

# **The Variation of Animals and Plants under Domestication**

**by**

**Charles Darwin**

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# The Variation of Animals and Plants

## FOREWORD

by  
Harriet Ritvo

Charles Darwin wrote *On the Origin of Species* in a hurry. He had, it was true, been formulating his ideas and arguments for several decades—since his round-the-world *Beagle* voyage of 1831-1836. These ideas and arguments had been slow to take definitive shape; Darwin had nurtured and reworked them, amassing evidence for what he projected to be a weighty magnum opus. Although he had shared his developing evolutionary speculations with his closest professional colleagues, Darwin was reluctant to publish them on several grounds. He was aware that his theory of evolution by natural selection (or descent with modification) was complex, that it rested on vast but not incontrovertible evidence, and that the chain of his reasoning was not uniformly strong. Further, his conclusions challenged not only the scientific assumptions of many fellow specialists but also the theological convictions of a much wider circle of fellow citizens.

In 1859, Darwin did not feel quite ready to expose his cherished theory to the harsh light of public scrutiny. In the introduction to the *Origin* he confessed that although his work on evolution by natural selection was "nearly finished," he would need "two or three more years to complete it." The *Origin* was, he suggested, merely a stopgap, a schematic "abstract" of a much longer and more fully supported treatise yet to come. He had been moved to preview his labors in this way, he explained, because his health was "far from strong" and, perhaps more importantly, because Alfred Russel Wallace, a younger naturalist working in isolation in southeast Asia, had sent a paper to the Linnean Society of London in which he "arrived at almost exactly the same general conclusions that I have on the origin of species." If Darwin had not gone public with his theory at this point, he would have risked losing credit for the work of many years.

As its reception showed immediately and has continued to show, the *Origin* benefited from the succinctness imposed by circumstances. Darwin himself may have appreciated this point; at any rate, he never produced the massive treatise, although he repeatedly issued revised editions of the *Origin*. But he did not abandon his intention to buttress his initial schematic presentation with additional evidence. In the course of the next two decades he published several full-length elaborations of topics summarily discussed in the *Origin: The Variation of Animals and Plants under Domestication; The Descent of Man, and Selection in Relation to Sex; and The Expression of the Emotions in Man and Animals*. In addition to fleshing out the *Origin*, these subsequent studies bolstered its arguments and responded to questions raised by critical readers, especially pragmatic questions about the way that descent with modification actually operated.

In *The Variation of Animals and Plants under Domestication*, which appeared first in 1868 and in a revised edition in 1875, Darwin developed a theme to which he had accorded great rhetorical and evidentiary significance. He had begun the *Origin* with a description of artificial selection as practiced by farmers, stock breeders, and pet fanciers, thus using a reassuringly homely example—one recognizable by the general public as well as by members of the scientific community—to introduce the most innovative component of his evolutionary theory. In addition, domesticated animals and plants, because they were numerous and available for constant observation, provided a readily available body of evidence.

Reassuring as it was, the analogy between natural and artificial selection was far from perfect. The point of Darwin's analogy was to make the idea of natural selection seem plausible by characterizing it as a grander version of a well-known process while emphasizing its efficiency and shaping power. He noted, for example, that some of the prize birds bred by London pigeon fanciers diverged so strikingly in size, plumage, beak shape, flying technique, vocalizations, bone structure, and many other attributes, that if they had been presented to an ornithologist as wild specimens, they would unquestionably have been considered to represent distinct species, perhaps even distinct genera. Darwin argued that if the relatively brief and constrained selective efforts of human breeders had produced such impressive results, it was likely that the more protracted and thorough-going efforts of nature would work still more efficaciously.

But as Darwin acknowledged, there were some fairly obvious reasons why the two processes might diverge. The superior power of natural selection—"Man can act only on external and visible characters: nature . . . can act on . . . the whole machinery of life. Man selects only for his own good; Nature only for that of the being which she tends" (*Origin*, chap. 5)—might constitute a difference of kind rather than of degree, as might the much greater stretches of time available for natural selection. Further, although the mechanism of the two processes appeared superficially similar, their outcomes tended to be rather different. Natural selection produced a constantly increasing and diversifying variety of forms; it never reversed or exactly repeated itself.

