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Darwin's Originality

Peter J. Bowler

Charles Darwin's theory of natural selection has been hailed as one of the most innovative contributions to modern science. When first proposed in 1859, however, it was widely rejected by his contemporaries, even by those who accepted the general idea of evolution. This article identifies those aspects of Darwin's work that led him to develop this revolutionary theory, including his studies of biogeography and animal breeding, and his recognition of the role played by the struggle for existence.

The publication of Charles Darwin's *On the Origin of Species* in 1859 is widely supposed to have initiated a revolution both in science and in Western culture. Yet there have been frequent claims that Darwinism was somehow "in the air" at the time, merely waiting for someone to put a few readily available points together in the right way [for instance (*1*)]. The fact that Alfred Russel Wallace (Fig. 1) independently formulated a theory of natural selection in 1858 is taken as evidence for this position. But Darwin had created the outlines of the theory 20 years earlier, and there were significant differences between the ways in which he and Wallace formulated their ideas. In this essay, I argue that Darwin was truly original in his thinking, and I support this claim by addressing the related issue of defining just why the theory was so disturbing to his contemporaries.

Darwin was certainly not the first to suggest the idea of evolution as an alternative to the creation of species by God. J. B. Lamarck's theory, published in 1809, had been widely discussed, although generally rejected (*2*–*4*). Robert Chambers's *Vestiges of the Natural History of Creation* of 1844 sparked a debate over the possibility that new species were produced from pre-existing ones in a progressive sequence leading up to humans (*5*). But if the general idea of evolution was not entirely new, Darwin's vision of how the process worked certainly was. Although the theory was eventually paralleled by Wallace, Darwin had conceived its basic outline in the late 1830s, after his return from the voyage of H.M.S. *Beagle*. He worked on it in relative isolation over the next 20 years, until the arrival of Wallace's paper in 1858 precipitated the flurry of activity leading to the publication of the *Origin*.

Historians have quarried Darwin's notebooks and letters to establish the complex process by which he developed his theory (*6*–*9*). Darwin was a highly creative thinker who synthesized a number of key insights, some derived from his scientific work and others from currents circulating in his cultural environment. Few would now accept the claim that evolution by natural selection was in the air. Darwin approached the subject in a way that was significantly different from any of the other efforts being made to explain the history of life on earth. He had a unique combination of scientific interests that alerted him to topics ignored by other naturalists. He certainly drew on ideas widely discussed at the time, but was forced by his scientific interests to use those sources of inspiration in a highly original way.

To some extent, Darwin may have been merely "ahead of his time," anticipating developments that would push other naturalists toward an evolutionary vision during the years he worked in isolation. By the late 1850s, the idea of progressive evolution was widely recognized, and the positive role of individual competition was being articulated by thinkers such as Herbert Spencer (Fig. 1). But key aspects of the Darwinian vision were truly original and would not have occurred to any other naturalist at the time. Here, Wallace provides a good comparison: He too moved toward the idea of branching evolution driven by local adaptation, but even he did not share Darwin's insight that the work of the animal breeders throws light on the process of natural selection.

The theory was both original and disturbing. It was not just that the idea of natural selection challenged the belief that the world was designed by a wise and benevolent God. There was a wider element of teleology or goal-directedness almost universally accepted at the time. Most thinkers—including Jean-Baptiste Lamarck and Chambers—took it for granted that the development of life on earth represents the unfolding of a coherent plan aimed at a predetermined goal. (This assumption is still preserved in the very term "evolution"; the Latin *evolutio* refers to the unrolling of a scroll.) The explanatory framework centered on the theory of natural selection challenged this vision of nature as an orderly pattern of relations.

Darwin's world view was profoundly different because he argued that the adaptation of populations to their local environment was the sole cause of transmutation. Many people found it hard to see natural selection as the agent of either divine benevolence or of a rationally structured cosmic teleology. Selection adapted species to an ever-changing environment, and it did so by killing off useless variations in a ruthless "struggle for existence." This did not seem the kind of process that would be instituted by a benevolent God, especially because its essentially "selfish" nature meant that a parasitic way of life was a perfectly natural adaptive response in some circumstances.

