

Charles O. Whitman's Theory of Evolution and Pigeons

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20세기 초 진화론의 발달: C. O. Whitman의 정향진화론을 중심으로

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요 약

다윈진화론(특히 자연선택 기제를 통한 진화과정)의 타당성이 쇠퇴되어 가는 20세기 초, 정향진화론은 중요한 대안으로 제시되었다. 미국 생물과학의 근대성을 추진시켰던 시카고 대학의 동물학 교수인 C. O. Whitman은 대표적인 정향진화론자이지만, 그는 동시대의 정향진화론자들과는 다소 그 지적 노선을 달리했다. 난할 중심의 세포연관 연구, 발생에 관한 그의 견해, 그리고 비둘기 날개깃털의 채색 변화의 경향을 종합하여, Whitman은 비둘기 그룹의 정향진화론을 주장했다. Whitman의 정향진화론은 신라마르크 진화론과 돌연변이설에 비판적이었지만, 반면 다윈진화론의 진영에 합류하여, 과학적으로 다윈의 연속변이를 채택하고 수사적으로 다윈의 자연선택을 그의 정향진화론에 적절하게 투영시켰다. 다윈진화론과 비다윈 진화론간의 이분화된 구도 속에서 규정했던 기왕의 진화사학자들과는 달리 Whitman의 정향진화론은 20세기 초 진화론의 복잡한 발달 속에서 이해되어야 한다.

주요어: 다윈진화론, 정향진화론, 위트만, 비둘기 진화패턴, 세포연관, 발생이론, 신라마르크진화론, 돌연변이설

Introduction

At the turn of the twentieth century, the period that Julian Huxley called the "Eclipse of Darwinism," Darwin's theory of evolution by natural selection had not received the support of the majority of the biological science community.¹⁾ Instead, three different theories of evolution emerged as alternatives: Lamarckism, mutationism, and orthogenesis. Because evolutionary theory focused on the problems associated with such factors as selection, adaptation, and variation, scientists could formulate various theories of evolution that reflected varying degree of emphasis on the different factors. Evolutionary biologists commonly used the concept of variation in formulating their theories of evolution, but they had different opinions as to the role variation plays in bringing about evolutionary change. Disputed issues included the continuous vs. discontinuous nature of variations, the linear vs. branching trend of evolution, and the primary force at work in evolution whether selection or adaptation. Also, teleology of evolution was questioned: were variations always useful or useless? As a result, at the turn of the century there were competing theories of evolution that reflected the complex interplay between these factors. Proponents of orthogenesis indicated that evolutionary change occurred in regular and linear trends. They argued that new variation occurred in certain directions controlled by forces internal to the organism (largely reinforced by environmental stimuli). One notable claim that orthogenesisists made was that their theory explained formation of nonadaptive characteristics which other competing theories of evolution could not explain. Perhaps because of the tendency of an internally driving force to result in directed variations, orthogenesis was seen as reestablishing "teleology" or "finalism" in the science of evolution.²⁾ Not all orthogenesisists had the same beliefs, however.

1) For the "eclipse of Darwinism," see Julian Huxley, *Evolution: The Modern Synthesis* (New York: Harper & Brothers Publishers, 1943), pp. 22~28; Peter Bowler, *The Eclipse of Darwinism: Anti-Darwinian Evolution Theories in the Decades around 1900* (Baltimore: Johns Hopkins Univ. Press, 1983).

2) Peter Bowler, *Evolution: The History of an Idea* (Berkeley: Univ. of California Press, 1989), p. 277.

In this paper, I discuss the theory of orthogenesis proposed at the turn of the century by a leading American biologist, Charles O. Whitman (1842-1910). As the first director of the Marine Biological Laboratory at Woods Hole and a professor of zoology at the University of Chicago, Whitman conducted research on pigeons to elucidate the mechanism of evolution. Early in his career, Whitman pioneered American biological research into cell lineage, in an attempt to understand the earliest development of an organism and the genetic continuity of the germ cell. Later, he re-analyzed Ernst Haeckel's biogenetic law (ontogeny recapitulates phylogeny) and made the reverse claim that ontogeny (individual development) was the basis for phylogeny (species development). Based on this theoretical premise, Whitman studied in detail the color pattern variations of pigeon wing feathers. After comparing varieties and species of pigeons, Whitman found that variations in the pigeon feather patterns tended to occur within a particular evolutionary direction, a tendency called orthogenesis by evolutionary biologists. The ideas about linear patterns, continuous variations, and nonadaptive characteristics that Whitman developed in his formulation of orthogenesis were different from those of other orthogenesisists at the time. In his theory of orthogenesis of pigeons, Whitman agreed with other orthogenesisists that directed variation was caused by forces internal to the organism, but disagreed with them in arguing that internal forces were independent of external influences. Instead, by claiming that the Darwinian component of evolution played a subsidiary role in directed variations, Whitman further utilized natural selection as a rhetorical tool to show that orthogenetic change was not teleological.

In the last twenty years, historians have begun to examine Whitman's biological research on pigeons. Richard W. Burkhardt Jr. has focused on Whitman's study of pigeon behavior, and argues that his research program on animal behavior constituted the first attempt to establish the new discipline of ethology in an American context.³⁾

3) Richard W. Burkhardt Jr., "Charles O. Whitman, Wallace Craig, and the Biological Study of Animal Behavior in the United States, 1898-1925," in Ronald Rainger, Keith R. Benson, and Jane Maienschein, eds., *The American Development of Biology* (Philadelphia: Univ. of Pennsylvania Press, 1988), pp. 185-218.

Eminent historians of biology Ernest Mayr and Peter Bowler have discussed Whitman's pigeon research, with particular emphasis on his ideas about evolution. Having discussed the fundamental tenets of Whitman's theory of orthogenesis—"a favored pathway of evolutionary variations set by the inherited genetic and developmental program of organism," Mayr has argued that Whitman's theory anticipated the modern idea of "restriction of variation," which holds that "the potential for variation in a phyletic line is very narrowly prescribed by the existing genotype" of the individual.⁴⁾ Bowler places Whitman's theory of orthogenesis in a historical context. Bowler's discussion of orthogenesis has focussed on the Lamarckian Theodor Eimer, who increased biologists' interest in orthogenesis in Germany, and placed Eimer's orthogenesis in a non-Darwinian framework. Although he has treated Whitman as a "somewhat unorthodox supporter of neo-Darwinism," Bowler does not however sufficiently support this assertion with concrete evidence. His two-page review of Whitman's work does not fully investigate Whitman's concept of orthogenesis.⁵⁾ Stephen Jay Gould has added the most penetrating analysis of Whitman's theory of orthogenesis and attempts to place him in the context of non-Darwinian ideas. Gould states that "I can't help thinking that the history of evolutionary thought might have been different had Whitman lived to promulgate and proselytize his non-Darwinian evolutionary ideas."⁶⁾

This paper, while acknowledging the contribution these historians have made to the study of the Whitman's work, seeks to rectify the relative neglect his pigeon research has suffered in recent scholarship on orthogenesis and to review the framework within which historians view his work. I will argue that Whitman's theory of orthogenesis does not fit into the simple dichotomy of Darwinian vs. non-Darwinian evolutionary theories. Whitman's views on orthogenesis based on pigeon

4) Ernst Mayr, "Charles Otis Whitman," *Dictionary of Scientific Biography* vol. 14 (New York: Charles Scribners Sons, 1974), pp. 313~315.

5) Peter Bowler, "Theodor Eimer and Orthogenesis: Evolution by 'Definitely Directed Variation'," *Journal of History of Medicine* 34 (1979), pp. 67~69; *idem*, *Eclipse of Darwinism*, pp. 159~160.

6) Stephen J. Gould, "What the Immaculate Pigeon Teaches the Burned Mind," *Natural History* (April, 1991), pp. 12~21, on p. 14.

research should instead be considered as theoretically related to his cell lineage research and his belief in the ontogenetic importance of recapitulation, neither of which fits neatly into Darwinian or non-Darwinian alignment.