Anyone familiar with artificial selection would have realized that, although new breeds were constantly being developed and although neither improved wheat nor improved cattle showed any tendency to revert to the condition of their aboriginal wild ancestors, the strains produced by human selection were neither as prolific nor as durable as those produced by nature. Indeed, the animals and plants celebrated as the noblest achievements of the breeder's art were especially liable to delicacy and infertility. Highly bred strains, long isolated from others of their species to preserve their genealogical purity, far from serving as a springboard for further variation, often had to be revived with infusions of less-rarefied blood. Yet any relaxation of reproductive boundaries threatened subsidence into the common run of conspecifics.

Darwin firmly connected *Variation* to the *Origin* by devoting its introduction to an overview of his theory of evolution by natural selection. In particular, the two volumes of *Variation*, clumsily organized and packed with zoological and botanical detail,

addressed some of the difficulties inherent in the attractive but paradoxical analogy between natural selection and artificial selection. For selection of any sort to operate, diversity already had to exist. With wild populations living under natural conditions, however, diversity was difficult to discern. It was widely believed that a heightened propensity to vary (at least in ways obvious to human observers) was one of the few general characteristics that differentiated domestic animals as a group from their wild relatives. This point was conventionally illustrated with reference to coat color and design. American bison, for example, were, on the whole, brown, and all Burchell's zebras shared similar black and white stripes. A single herd of either *Bos taurus* or *Equus caballus* (domestic cattle or horses), on the other hand, could display colors ranging from white through yellow, red, and brown to black, as well as a variety of spotted and blotched patterns.

In order to demonstrate that such populations spontaneously produced sufficient variation to support artificial selection, Darwin devoted most of the first volume of *Variation* to a species-by-species survey of domesticated plants and animals. He began with the dog, the breeds of which differed so greatly in size, shape, disposition, talents, and every other characteristic that Darwin attributed its exemplary plasticity to its derivation from several different species of wild canines. Domestic cats, on the other hand, differed relatively little from one another, at least, their variation tended to be individual, rather than consolidated into breeds. Darwin attributed this to the minimal influence exerted by cat owners over the mating behavior of their animals, so that, alone among fully domesticated animals, cats could not be said to have undergone a genuine process of artificial selection.

Farmyard ungulates, however, had all proved more susceptible to human manipulation, whether through the gradual enhancement of inherent tendencies, such as the relatively early maturation that distinguished shorthorn cattle, or through the preservation of spontaneously arising monstrosities, such as the short, broad foreheads and protruding lower jaws of the niata cattle of South America, the bulldogs of the bovine world. Among animals, fancy pigeons, with their short generations, devoted breeders, and lack of any pragmatic constraints on their extravagant deformations, provided Darwin with his most abundant material. He allotted less space to his survey of domesticated plants, although, with the exception of trees, they tended to be much shorter lived and more variable even than pigeons. For example, as Darwin pointed out, a single long-cultivated species—*Brassica oleracea*, the ordinary cabbage—had given rise to strains as distinctive as Brussels sprouts, cauliflower, broccoli, and kohlrabi.

Darwin crammed in so much information of this sort that, in order to confine *Variation* to two volumes of manageable size, less crucial evidence was relegated to a smaller typeface. And so compendious was his survey of domesticates that he felt constrained to deny that it was intended to be an exhaustive catalog. After all, many such catalogs, devoted merely to the accumulation of species- or breed-specific data, existed already; Darwin cited them generously in his footnotes. The material included in *Variation* had been chosen to fulfill a more focused argumentative purpose. Darwin's theory of descent with modification required something further than the simple demonstration that

abundant variation existed among domesticated animals and plants. The accumulated experience of naturalists and breeders offered no clear explanation of the causes of variation; indeed, no consensus existed on this issue. Variation under domestication was frequently attributed to accidental external influences, especially climate and food. But environmentally induced variation was not of much use to Darwin. Instead, he sought evidence not only that the tendency to vary was inherent in domesticated animals and plants but also that specific variations were inherited.