More seriously for the idea of cosmic teleology, Darwin's supposition that the production

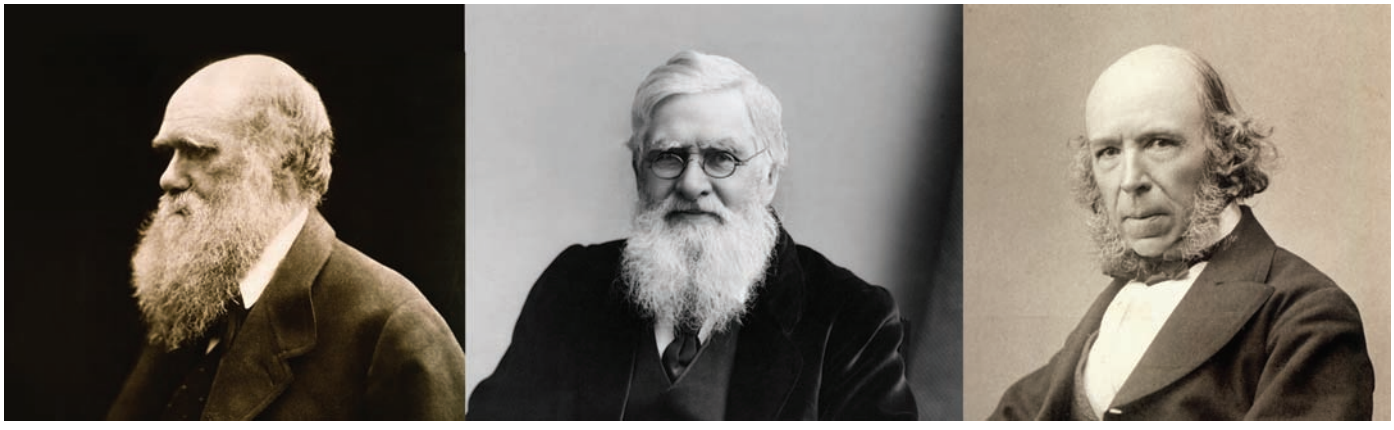

Fig. 1. Charles Darwin, Alfred Russel Wallace, and Herbert Spencer.

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of the individual variants in a population was essentially undirected ruled out any possibility that evolution could be shaped by a predetermined developmental trend. There was no obvious goal toward which it was aimed, and it did not produce an orderly pattern of relations between species. The accusation that the theory depended on "random" variation indicated the concerns of his opponents on this score. As Darwin himself made clear, variation was certainly caused by something (later identified as genetic mutations), but it was not aimed in any one direction and, thus, left adaptive evolution essentially open-ended. He allowed a limited role for variation shaped by the organisms' own activities (the so-called Lamarckian effect), but this too permitted multiple vectors of change. Evolution had to be depicted as a branching tree in which each act of branching was the result of a more or less unpredictable migration of organisms to a new location. At the same time, Darwin's theory undermined the old idea that species were idealized types, fixed elements in a clearly defined natural order. Species had to be treated as populations of varying individuals, with no fixed limit on the range of possible variation.

The Tree of Life

One innovation at the heart of Darwin's theory seems so obvious today that it is hard for us to appreciate just how new and how radical it was at the time. Lamarck had proposed that there might be natural processes adapting species to changes in their environment. But Darwin was perhaps the first to realize that if adaptation to the local environment was the only mechanism of evolution, there would be major implications for the whole system by which species are classified into groups. Darwin's mentor in geology, Charles Lyell, had shown how his uniformitarian theory would allow the biogeographer to reconstruct the migrations of species on an ever-changing earth. Populations could sometimes become divided by geographical barriers, so that what was once a single species could split into multiple branches adapting to separate environments (*10*). Evolution would become a divergent process, with some branches splitting over and over again, whereas others came to a dead end through extinction.

The image of the tree of life had appeared in Darwin's notebooks of the late 1830s (Fig. 2) and was proposed independently by Wallace in a paper published in 1855. Both realized that it explained why naturalists were able to arrange species into groups within groups, using descent from a common ancestor to explain the underlying similarities. Closely related species have diverged recently from a common ancestor, whereas the ancestry of more distantly related forms must be traced further back down the family tree to find the common point of origin.