Having thoroughly read the theories of development and heredity available in his time, Whitman believed that the primordial germ cell formed the basic organization of an organism and dominated its development and heredity as well. Arguing that in the fertilized egg the germ cell's genetic continuity was barely affected by external influences, Whitman claimed that germinal variation in ontogeny was the source of all phyletic deviation. With this theoretical presupposition Whitman reacted critically to Lamarckian ideas because he denied the transmission of acquired traits through the cumulative effects of use and disuse and the environmental influences on phylogeny. At the same time, he rejected mutation theory with its emphasis on discontinuous variations because he believed that the apparent mutations were actually genetically linked together by a continuous differentiating process. Instead, Whitman remained in support of a Darwinian mechanism of evolution, utilizing it scientifically and rhetorically in his formulation of orthogenesis.

Whitman's Career

Charles Otis Whitman was born on December 14 1842, in Woodstock, Maine. Having been interested in natural history since childhood, and attending Louis Agassiz's Anderson School of Natural History at Penikese Island in 1873, he decided to study biology and went to Germany to work under Rudolf Leuckart, the leading zoological teacher of his time. In 1878 Whitman received a Ph. D. from the University of Leipzig. After returning to America, Whitman contributed to the modernization of American biology by bringing to America the traditions of experimentalism already well known to European biologists. Whitman advanced biological research by directing the leading research institution, the Marine Biological Laboratory (MBL) at Woods Hole, from its founding in 1888. After serving as the first chair of the Department of Zoology at Clark University, he assumed the first

chairmanship of the University of Chicago Department of Biology in 1892 (later the Department of Zoology). To provide a forum for the biological science community, he founded the *Journal of Morphology* in 1887, and was an important figure in establishing the American Morphological Society in 1890, which became the American Society of Zoologists after 1902.⁷⁾

In America, Whitman was instrumental in developing a pioneering research program of embryology and his research on cell lineage at the Marine Biological Laboratory, which in turn stimulated the studies on the relationship to heredity and evolution. During his stay in Germany, Whitman's doctoral research concerned the embryology of the parasitic leech *Clepsine* in the annelid phylum. Like other biologists of the time in Germany, he concentrated on cell lineage by analyzing the processes of cell cleavage: he studied the developmental processes of the earliest cell of a fertilized egg and its division within each individual blastomere, that is, from the one-cell, unsegmented egg stage through the gastrular stage to the germ layer stage, after which the principal organs were formed. In his paper entitled "The Embryology of *Clepsine*," Whitman argued that it was the fertilized egg, not the germ layer as commonly believed, which was primary importance for tracing the development of the future whole organism. He wrote that "In the fecundated egg slumbers potentially the future embryo. While we cannot say that the embryo is predelineated we can say that it is perdetetermined."⁸⁾ He further asserted that the fertilized egg cell contained the predetermined characteristics which guided its species-specific development. By putting great emphasis on individual development of the organism, Whitman went so far as to reformulate Haeckel's biogenetic law, stating that ontogeny, rather than phylogeny, was a theoretical key for understanding

7) Ralph W. Dexter, "Charles O. Whitman and the American Society of Zoologists," *American Zoologist* 19 (1979), pp. 1251~1253; Frank R. Lillie, "Charles Otis Whitman," *Journal of Morphology* 22 (1911), pp. xv-lxvii; *idem*, "Charles Otis Whitman," *Science* 33 (1911), pp. 54~56; A. P. Mathews, "Charles Otis Whitman," *Science* 33 (1922), pp. 56~58; E. S. Morse, "Charles Otis Whitman, 1842-1910," *National Academy of Science Biographical Memoir* 7 (1912), pp. 269~288.

8) Lillie, "Whitman," *Journal of Morphology*, pp. xlviii-xlix.

evolutionary phenomena.⁹⁾ As we will see, Whitman's research on cell lineage would hold significance for his understanding of the developmental mechanism and heredity responsible for his formulation of orthogenesis.

In addition to research on cell lineage, Whitman developed various lines of biological research on pigeons including their natural history, hybridization, heredity, and behavior. Having been captivated since a boy with all kinds of birds, especially pigeons, Whitman began full time research to establish his particular theory of the evolution of pigeons when he became professor of zoology at the University of Chicago. The scope of his research was extensive. He collected representatives of six hundred wild and two hundred domestic pigeon species from all over the world, and set up an elaborate breeding pen in his yard, where he hybridized approximately forty wild species. Whitman almost always took care of the birds himself and was able to capture and handle them without a struggle. He gathered, classified, and documented the things that captured his interest and kept extensive notes on all aspects of the life history of pigeons. He also hired two Japanese artists to help with his research by drawing pigeons and doves as well (Perhaps because of his teaching experience in Tokyo University in Japan, he seemed to be associated with Japanese illustrators). Although he examined all aspects of the species for decades, Whitman specifically studied the development of individual pigeons and the evolutionary relationships in the characters of color patterns among pigeons.¹⁰⁾

Oscar Riddle, one of Whitman's students, who later took over his research on pigeons at the Station for Experimental Evolution at Cold Spring Harbor, Long Island, New York, reported on Whitman's investigative zeal:

The patterns were studied from the living birds; male and female were compared; the sequence of pattern in the plumages from young to old was accurately observed; thoughtful experiments were devised

9) Frank R. Lillie, *The Woods Hole Marine Biological Laboratory* (Chicago: Univ. of Chicago Press, 1944), p. 124; Jane Maienschein, "Cell Lineage, Ancestral Reminiscence, and the Biogenetic Law," *Journal of the History of Biology* 11 (1978), pp. 129~158.

10) Lillie, "Whitman," *Journal of Morphology*, pp. lxiv, lxxi; R. M. Strong, "Some Reminiscence of the Late Professor Charles Otis Whitman," *The Auk* 29 (1912), p. 15.

to bridge the gap between the molts and thus replace apparent discontinuities with evident continuities; the behavior of many characters in hybridization was extensively studied; and the primitive pattern of several diverse orders of birds was ascertained.¹¹⁾

Perhaps because of the wide scope of his project, Whitman did not completely finish it. He never formulated his final conclusions, but published only a few preliminary works. Apart from his two lectures on pigeon behavior, two short papers on incomplete research were his only publications on pigeons.¹²⁾ Riddle and Harvey Carr, both of whom were Whitman's students, gathered Whitman's notes and data into a three-volume posthumous work on pigeons that was published in 1919. This compendium of material constructed from many sources includes Whitman's observations and analyses of birds and is supplemented by illustrations drawn by scientific artists. Whitman had described the varieties and species of pigeons in great detail. He used this evidence to support his theory of orthogenesis.¹³⁾

Background: Theories of Evolution in Contention

In order to understand Whitman's theory of orthogenesis, his theory must be examined in connection with the various attributes of contemporary evolutionary views. Darwin's theory of evolution by natural selection had already begun to be

11) Charles O. Whitman, *Posthumous Works: Orthogenetic Evolution in Pigeons*, Oscar Riddle and Harvey Carr, eds, vol. 1 (Washington: Carnegie Institution, 1919), editorial statement.

12) On the first two animal behavior studies, see Charles O. Whitman, "Animal Behavior," *Biological Lecture at Marine Biological Laboratory* (1898), pp. 185~338; *idem*, "Myths in Animal Psychology," *Monist* 9 (1899), pp. 524~537; On pigeon evolution, see Charles O. Whitman, "The Origin and Relationship of the Rock Pigeons as Revealed in Their Color Patterns," *Biological Bulletin* 6 (1905), pp. 307~308; *idem*, "The Origin of Species," *Bulletin of Wisconsin Natural History Society* 5 (1906), pp. 6~14.

13) Whitman, *Posthumous Works*, Oscar Riddle edited volumes 1 and 2, while Harvey Carr edited volume 3: The first volume was on "Orthogenetic Evolution in Pigeons"; the second was on "Inheritance, Fertility and the Dominance of Sex and Color in Hybrids of Wild Species of Pigeons"; the third was on "The Behavior of Pigeons."

challenged. As Vernon L. Kellogg, professor of entomology at Stanford University, noted in 1907, "when one reads of the 'death bed of Darwinism,' it is not of the death bed of organic evolution or of the theory of descent that one is reading... [Rather], many reputable biologists to-day strongly doubt that commonly reputed effectiveness of the Darwinian selection factors."¹⁴ At about the same time, a larger number of evolutionary scientists took up new kinds of problems relating to evolutionary phenomena, providing alternative theories of evolution.