As a result, Darwin's wealth of detail in *Variation* disproportionately featured strong—as well as puzzling, problematic, or even questionable—versions of inheritance, in addition to the unsurprising, if still not completely understood, likelihood that children would resemble their parents. For example, he devoted an entire chapter to what he termed "atavism" or "reversion"—that is, the tendency for offspring to manifest traits apparently derived from their grandparents, collateral relations, or even remote ancestors, rather than from their mothers or their fathers. The existence of this tendency in the lineages of individuals, he argued, incontrovertibly demonstrated the fact of heritability; and in an extended or exaggerated version it also demonstrated evolutionary relations between species. Thus, many breeds of domesticated chickens revealed their ultimate ancestry by producing occasional sports with the red and orange plumage of the original *Callus bankiva*, or jungle fowl.

Like many other naturalists of his time, Darwin was receptive to the idea of telegony, also known as "the influence of the previous sire." He retailed the famous story of Lord Morton's mare, a chestnut of seven-eighths Arabian blood, whose first foal had been sired by a quagga (a now-extinct relative of the zebra) her owner was attempting to domesticate. It was not surprising that the young hybrid faintly echoed his father's stripes, but the fact that her next two foals, both sired by a black Arabian horse, also seemed to resemble the quagga in this regard, was more remarkable. Darwin pointed out that atavism offered one possible explanation of this phenomenon—infant horses and donkeys often showed evanescent striping, which might indicate the pattern of their ancient shared progenitor—but he was also drawn to the notion that the first male to impregnate a female left some permanent, heritable trace of himself behind.

He offered analogous examples from the vegetable kingdom, where the pollen of related varieties of apples, corn, or orchids, could not only produce hybrid offspring but occasionally also physically alter the reproductive tract of the female. Plants also, and more regularly, demonstrated a kind of variability that could arise independently of sexual reproduction, such as "bud variation," whereby what Darwin called a "monstrosity" might appear on a single branch or flower and then be transmitted, sexually or asexually, to future generations.

As he documented the profusion of variation among domesticated animals and plants, and the tendency of organisms to transmit these variations down the generations, Darwin did more than demonstrate that there was ample grist for the mill of natural selection. He also addressed the most serious weakness in the argument of the *Origin*. Despite the incompleteness of the fossil record, plenty of evidence suggested that evolution had taken

place; indeed the idea of evolution had been current in one form or another for a century before 1859. Darwin's explanation of the way that natural selection should operate was also widely persuasive. The competitive metaphors with which he characterized it, especially the "struggle for life" prominently featured in the *Origin's* subtitle, fit well with Victorian understandings about how things worked in the human arenas of industry, commerce, and geopolitics. There was, however, a problem that troubled those inclined to sympathize with Darwin's reasoning as well as those inclined to reject it. The efficacy of natural selection, like that of artificial selection, depended on the inheritance of particular traits. But before the modern understanding of genetics became available, no satisfactory mechanism had been adduced to explain this phenomenon.

No consensus yet existed about the way that sexual reproduction worked, so there was also disagreement about which characteristics were inherited and which were the result of environment, and what could be contributed by the male as opposed to the female parent, let alone why offspring sometimes resembled a grandparent or some more distant relative rather than their parents. The special difficulty of accounting for the sudden emergence of monstrosities, or even less dramatically novel traits, led Darwin, in later editions of the *Origin* as well as in *Variation*, to become increasingly receptive to the notion that characteristics acquired by one generation might be inherited by the next.

In the penultimate chapter of *Variation*, Darwin attempted to strengthen the weak link in his chain of argument by proposing a mechanism for inheritance. He called his theory "pangenesis," and he claimed that it explained not only ordinary inheritance—the influence of parents on their children—but also reversion, telegony, the regeneration of amputated limbs in some kinds of animals, the inheritance of acquired characteristics, and the relationship between sexual and asexual modes of reproduction and inheritance. The operation of pangenesis depended on the posited existence of unobservable units that Darwin called "gemmules," tiny granules that were thrown off by individual cells and then circulated through the body.