The idea of common descent now seems so obvious that we might wonder what alternative models could have been proposed to account for the relations among species. Several proposals available in the 1830s deflected attention away from the model of the branching tree (*11*). William Sharp Macleay's quinary or circular system of classification supposed that every genus contained five species that could be arranged in a circle; each family five genera, and so on through the taxonomic hierarchy. Chambers's *Vestiges of the Natural History of Creation* depicted evolution in terms of parallel lines advancing through a predetermined sequence of stages within each family, driven by force derived from individual development.

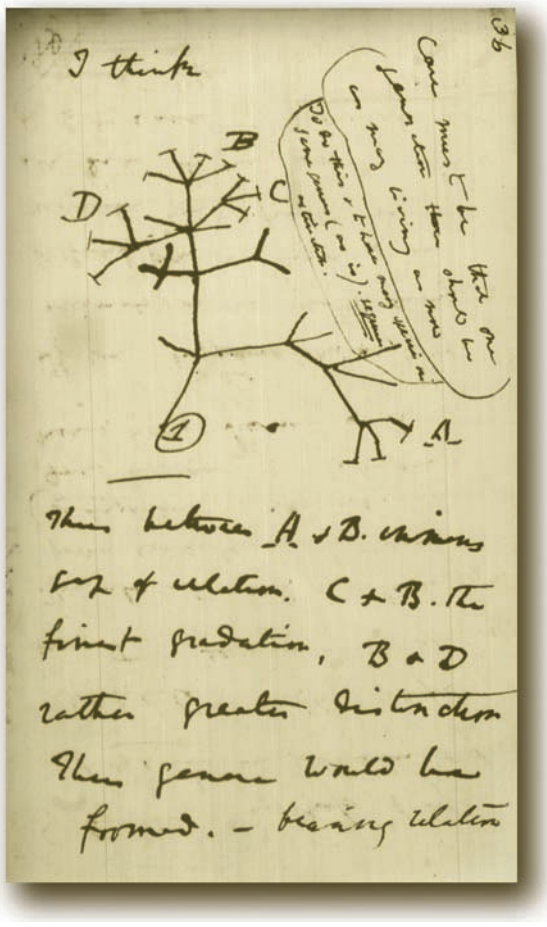

Fig. 2. Tree of Life, from Darwin's notebooks (*22*).

These rigidly structured models of taxonomic relations and evolution made good sense to anyone embedded in a vision of nature as a predictable, orderly system governed by a divine plan. Such a world view made it difficult to accept that the history of life on earth might be essentially irregular and unpredictable, dependant on the hazards of migration, isolation, and local adaptation. Darwin was led toward his alternative model in part because he was more interested in adaptation than cosmic teleology, thanks to the influence of William Paley's natural theology. Natural selection replaced divine benevolence as an explanation of adaptation. Unlike Macleay and Chambers, Darwin did not expect his theory to predict an orderly pattern of relations.

It has been argued that Darwin's move to a more historical viewpoint was inspired by German romanticism [e.g. (*12*)], but a more practical incentive was provided by the biogeographical insights gained on the *Beagle* voyage (1831–36). The Galapagos species provided the most obvious example of how the relations within a group can be explained by supposing that an original population became divided up, in this case by independent acts of migration to oceanic islands. Here, Darwin followed Lyell in seeing that biogeography must become a historical science, explaining present distributions in terms of past migrations, extinctions and (for Darwin but not for Lyell) evolutionary adaptations. Populations divided by geographical barriers will develop independently as each adapts to its new environment in its own way, and the possibility that barriers can be crossed occasionally allows for the branching process of evolution that Darwin conceived in the late 1830s. It was by approaching the problem of the origin of new species through a study of biogeography that Darwin was led to construct his model of open-ended, divergent evolution. Wallace developed a similar model and tested it during his explorations in South America and the Malay Archipelago (modern Indonesia).

Adrian Desmond and James Moore have recently proposed that Darwin's hatred of slavery prompted his move toward evolutionism (*13*). Because many slaveholders argued that the black race was separately created from the white, Darwin wanted to show that all races share a common ancestry, and he realized that this claim could be defended by extending the idea throughout the animal kingdom. As a basis for his thinking, this thesis is sure to generate much controversy, but if accepted it would emphasize the crucial role played by his move toward a model of branching evolution based on geographical diversity.