For several decades after the publication of the *Origin of Species* in 1859, Darwin and Darwinians regarded natural selection as the primary force that drove evolution. According to Darwin, in normal circumstances variations occurred randomly, and thus could appear in any direction. Darwin contended that species were produced through repeated selection of the fittest variants, and evolutionary processes were continuous. Darwin's theory of natural selection was strengthened by the German biologist, August Weismann, who promoted the concept of neo-Darwinism. By studying the relationship between variation and heredity, Weismann formulated the concept of germinal selection. He described the hereditary substance in the germ cell, which he called germ plasm, as being distinct, and he explained how selected variations in the germ plasm were inherited.

To some evolutionary biologists, Darwinian selectionism offered an insufficient account of all evolutionary phenomena. Natural selection could not explain neatly the origin of the variations or the accumulation of adaptive modifications of species. Those who objected to Darwinian ideas began to reconsider the Lamarckian principles of the inheritance of acquired characteristics as the essential process for inducing evolutionary change. These Lamarckians argued that new species were formed by adapting and adjusting themselves to environmental changes and through the effects of use and disuse of organs. A group of American neo-Lamarckians emphasized the overarching importance of environmental influences in progressive and linear trends of evolution. While the Lamarckians conceived of "adaptation" and "species-forming" as identical processes, this view was influential on Darwinians

14) Vernon L. Kellogg, *Darwinism To-day* (New York: Henry Holt and Company, 1907), p. 3.

because they both regarded "adaptation" as being a powerful mechanism for explaining evolution.¹⁵⁾

Those Darwinians had argued that based on the cumulative selection and inheritance of useful variations, evolution would still be a continuous process because of the natural selection of minute variations. But many variations came to be seen as discontinuous, which appeared to be the result of mutation. Hugo de Vries, who argued for mutation as a source of new species, stated that mutations periodically occurred "due to changes in the germ plasm," not in response to environmental conditions. After Gregor Mendel had first introduced the new concept of the hereditary particle as a biological unit, de Vries subsequently developed the idea of "germinal units" that were combined and recombined to produce sudden change for each characteristic.¹⁶⁾

Evolutionary biologists also had to address the mode of producing new variations by questioning why some variations occurred in any particular direction and were not necessarily useful. Both Darwinians and Lamarckians felt that adaptation to external influences was so significant that it could induce new useful variations. Not every new species was formed through adaptive modification, however. The Lamarckians in particular could not entirely explain how some of the so-called nonadaptive variations could be sources of new species. By contrast, the emerging mutationists explained that the occurrence of nonadaptive characters of the organism could result in part from the random combination of genetic forces such as "germinal units."¹⁷⁾

The best way to explain nonadaptive characteristics came from a group of orthogenesisists in Germany and America. Carl von Naegeli, a German plant biologist, asserted that variations were governed by some unknown forces within the germ plasm that were oriented in definite directions. Through his research on evolutionary trends in butterflies and lizards, the German Theodor Eimer also found that

15) Philip G. Fothergill, *Historical Aspects of Organic Evolution* (London: Hollis and Carter, 1952), p. 168; Kellogg, pp. 265~266, 274.

16) Kellogg, pp. 170~181, 274, 337-343; Bowler, *Evolution: The History of an Idea*, pp. 270~281.

17) Kellogg, p. 272.

variations occurred in a few definite directions. Eimer argued that the internal force of an organism interacting with environmental stimuli caused it to form nonadaptive characteristics. Like the Lamarckian Eimer, American orthogenesisists (including Edward D. Cope), known as neo-Lamarckians, made a similar argument for nonadaptive characteristics due to the organism's response to its environmental influences and inheritance of acquired characteristics. Most orthogenesisists believed that their theory fit well with Lamarckian ideas, and had no recourse to Darwinian selective forces for explaining nonadaptive characteristics.¹⁸⁾

Whitman's theory of orthogenesis contrasted with others of his day. By taking up the complex issues and problems evolutionary biologists had been engaged in, Whitman was extensively engaged in research on pigeons in connection with their variation, inheritance, and evolution. He formulated a theory of orthogenesis in company with Darwinian tradition.

The Pattern of Evolution in Pigeons

Pigeons had long been a favorite animal of both fanciers and naturalists. Darwin himself had used them in both the *Origin of Species* and *The Variation of Animals and Plants under Domestication* as part of the empirical support of his theory for evolution by natural selection. In pigeons, there are two basic color patterns, chequered and barred, and these two patterns often occur together in the same species. In the chequered-pattern pigeons, the two bars and chequers (sometimes referred to as spots) cover almost all the wing feathers (fig. 1 b). In barred-patterned pigeons, there are two bars on the front part of the wings and a uniform gray color on the rest of the wings. These apparent bars, however, are actually

18) Theodor Eimer, "Further Remarks on the Causes Which Change the General Colouring of Animals," in *Organic Evolution as the Result of the Inheritance of Acquired Characters according to the Laws of Organic Growth*, trans., J. T. Cunningham (London: Macmillan and Co., 1890), pp. 135~139; Kellogg, pp. 285~287; Robert C. Richardson & Thomas C. Kane, "Orthogenesis and Evolution in the Nineteenth Century," in Matthew H. Nitecki, ed., *Evolutionary Progress* (Chicago: Univ. of Chicago Press, 1988), p. 152.

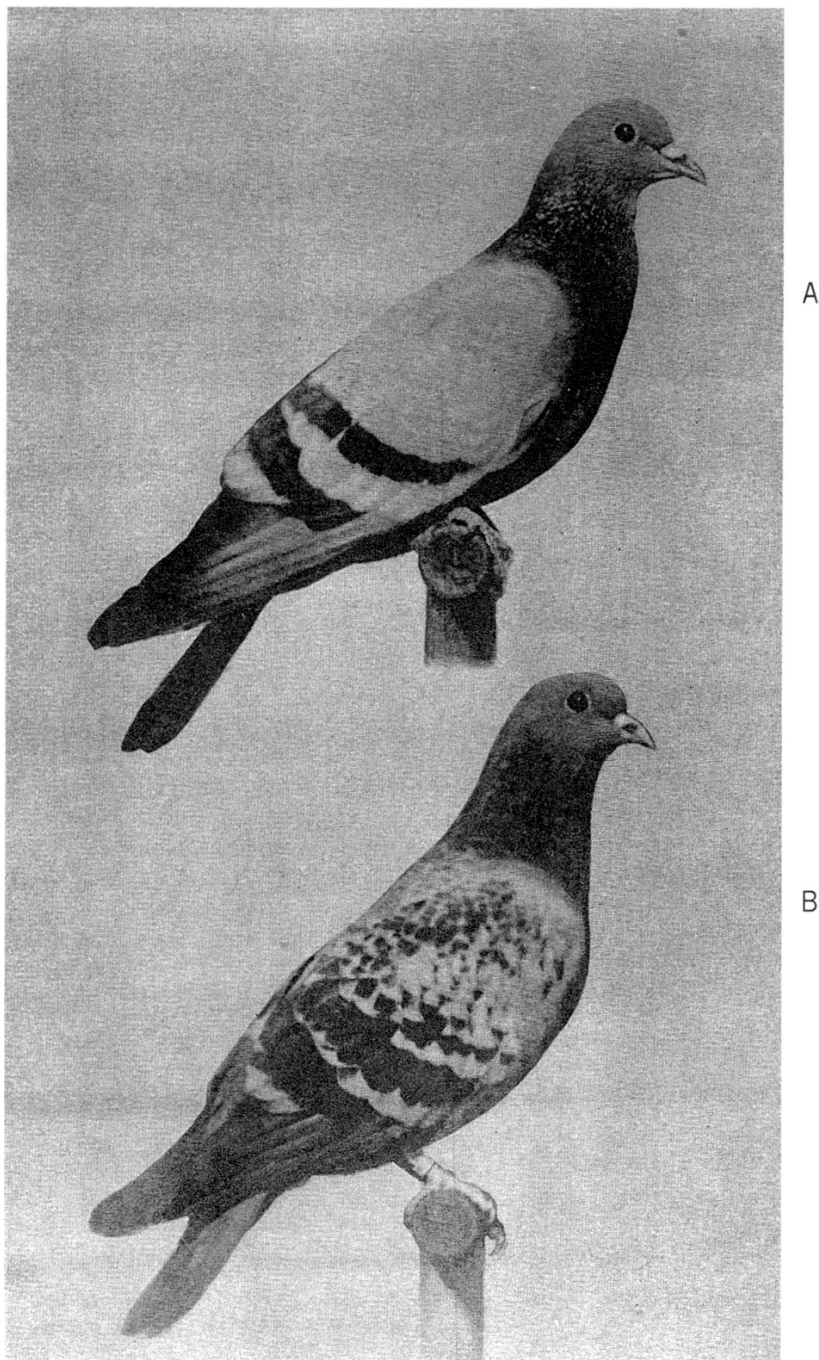


Fig. 1 A: Adult male two-barred rock-pigeon, *Columba livia*
B: Adult male chequered wild rock-pigeon, *C. affinis*

Source: C. O. Whitman, *Posthumous Works: Orthogenetic Evolution in Pigeons*, Oscar Riddle and Harvey Carr, eds., Vol. 1(Washington: Carnegie Institution, 1919). Following figures come from the same source.

composed of chequers on several feathers, which when grouped produce what looks like a continuous stripe (fig. 1 a).

