the interior with a hand lens or dissecting



External and internal anatomy of a generalized acorn barnacle. Drawing by Leslie C. Costa.

microscope. The space within the aperture is called the *mantle cavity*, a term associated with mollusk anatomy. (This is a holdover from a time when barnacles were classified as mollusks. Note the superficial similarity of the Acorn barnacle to the **limpet**, if one is available, which is a mollusk.)

6. Use the C-clamp to loosen the articulations between the adjacent wall plates: carefully place the clamp jaws on opposite sides of the shell and apply pressure slowly until the wall plates give way and separate. Remove the clamp and repeat at intervals around the circumference until all the plates are loose.
7. Carefully remove one or two of the wall plates, and the opercular plates. Sketch the scutal and tergal plates.
8. Within the mantle cavity, note the appendages arising along the ventral (upper!) surface of the body; these are the cirri. How many pairs are present? (You should find six pairs.)
9. Carefully remove one of the cirri (singular: cirrus), and note that it has two arms (*biramous*). Place a cirrus on a glass slide and apply a drop of water to observe the fringe of hairs, or *setae*. Three of the paired cirri capture food particles in the water column, while the other three function to scrape the particles into the mouth. There are many excellent video clips online showing how the cirri function in feeding, such as this one at the Snail's Odyssey website: www.asnailsodyssey.com/VIDEOS/BARNACLE/barnacleFeed.html.
10. Select a stalked **gooseneck barnacle**. The first difference to note with respect to acorn barnacles is the *peduncle*, or stalk. This functions mainly for attachment but does house muscles and ovaries. (The peduncle of some species is covered with small round calcareous plates called *ossicles*.) Atop the peduncle is the part you think of as the barnacle proper: the *capitulum*.
11. Note that the exoskeleton is flexible; it consists of a thin membrane of chitin (the material that forms the exoskeleton of most arthropods) and protein.
12. Orient yourself to gooseneck barnacle structure starting from



External and internal anatomy of a generalized gooseneck barnacle. Drawing by Leslie C. Costa.

the aperture at the top of the capitulum. As in acorn barnacles, the aperture is opened and closed with opercular plates. In gooseneck barnacles, however, these plates are very large and form part of the exterior body wall. The scutal plates are the largest plates, sitting more or less atop the peduncle. The tergal plates are next largest, just above and sometimes slightly to one side of the scutal plates. The largish plate just below the tergum is called the *carina*.

13. Carefully pull open the aperture with your forceps or fingers. Inside is the dark mantle cavity, and you may see the cirri within.
14. The pointy tergal side of the body is the posterior of the animal. Placing the barnacle on its side, posterior to the right and peduncle toward you, use the scissors to carefully cut the membrane *between* the large plates, taking care not to thrust the blade of the scissors more deeply than necessary to cut the membrane.
15. Lift the cut membrane with the forceps. You will find a large muscle running transversely between the scutal plates. This is

the adductor muscle, which controls the aperture. Cut this muscle to free the body wall membrane, and remove this to expose the mantle cavity within.

16. Observe the six pairs of large cirri, each two-branched (biramous). Remove a cirrus at the base and observe the two long and curled branches covered with long setae.
17. Compare the scutal and tergal plates and cirri of the acorn and gooseneck barnacles. These structures are *homologous* between the two barnacle groups, their different morphologies reflecting variation on a theme.

For further dissection, consult the barnacle section of a manual such as *Observing Marine Invertebrates* by Donald P. Abbot (Stanford, CA: Stanford Univ. Press, 1987) or *Invertebrate Zoology: A Functional Evolutionary Approach*, 7th edition, by Edward E. Ruppert, Richard S. Fox, and Robert B. Barnes (Belmont, CA: Thomson, Brooks-Cole, 2004).

See also:

M. Lowe and C. J. Boulter, "Darwin's Barnacles: Learning from Collections," in *Darwin-Inspired Learning*, ed. M. J. Reiss, C. J. Boulter, and D. L Sanders (Rotterdam: Sense Publishers, 2015), 273–284.

"Barnacles" at the Darwin Correspondence Project: www.darwinproject.ac.uk/learning/universities/getting-know-darwins-science/barnacles.