This model was so radical that many late 19th-century evolutionists were unable to accept it in full. Ernst Mayr argued that the theory of common descent was one of Darwin's greatest achievements, in addition to natural selection itself (*14*). So it was, but I think Mayr overestimated the rapidity with which other naturalists were converted to the theory. Many of the non-Darwinian theories of evolution proposed during the "eclipse of Darwinism" in the late 19th century were introduced with the aim of subverting the implications of the principle of common

descent (*15*). The American neo-Lamarckians Edward Drinker Cope and Alpheus Hyatt proposed that the evolution of each group should be seen as a series of parallel lines moved through the same hierarchy of developmental stages, an updated version of the idea suggested in Chambers's *Vestiges*. The similarities linking the species in a genus were due not to a recent common ancestry, but to parallel trends independently reaching the same stage of development. Like Chambers, they endorsed the recapitulation theory (ontogeny recapitulates phylogeny, in the terminology introduced by Ernst Haeckel) and saw evolution as the addition of preordained stages to ontogeny. Adaptation was not crucial once the basic character of the group was established, and the linear, orthogenetic evolution of the group might eventually generate bizarre nonadaptive characters as a prelude to extinction—the theory of "racial senility." Darwin could make no sense of the theory proposed by Cope and Hyatt, because he could not imagine an evolutionary process driven by predetermined trends. But the fact that such theories flourished in the late 19th century demonstrates just how radical the theory of open-ended, divergent evolution was to the naturalists of the time.

Artificial Selection

These non-Darwinian models were ultimately marginalized by the synthesis of the selection theory and genetics in the early 20th century. Genetic mutations seemed to be essentially pluralistic and undirected, providing just the source of "random" variation that Darwin's mechanism required as its raw material. This later development highlights the importance of another insight gained by Darwin in the late 1830s, his decision to investigate the work of the animal breeders (Fig. 3) and his recognition that their method of artificial selection offered a useful way of understanding how the equivalent natural process operated. The exact role played by Darwin's study of breeding in the formulation of his theory is much debated by historians (*16*–*17*), but there can be little doubt of how important the analogy between artificial and natural selection became in his later thinking. In this case, Darwin was truly unique, because even Wallace did not take this step and dissociated himself from the link with artificial selection expressed in Darwin's later writings.

Darwin turned to the breeders in search of a clue as to how a population could be changed—here at least was a situation where modifications were actually being produced on a human time scale and that could be investigated directly. There was a well-developed network of breeders by this time, and although their ideas about heredity and variation were distinctly pregenetical (like Darwin's own), they had a very clear appreciation of how they produced changes in their artificially small populations. The insight that they worked by selection may have been important (this is the point of contention among experts studying Darwin's notebooks), but the breeders certainly taught him one thing. He realized that in a domesticated population there is always a fund of apparently purposeless and undirected variation among individual organisms. Although convinced that the degree of variability was artificially enhanced under domestication, Darwin, nevertheless, accepted that there must be some equivalent variability in every wild population. The analogy with artificial selection then allowed him to depict natural selection as a parallel process in which a few variant individuals, in this case with characters useful to the species rather than the human breeder, survive and reproduce. Those with harmful characters are eliminated by the struggle for existence, just as the breeder will not permit any animal to reproduce if it does not have the character he wants. It was the breeders who taught Darwin that variation is not directed toward some preordained goal, allowing him to build on his existing conviction that adaptive evolution must be an open-ended, branching process.

At the same time, the breeders' attitude toward variation pushed Darwin toward the view that the species is just a population of interbreeding individuals. Traditionally, species were treated as idealized types with a fixed essence, any variation from the norm being trivial and impermanent. The breeders knew that they could produce huge changes in structure by accumulating normal variations over a number of generations. When Darwin linked this information with his conviction that species could change indefinitely over time, he was driven toward a new form of species concept in which the population becomes paramount. The natural range of variability becomes part of the species' character, not the result of accidental deviations from a fixed norm. This is what Mayr called the transition from typological thinking to population thinking, and although he may have exaggerated the extent to which Darwin himself made the conceptual transition, the subsequent development of the selection theory brought this implication out more clearly.