Darwin knew that pigeons interbreed easily, and he found that chequered pigeons often appeared among the offspring of barred pigeons. He believed that the chequers could be "homologous" with the spots of barred pigeons; the real difference lay in the number of color markings. Chequers, for Darwin, thus represented the result of a gradual modification through the intensification of the color of the bars. He wrote: "The chequering arises merely from an extension of these marks to other parts of the plumage."¹⁹⁾ Thus, Darwin inferred that rock pigeons with two bars (*Columba livia*) were ancestral to those with the other pattern. Like other English naturalists of his time, Darwin had not considered the color pattern of wing feathers as being more important than other organic characters, but he nevertheless understood pigeon coloration in evolutionary terms, contending that all domesticated pigeons belonged to the same species and were variations of a common ancestor—the rock pigeon with two bars.²⁰⁾

Nearly half a century after Darwin developed his theory of evolution, Whitman challenged his hypothesis concerning pigeon evolution at the Congress of Arts and Sciences at the Universal Exposition at St. Louis in 1904.²¹⁾ He argued against the origin of the two barred pigeon that Darwin had proposed. In doing so, Whitman chose as his research problem the natural variations of color patterns of pigeons. Unlike naturalists and pigeon breeders of his day, Whitman argued that coloration could become a specific fixed characteristic like other particular parts through organic evolution, since he observed that wild pigeon species always maintained a constant color in nature. Furthermore, he argued, this constancy was clear visual evidence of evolution.²²⁾

19) Charles O. Darwin, *The Variation of Animals and Plants under Domestication with a Preface by Asa Gray* (New York: Orange Judd & Company, 1868), p. 225.

20) *Ibid*; James A. Secord, "Nature's Fancy: Charles Darwin and the Breeding of Pigeons," *Isis* 72 (1981), p. 170.

21) This paper was actually published in the *Bulletin of Wisconsin Natural History* 5 (1906), pp. 6~14.

22) Whitman, *Posthumous Works*, vol. 1, p. 181.

Starting with Darwin's conclusion about the origin of the two-barred pigeon, Whitman identified two key questions: What was the initial stage in the evolutionary process; and how did the two patterns of chequered and barred develop? He then raised theoretical questions concerning the laws by which variations worked in evolutionary change. To decide which species of pigeon was the ancestral type, he assumed each species could develop in its own way, and he compared individual pigeons within one species or between different species to guide his work. Taking phylogeny as the starting point, he compared the maze of patterns existing among 500 or more species of pigeons, and even traced affinities farther back in the bird world.²³⁾

While observing the pigeons whose patterns fell between the chequered and the barred types, Whitman could see a great number of new variations in the pigeon groups. He noticed that wing feather patterns were an especially important site for changes and that the size and shape of wing markings tended to change continuously among varieties and species as well. He found regular sequences of color pattern modification in a given group and the same sequences were parallel to other allied species or genera.²⁴⁾ The basic sequence was, according to Whitman, a progression from an initial pattern of black chequers on all feathers to the concentration of color in certain areas (chequers plus many bars), the reduced chequers plus reduced bars, and finally to the elimination of all chequers with only bars. In Whitman's own words,

The process of evolution in color patterns has been a sweeping one, ... taking the same general direction. The stages reached are various, ranging all the way from the full-chequered to the wholly unchequered state; from chequers and bars combined in different proportions to bars alone; from many bars to three, two, one, a remnant, or none; and in all shades of brown, black, gray, red, to pure white²⁵⁾

23) *Ibid.*, pp. 7, 13, 15, 35.

24) *Ibid.*, p. 49.

25) Whitman, *Posthumous Works*, vol. 1, p. 55.

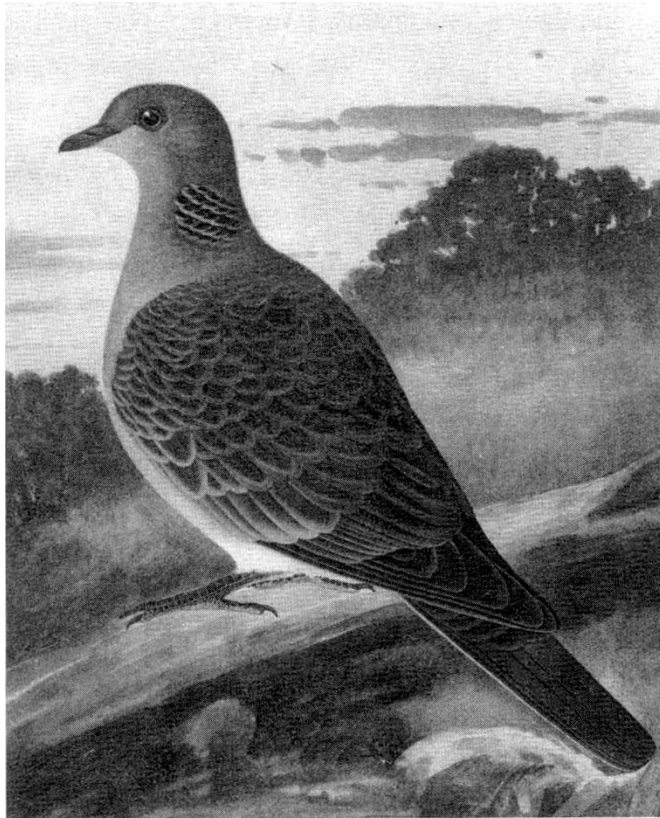


Fig. 2 Adult female Japanese turtle-dove, *Turtur orientalis*

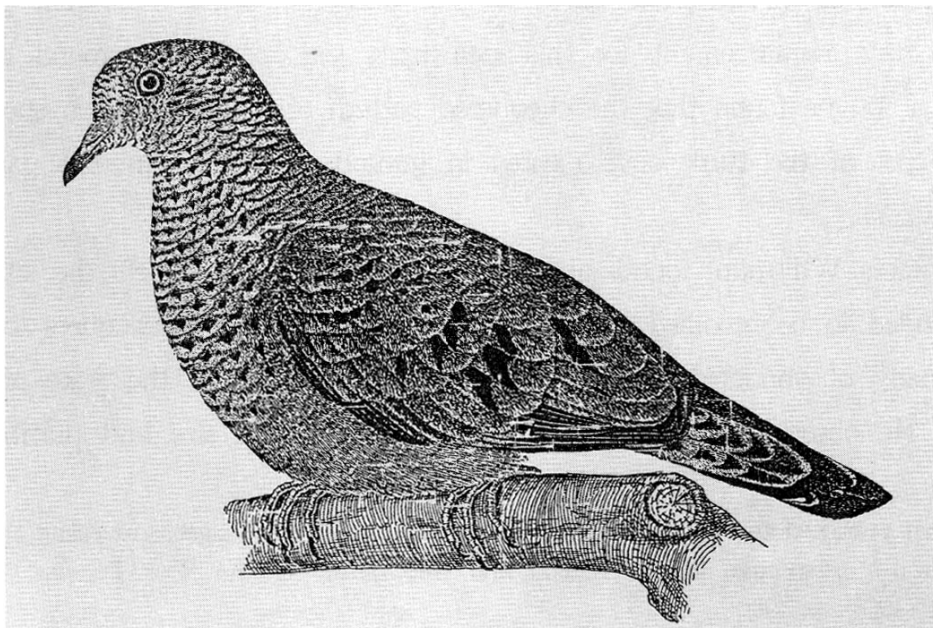


Fig. 3 Adult female Florida ground-dove, *Chamoepelia passerina*

In 1908 when he published a preliminary two-page report on his work, Whitman's views were clearly opposed to Darwin's. Whitman wrote:

The latter [two-barred] was regarded by Darwin as the typical wing pattern for *Columba livia*; the former [chequer] was supposed to be a variation arising therefrom, a frequent occurrence but of no importance. Just the contrary is true; the chequered pigeon represents the more ancient type from which the two barred type has been derived²⁶⁾

In his detailed comparison, Whitman traced the chequers of rock pigeons back to the uniform spots of some species—the “turtle-dove patterns,” which he identified as an ancestral type for the pigeon (fig. 2).²⁷⁾ In many of the new variations, he was able to observe that a single dark spot of turtle dove pattern was gradually modified into the two spots or chequers on each feather of the rock pigeon. He wrote that: “The transitional stages between the turtle dove pattern and the chequered pattern of the rock pigeons are exhibited as we pass from one species to another.” He further argued that a similar change between these two patterns could be seen in the transitional stages from the juvenile to the adult plumage of developing individuals and/or in different parts of one and the same individual plumage. Whitman drew reinforcement for this idea from the species of ground doves in Florida (fig. 3); he found that the chequered pattern of the rock-pigeon species and the dark spot of the turtle-dove existed in ground doves on different parts of a single individual.²⁸⁾

Furthermore, Whitman found another tendency, one in which the chequered pattern tended to be modified in time from a large number of chequers to smaller ones in many of variation he observed, eventually arriving at the state of having two bars. He observed that as the chequers decreased in size and number, each

26) Whitman published the abstract on his research results on rock pigeon, revealing the reverse of Darwin's perspective in the “Origin and Relationship of the Rock Pigeons,” *Biological Bulletin* (1908), p. 308.

27) Doves are one of the principal groupings of pigeons.

28) Whitman, “Origin of Species” (1906), p. 13.

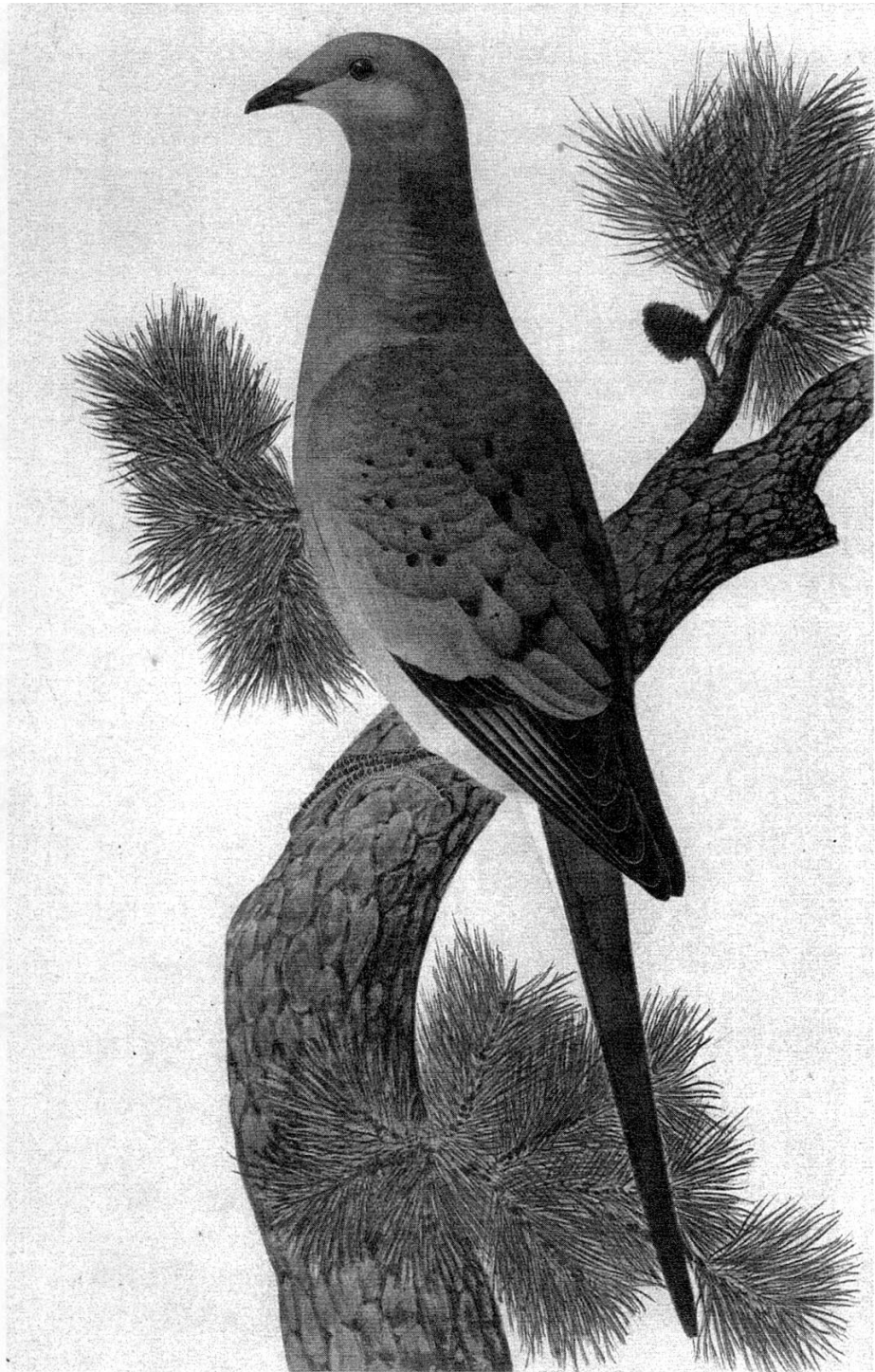
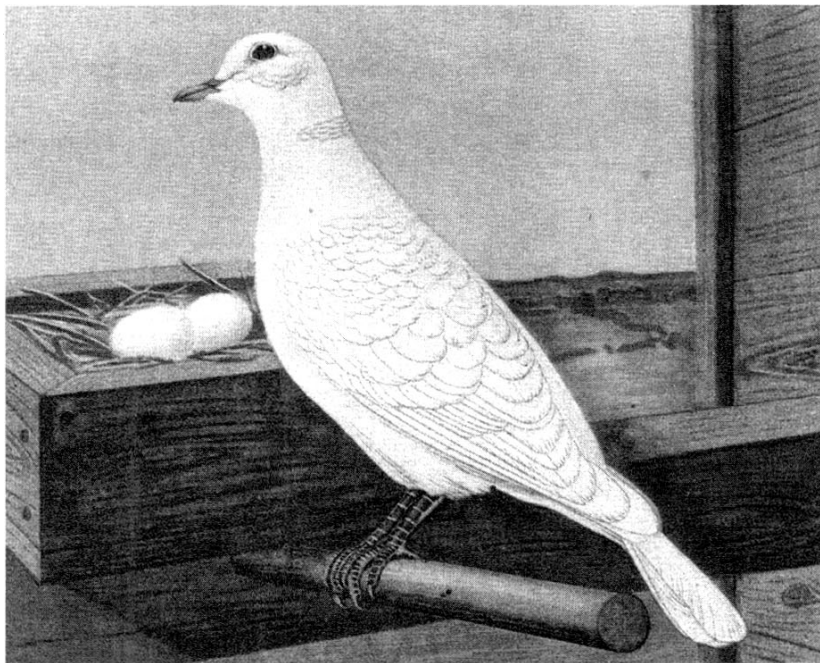
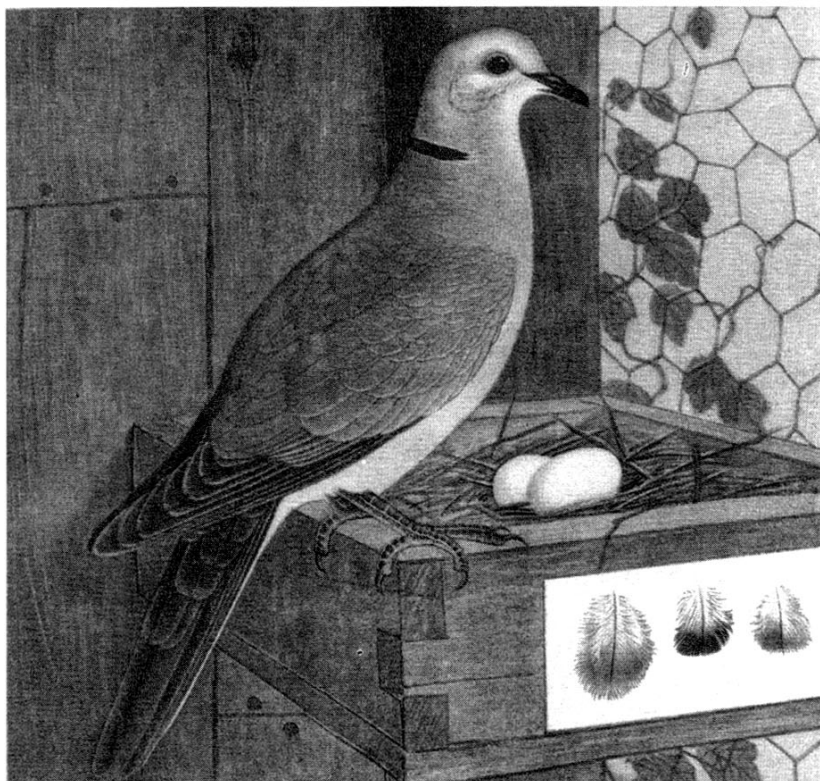