They had, however, an affinity for each other, which led to their aggregation in the reproductive organs or in parthenogenetic buds. They could remain latent for years, until an organism reached a certain stage of development, or for generations, until they encountered other gemmules to which they bore some special relationship. In this way a long-dormant greatgrandparental gemmule might suddenly manifest itself in a child. Since gemmules could be altered by environmental influences, they could convert acquired characteristics into the stuff of heredity. And since they were vulnerable to error, they could occasionally make mistakes, causing organs, such as limbs or tails or even heads, to develop in inappropriate numbers or in the wrong places.

It has doubtless been fortunate for Darwin's reputation that his theory of pangenesis is not as well remembered as his theory of evolution by natural selection. As vague in detail as it was ambitious and comprehensive in scope, it was unpersuasive at the time and has since been proven completely wrong. But like *Variation* as a whole, which similarly illustrated the limitations of its author as well as his strengths, pangenesis does not therefore lack interest or significance. Despite recent excellent and well-appreciated



studies of his entire life and extended *oeuvre* (Janet Browne, *Charles Darwin: Voyaging* [New York: Knopf, 1995] and Adrian Desmond and James Moore, *Darwin* [London: Michael Joseph, 1991], Darwin is known primarily as the author of the *Origin*, which is unrepresentative in its economy of structure, argument, and evidence, as well as on account of its historical notoriety. Its enforced streamlining has helped to preserve the *Origin's* accessibility, but its relative paucity of examples was particularly uncharacteristic of Darwin. *Variation*, with its accumulation of evidence about everything from the webbing between dogs' toes to the weight of gooseberries, was much more typical; in addition, it placed Darwin firmly—indeed, irretrievably—within his time, rather than in an achronological limbo reserved for intellectual heroes. As a graduate student from the People's Republic of China told me several years ago, after having participated in a seminar that read excerpts from *Variation* and *The Expression of the Emotions*, if the leaders of his government knew that Darwin had written such books, he would not be officially admired.

In science as in politics the victors tend to write the history books. As a result, the record of the past is edited, intentionally or unintentionally, so that it focuses mainly on the precursors of contemporary orthodoxy. Such a focus may accurately represent the genealogy of modern ideas, but it almost inevitably misrepresents the historical experience of their progenitors. Viewed without the benefit of hindsight, the marketplace of Victorian ideas seemed much more competitive than it does to us.

Even the powerful, persuasive, and ultimately triumphant theory of evolution by natural selection required not only defense, but repeated buttressing and revision. *Variation* showed Darwin hard at work on this rearguard action, using the materials he had at hand—for the most part, homely details about the domesticated animals and plants with which his audience was most familiar. His information was gleaned from the observations of fanciers, breeders, and amateur naturalists, as well as from the treatises of those on the cutting edge of zoology and botany. As hindsight narrows the historical spotlight, it imposes its own sense of hierarchy on the preoccupations of the past. But Darwin was interested in all of these topics, valued all of these sources, and belonged, to a greater or lesser extent, to all of these communities.

The author of *Variation* was a Victorian country gentleman, a lover of dogs and horses, a breeder of pigeons and peas. He was also, and equally, the author of *On the Origin of Species*.

## **PREFACE TO THE SECOND EDITION**

During the seven years which have elapsed since the publication in 1868 of the first edition of this Work, I have continued to attend to the same subjects, as far as lay in my power; and I have thus accumulated a large body of additional facts, chiefly through the kindness of many correspondents. Of these facts I have been able here to use only those which seemed to me the more important. I have omitted some statements, and corrected

some errors, the discovery of which I owe to my reviewers. Many additional references have been given. The eleventh chapter, and that on Pangenesis, are those which have been most altered, parts having been remodelled; but I will give a list of the more important alterations for the sake of those who may possess the first edition of this book.

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