In the debates that followed the publication of *On the Origin of Species*, the analogy with artificial selection continued to play a key role by forcing even Darwin's critics to think about the problems of heredity and variation in a new way (*18*). Opponents such as Fleeming Jenkin, who saw selection working on large variations or "sports of nature," were, nevertheless, still working within the framework defined by this analogy. For supporters such as Francis Galton, artificial selection helped to clarify the nature of both heredity and selection, paving the way for the revolutionary impact of Mendelian genetics. The notion of "hard" heredity was introduced in opposition to the "soft" form of

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Fig. 3. Pigeons (*23*).

inheritance implied by the Lamarckian process. The undirected nature of variation was clarified both through the study of large populations by Galton and through the breeding studies of the geneticists. Although it took some time for the geneticists to accept the situation, their studies of mutation ultimately endorsed Darwin's claim that the only way the environment could affect the population was by selection. Modern evolutionary developmental biology has reopened the question of whether variation and evolution can be quite as open-ended as Darwin and his followers believed. But the non-Darwinian vision of evolution unfolding to an orderly, predictable plan has been essentially marginalized by acceptance of the key insights on which Darwin based his theory of natural selection.

The Struggle for Existence

One of the most disturbing aspects of Darwin's theory was its appeal to the struggle for existence as the natural process that equates with the breeder's activity as a selecting agent. This very harsh vision of nature certainly threatened the traditional belief in a benevolent Creator. The term "struggle for existence" occurs in Thomas Robert Malthus's *An Essay on the Principle of Population*, although used in the context of tribal groups competing for limited resources. Darwin saw that population pressure would lead to competition between individuals and was perhaps the first to realize that it might represent a means by which the population could change through time (*19*, *20*). The process worked by eliminating the least fit variants within the population and allowing the better adapted to survive and breed. This was what the philosopher Herbert Spencer would later refer to as the "survival of the fittest." Strictly speaking, natural selection requires only differential reproduction among variants, but Darwin thought that the pressure of competition was necessary to make it effective. It seems that without the input from Malthus, he would not have come up with the theory.

The idea of struggle was pervasive in the literature of the period, but could be exploited in many different ways. In the 1850s, Spencer had already seen how competition could be turned into a very different, and in some respects less disturbing, mechanism of progress (*21*). For Spencer, the interaction between individuals stimulated their efforts to adapt to the changing social and physical environment. He then invoked Lamarck's concept of the "inheritance of acquired characteristics" to explain how these self-improvements accumulated over many generations, leading to biological evolution and social progress. Spencer's self-improvement model of progress became immensely popular in the later 19th century, and because it too seemed to rely on struggle as the motor of change, it was often confused with the Darwinian mechanism. In fact, Spencer thought that all humans will eventually acquire the faculties needed to interact harmoniously with one another. But his occasional use of highly individualistic language allowed him to be perceived as the apostle of free enterprise. Much of what later became known as "social Darwinism" was, in fact, Spencerian social Lamarckism expressed in the terminology of struggle popularized by Darwin.

This point is important in the context of the charge raised by modern opponents of Darwinism that the theory is responsible for the appearance of a whole range of unpleasant social policies based on struggle. Darwin exploited the idea of the struggle for existence in a way that was unique until paralleled by Wallace nearly 20 years later. Their theory certainly fed into the movements that led toward various kinds of social Darwinism, but it was not the only vehicle for that transition in the late 19th century. It did, however, highlight the harsher aspects of the consequences of struggle. The potential implications were drawn out even more clearly when Galton argued that it would be necessary to apply artificial selection to the human race in order to prevent "unfit" individuals from reproducing and undermining the biological health of the population. This was the eugenics program, and in its most extreme manifestation at the hands of the Nazis, it led not just to the sterilization but also to the actual elimination of those unfortunates deemed unfit by the state. Did Darwin's emphasis on the natural elimination of maladaptive variants help to create a climate of opinion in which such atrocities became possible?

It has to be admitted that, by making death itself a creative force in nature, Darwin introduced a new and profoundly disturbing insight into the world, an insight that seems to have resonated with the thinking of many who did not understand or accept the details of his theory. Darwinism was not "responsible" for social Darwinism or eugenics in any simple way. After all, some early geneticists endorsed eugenics by analogy with animal breeding even while dismissing natural selection as the mechanism of evolution. And the Nazis wanted to purify a fixed racial type, which they certainly did not want to admit had evolved gradually from an ape ancestry. But by proposing that evolution worked primarily through the elimination of useless variants, Darwin created an image that could all too easily be exploited by those who wanted the human race to conform to their own pre-existing ideals. In the same way, his popularization of the struggle metaphor focused attention onto the individualistic aspects of Spencer's philosophy.