Fig. 4 Adult male passenger pigeon, *Ectopistes migratorius*



A



B

Fig. 5 A Adult female white ring-dove, *Streptopelia alba*
B Adult female blond ring-dove, *Streptopelia risoria*

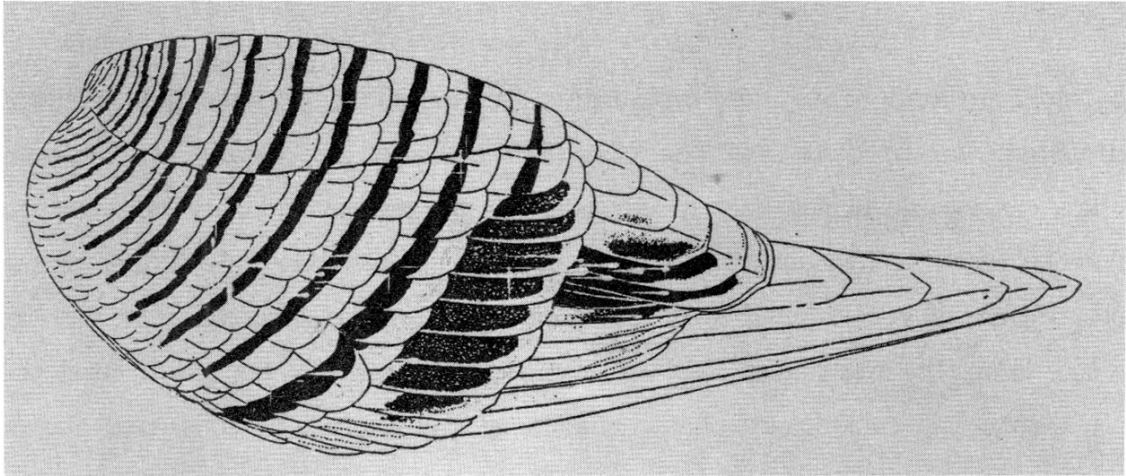


Fig. 6 Adult female crested pigeon, *Ocyphaps lophotes*

species presented a different number of chequers and bars, all composed of similar chequers. Whitman stated that chequers appeared and became increasingly strong in the species of rock pigeons with chequers (fig. 1 b); many chequers were lost in the passenger pigeon species (fig. 4); and in the ring dove species there were no chequers at all (fig. 5). At the same time, the number of bars was reduced successively from species to species. While the crested pigeon had twelve bars (fig. 6), the passenger pigeon showed two bars (fig. 4). Furthermore, some species of the ring doves had no bar, showing more or less uniform color; this dove, Whitman thought, represented an end point in his orthogenetic trend (fig. 5). Through careful observations, Whitman discovered orthogenetic evolutionary change in pigeons, proceeding from the chequered to the barred type and taking place in wild as well as domestic pigeons. Considering the turtle dove as the ancestral type from which all other species derived, he argued that the progression he observed from the turtle dove pattern through the rock pigeon and passenger pigeon to ring doves had parallels in other series of varieties and species also deriving from the turtle dove.²⁹⁾

29) Whitman, "Origin of Species" (1906), p. 12; *idem*, *Posthumous Works*, vol. 1, p. 7.

Presuppositions for Whitman's Theory of Orthogenesis

In order to understand the evolutionary sequences of pigeons that Whitman formulated, we need to examine how he came to incorporate his theoretical justifications into an evolutionary mechanism. As we saw, evolutionary biologists were concerned with the relationship between variation and evolution. One further pressing problem that they confronted was to understand how the inheritance of variations worked. Soon, the relationship between variation and heredity became a focal point for understanding evolutionary phenomena. In general, those who considered Darwin's explanation of heredity insufficient came to think that the theoretical advancement of cytology occurring at the same time was heuristic for understanding the complex interrelationship among variation, heredity, and development. Weismann, for instance, attempted to uncover hereditary determinants in the germ plasm, which, located in the chromosome in the cell nucleus, was responsible for inheritance. Weismann then argued that these determinants were conveyed to the offspring and were automatically transmitted into different individual cells in the course of development.

In his further attempt to understand the transmission mechanism by which the hereditary information of the germ plasm was passed to the next generation, Weismann took up the idea of germ cell continuity that had been discussed in late 19th century Germany. According to the concept's proponents, germ cells located in ovary persisted from early cleavage to gamete production and remained uninfluenced by the events of the organism's development. In regard to germ cell continuity, Weismann argued that only chromosomes in the cell nucleus (that is, germ plasm) were responsible for heredity throughout the life of the organism. But he claimed that somatic cells were unable to transmit new characteristics, acting only as hosts for sustaining the germinal materials. American biologists, on the other hand, held that hereditary information in the germ cell would be subject to change during individual development. For instance, E. B. Wilson argued that the predetermined germ cell might be influenced through subsequent cell division and by cell interaction. As a consequence, Wilson argued that hereditary features in the germ

cell might be transformed over time.³⁰⁾

Whitman had been interested in formulating his theoretical position on heredity and development mechanisms. By the time he worked on cell lineage, Whitman challenged many assumptions of 19th century biology, and he established his own independent positions. Although there had been the consensus that the cell was the fundamental unit in understanding heredity and development, Whitman believed that the process of cell development had been understood inadequately. Instead of emphasizing the importance of the cell itself, he presented the concept of "organism development," claiming that organization—the original constitution of the germ cell—"precedes cell formation and regulates it."³¹⁾ He further wrote that "an organism is an organism from the egg onward, quite independent of the number of cells present, that cleavage is not a process by which organization arises, but that organization precedes cleavage." His research on cell lineage was significant because it demonstrated the patterns by which the fertilized germ cell already retained the organization of the whole organism. Whitman asserted that the germ cell only dominated and controlled the organism's development, which to him would be the basis of heredity.³²⁾

Arguing that the germ cell was the key to understanding heredity and development, Whitman discussed a law of genetic continuity. Of this law, he wrote:

It abolished the miracle of original creation. It enables us to view germs, not as de novo creations, but as complex products, embodiments of work previously done. It puts in a clear light the fact that organization can be, and actually is, directly transmitted. It shows us how the whole

30) For Weismann's germ cell continuity, see Frederick Churchill, "From Heredity Theory to Vererbung: The Transmission Problem, 1850-1915," *Isis* 78 (1987), pp. 337-364; For Weismann's germplasm doctrine, see Bowler, *Eclipse of Darwinism*, pp. 40-41; *idem*, *Evolution: The History of an Idea*, pp. 250-253.

31) Charles O. Whitman, "The Inadequacy of Cell Development," *Biological Lecture at Marine Biological Laboratory* (1894), pp. 105-124; quotation on Lillie, "Whitman," *Journal of Morphology* (1911), p. xlix.

32) Whitman, "Inadequacy of Cell Development," pp. 112, 123; *idem*, "Evolution and Epigenesis," *Biological Lecture at Marine Biological Laboratory* (1895), p. 213.

organic world hands on the power of growth and self-division in its primordial units. It teaches us that the germ may stand for two things; namely, something already accomplished as well as something yet to be accomplished.³³⁾

Additionally, with his theoretical premise of a law of genetic continuity of the germ cell, Whitman formulated a different developmental mechanism, which in turn became valuable for explaining his theory of orthogenesis. Evolutionary biologists in the 19th century had believed that the study of individual development could contribute to the understanding of ancestral evolutionary relationships. They found a theoretical justification for this idea in Ernest Haeckel's biogenetic law, which stated that ontogeny (individual development) recapitulated phylogeny (species development). As Whitman understood him, Haeckel placed causal weight on phylogeny rather than on ontogeny, because ontogeny provided only a specific developmental process for an individual species.

Initially, Whitman disagreed with Haeckel's assertion, which, according to Whitman, held that "phylogeny was the primary fact upon which ontogeny was causally founded, being conditioned by heredity and adaptation."³⁴⁾ Whitman reversed the causal relationship of Haeckel's biogenetic law, giving the ontological primacy to ontogeny, which explained evolutionary phenomena. He believed that not only the primordial germ cell predetermined the organism's development but also distinguished each species from other species. For Whitman, if changes in germinal materials were produced, the whole development process of the individual organism would be influenced by this change. Because such changes did not occur spontaneously and the cause of such changes must lie in the germ cell, new variations could be passed on only if they occurred early in ontogeny. Whitman claimed this, writing that "germ variation[s] in ontogeny became important sources for phyletic departures, for it was the only variation that can be hereditarily recapitulated and thus perpetuated." Having formulated the idea that recapitulation was repetition of the reproductive

33) Whitman, "Evolution and Epigenesis" (1895), pp. 214~215.

34) Whitman, *Posthumous Works*, vol. 1, p. 177.

process and thus ontogeny was reproductive recapitulation, Whitman stated that phylogeny was a consequence of ontogeny itself and ontogeny preceded phylogeny ontologically.³⁵⁾ Consequently, if individual development was clearly understood, for Whitman, an evolutionary change of species would proceed in the same way as ontogeny did.

Based on his idea of development as the hereditary mechanism, Whitman sought concrete evidence for explaining the evolution of pigeons through scientific observation of individual pigeon development. After observing that individual pigeons passed through a succession of different patterns in their plumages, reaching the adult pattern through several molts, either partial or total, he insisted that the comparative anatomy and embryology of individual species would give clues to understanding their phylogeny.³⁶⁾ He focused on two kinds of observations: he compared young and old pigeons within and between domestic species, and he compared the various stages of wild species that were marked with spots and bars because of his assumption that the evolutionary process should be occurring in birds in the wild and not just in domestic birds. Whitman claimed that he had a crucial experiment: as he plucked "a few juvenile feathers at points and time-intervals," he found that "the new feathers developing in the places of those removed would appear at successively later ages, each unfolding a pattern in a state of evolution corresponding to its age." After commissioning scientific artists to delineate the development of different stages of individual pigeons among varieties and species, he insisted that "We have pictured before our eyes the progressive transformation by which the earlier pattern is converted into the later pattern."³⁷⁾ As a consequence, he was able to prove the sequence in the majority of variations that a juvenile bird with chequered feathers would molt and grow into an adult with two-barred plumage.

Whitman's conclusion that orthogenetic change proceeded from chequered to barred came in part from his concurrent breeding experiments. In one experiment,

35) *Ibid.*, p. 180.

36) *Ibid.*, pp. 8, 50.

37) Whitman, *Posthumous Works*, vol. 1, p. 7.

where he used the chequered pigeons in each generation, he obtained a two barred variety from chequered parents. In another experiment, Whitman took barred pigeons and kept them isolated from chequered pigeons, but he could never produce chequered birds from the two barred parents. He wrote that no variation appeared in the direction from barred to chequered but that the opposite direction from chequered to barred did take place.³⁸⁾

Moreover, Whitman was able to explain the appearance of directed variations by postulating an internal driving force at work in orthogenetic change. In other words, his treatment of the genetic continuity of the germ cell led him to claim that the existing organization of the germ cell induced variations that always proceeded in definite, restricted directions. He claimed that germ cells acted "in organized unison towards a definite end—that end being prescribed, not teleologically but constitutionally, as the fruit of all that inheritance has preserved of ancestral progress."³⁹⁾ As we have seen so far, Whitman's orthogenesis arose from his research on cell lineage and developmental mechanism.

Critique and Response:

Whitman's Theory of Orthogenesis in Intellectual Context

Whitman's research on the evolutionary mechanism of orthogenesis among pigeons responded and reacted to the competing theories of evolution of his time. I believe that Whitman's theory of orthogenesis should be cast in a larger context than the Darwinian vs. non-Darwinian framework that historians of evolutionary biology have erected.

It has been argued that orthogenesis and Lamarckian theory of evolution have common underpinnings. In general both groups denied the occurrence of the random variations that induce branching trends of evolutionary change according to

38) *Ibid.*, p. 16.

39) Whitman, "Evolution and Epigenesis" (1895), p. 222.

Darwinians, and instead emphasized linear and regular trends in evolution. A number of leading orthogenesisists in Germany and America adopted the Lamarckian concepts of inheritance of acquired characteristics, and environmental stimuli were seen as influential in eliciting orthogenetic change. Whitman disagreed with those Lamarckian orthogenesisists. In fact, he completely refused to accept the Lamarckian concept, which largely held that ontogeny came to repeat changes occurring due to somatic modifications. Furthermore, he stated that phylogeny could not be explained by the "transmission of characters acquired in the Lamarckian sense," instead asserting that "only germinal variations are hereditary" and that all so-called "acquired characteristics of somatic origin were not transmissible and therefore without specific significance."⁴⁰⁾

In his theory of evolution, Whitman claimed that the mode of producing new variations in orthogenesis was based on a progressive continuity in which variations evolved from the gradual modification out of existing species rather than as abrupt discontinuities. Having accepted the Darwinian concept of continuous variations, Whitman went so far as to oppose the emerging mutation theory of evolution, according to which the mutationist de Vries, for instance, believed that small variations were not enough to bring about permanent changes for shaping new species. Whitman clearly understood de Vries's stance against Darwinian continuous variation and evolution, and he wrote that de Vries said that "species have not arisen through gradual selection continued for hundreds or thousand of years, but by jumps through sudden transformations." In contrast to variations that advanced in a linear direction, Whitman understood de Vries to claim that mutations diverged in new directions and that these mutations took place without definite direction."⁴¹⁾

Indeed, in his research on the wing feather patterns of pigeons, Whitman did see something like mutants when he distinguished mutant plumage from that of normal plumage. For instance, when the light-colored edge in each feather of the turtle dove disappeared with the molt of the juvenile feathers, it might modify its form

40) Bowler, *Eclipse of Darwinism*, pp. 141~142; quotation on Whitman, *Posthumous Works*, vol. 1, p. 5.

41) Whitman, *Posthumous Works*, vol. 1, p. 9.