Modern science recognizes the importance of Darwin's key insights when used as a way of explaining countless otherwise mysterious aspects of the natural world. But some of those insights came from sources with profoundly disturbing implications, and many historians now recognize that the theory, in turn, played into the way those implications were developed by later generations. This is not a simple matter of science being "misused" by social commentators, because Darwin's theorizing would almost certainly have been different had he not drawn inspiration from social, as well as scientific, influences. We may well feel uncomfortable with those aspects of his theory today, especially in light of their subsequent applications to human affairs. But if we accept science's power to upset the traditional foundations of how we think about the world, we should also accept its potential to interact with moral values.

References

1. L. Eiseley, *Darwin's Century: Evolution and the Men Who Discovered It* (Doubleday, New York, 1958).
2. P. Corsi, *The Age of Lamarck: Evolutionary Theories in France, 1790–1830* (Univ. of California Press, Berkeley, 1988).
3. A. Desmond, *The Politics of Evolution: Morphology, Medicine and Reform in Radical London* (Univ. of Chicago Press, Chicago, 1989).
4. P. J. Bowler, *Evolution: The History of an Idea* (Univ. of California Press, Berkeley, ed. 3, 2003).
5. J. A. Secord, *Victorian Sensation: The Extraordinary Publication, Reception, and Secret Authorship of Vestiges of the Natural History of Creation* (Univ. of Chicago Press, Chicago, 2000).
6. D. Kohn, Ed., *The Darwinian Heritage*: *A Centennial Retrospect* (Princeton Univ. Press, Princeton, NJ, 1985).
7. J. Browne, *Charles Darwin: Voyaging* (Jonathan Cape, London, 1985).
8. C. Darwin, *The Power of Place* (Jonathan Cape, London, 2002).
9. M. J. S. Hodge, G. Radick, Eds., *The Cambridge Companion to Darwin* (Cambridge Univ. Press, Cambridge, 2003).
10. M. J. S. Hodge, *Stud. Hist. Biol.* **6**, 1 (1982).
11. P. F. Rehbock, *The Philosophical Naturalists: Themes in Early Nineteenth-Century British Biology* (Univ. of Wisconsin Press, Madison, 1983).
12. R. J. Richards, *The Meaning of Evolution: The Morphological Construction and Ideological Reconstruction of Darwin's Theory* (Univ. of Chicago Press, Chicago, 1992).
13. A. Desmond, J. R. Moore, *Darwin's Sacred Cause: Race, Slavery and the Quest for Human Origins* (Allen Lane, London, 2009).
14. E. Mayr, *One Long Argument: Charles Darwin and the Genesis of Evolutionary Thought* (Harvard Univ. Press, Cambridge, MA, 1991).
15. P. J. Bowler, *The Eclipse of Darwinism: Anti-Darwinian Evolution Theories in the Decades Around 1900* (Johns Hopkins Univ. Press, Baltimore, MD, 1983).
16. R. J. Richards, *Stud. Hist. Philos. Sci.* **28**, 75 (1997).
17. M. Ruse, *J. Hist. Ideas* **36**, 339 (1975).
18. J. Gayon, *Darwinism's Struggle for Survival: Heredity and the Hypothesis of Natural Selection* (Cambridge Univ. Press, New York, 1998).
19. P. J. Bowler, *J. Hist. Ideas* **37**, 631 (1976).
20. A. Desmond, J. R. Moore, *Darwin* (Michael Joseph, London, 1991).
21. M. Francis, *Herbert Spencer and the Invention of Modern Life* (Acumen, Stocksfield, UK, 2007).
22. C. Darwin, *Transmutation Notebook D*, from *Natural Selection* portfolio (Cambridge Univ. Library, Cambridge, 1838); P. H. Barrett, P. J. Gautrey, S. Herbert, D. Kohn, S. Smith, transcribers and Eds., *Charles Darwin's Notebooks* (British Museum of Natural History, Cornell Univ. Press, Ithaca, NY, 1987); available at the Darwin Digital Library, http://darwinlibrary.amnh.org/.
23. G. Neumeister, *Das Ganze der Taubenzucht* (B. F. Voigt, Weimar, 1876).

10.1126/science.1160332