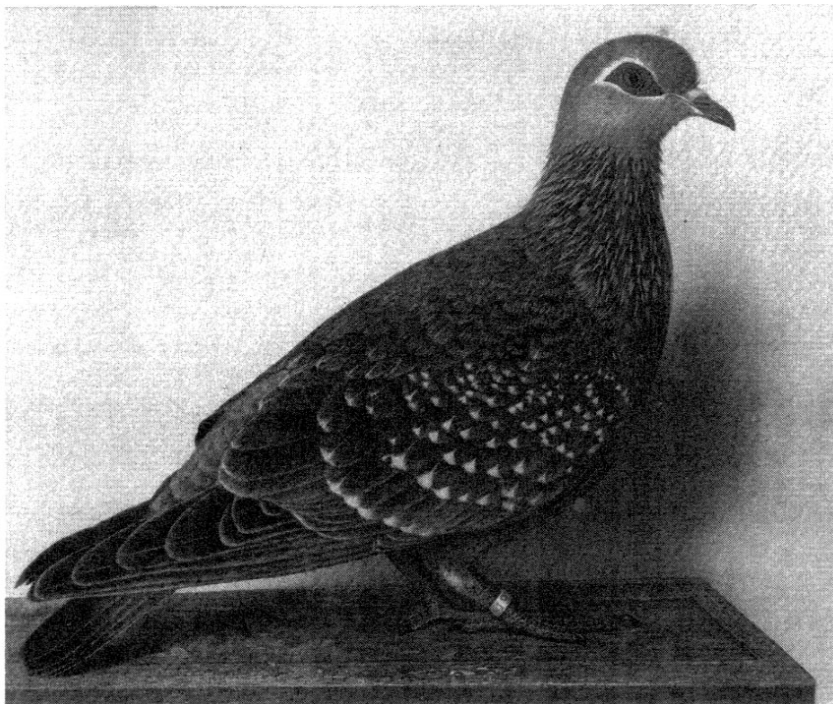


Fig. 7 Mate of guinea mutant, *Columba guinea*

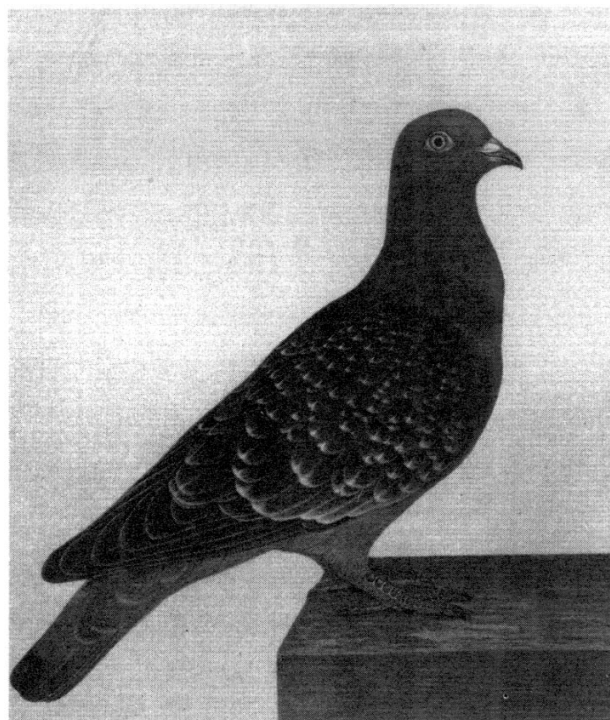


Fig. 8 Adult spotted pigeon, *Columba maculosa*

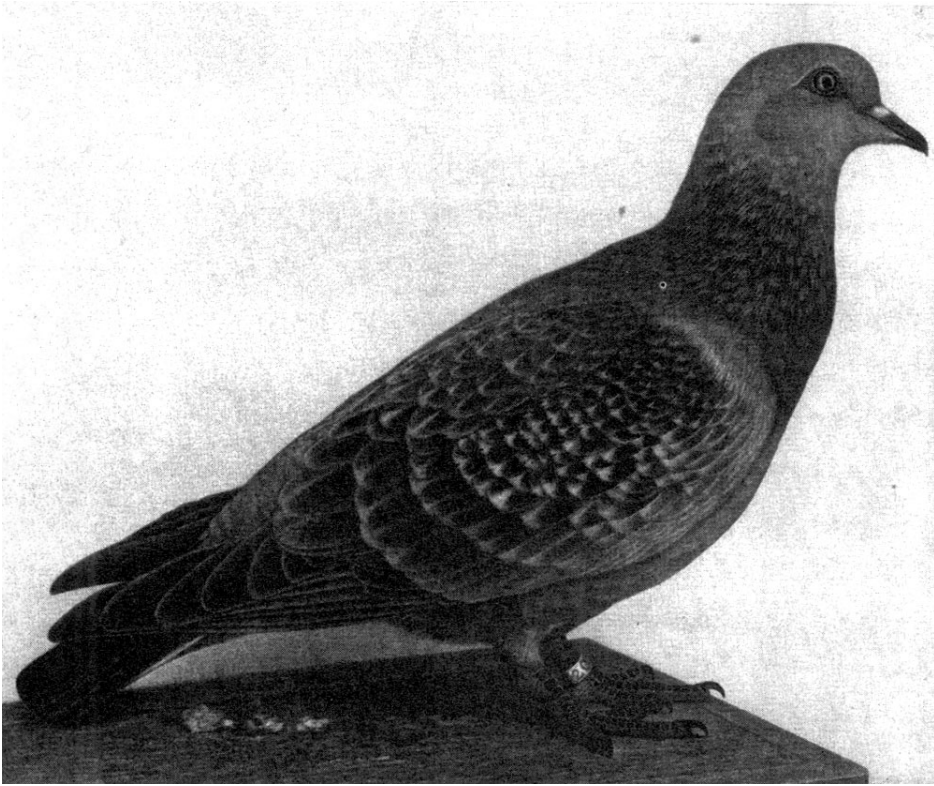


Fig. 9 mutant of *Columba guinea*

into "a narrow crescent, more or less thickened at the middle" (fig. 7), or it might change into the form of "a triangular spot," which Whitman called a "guinea mark," as in the *Columba guinea* of Africa (fig. 8), or it might be "more obtusely pointed," as in the chequered pigeon of south America (fig. 9). Whitman thought that the difference was so wide between the two successive plumage stages that mutationists would naturally recognize these contrasting color patterns as mutations to show a discontinuity in evolution.

For his part, Whitman argued against de Vries's concept of unit characters (along with the Mendelian one in general), the segregation of which could produce mutations. His analysis of germinal material in the germ cell did not fit well with de Vries's concept of unit characters. As we have seen, Whitman emphasized the genetic continuity of germ cell, claiming that the germ cell stood for "an organized whole. It is a unit organism, not an organism of units: all the features that arise in the course of development are within the sphere of the individual unity and integral

parts of it,"⁴²⁾ Whitman continued to emphasize the futility of analyzing unit characters, writing that:

[The] conception of [unit characters of mutation] implies that every character of the adult organism pre-exists in some rudimentary form in the germ cell from which the organism develops. These assumed rudiments of unit-characters must be as fixed in number and constitution in the fertilized egg as in the adult. Unless we assume that these units may mutate at any stage of development, we must suppose that all mutations destined to appear in adult stages must have originated in the very first stage of existence of the primordial units. Thus mutations would be carried back to the pre-mutation forever beyond the reach of investigation.⁴³⁾

Further, Whitman suggested that his breeding data of pigeons did not support the segregation principles. At the Biological Lecture at Woods Hole, he reported on crossing-breeding experiments between pigeons.

The most remarkable case was a male hybrid between a male chequered rock pigeon and a female oriental turtle dove. The offspring of this hybrid, mated with the domestic pigeon, exhibited segregation; but neither in the first nor the second generation were there "dominants," and "recessives" in the Mendelian sense.... Segregation is probably never complete; and in some cases at least the intermediate [blending chequer with bar] character seems to be permanent.⁴⁴⁾

In a nutshell, Whitman stressed that mutationists failed to analyze properly the appearance of apparent mutations which to him merely reflected many transitory stages evolution must have followed. He stated that an adult pattern which looked like an obvious mutation was "only an end-stage in a continuous process of

42) Whitman, *Posthumous Works*, vol. 1, p. 6.

43) Whitman, "Origin of Species" (1906), p. 10.

differentiation. There are no kaleidoscopic leaps to interrupt the sequence." Whitman wrote that "[T]he evidence showing such a gradual transmutation [is] still to be seen, and in such profusion as to wholly exclude doubt. Hundreds of species have been formed in this simple way[,] leaving no room for the claim of sudden, nontransitional mutation."⁴⁵ As a consequence, because he firmly believed in the nature of continuous variations and evolution, Whitman completely rejected mutation theory.

Whitman's critique of de Vries's mutation theory and Lamarckism led him to ally himself with Darwinian selectionism. Whitman's scientific training and experience in Germany kept him in contact with the neo-Darwinism that Weismann promoted. Also, Whitman's law of genetic continuity in the germ cell was in agreement with Weismann's germ cell continuity despite slight differences in their analysis of germinal materials. While both believed in the predetermined nature of the germ cell, Whitman did not completely agree with Weismann's sort of preformation position. I would argue here that rhetorically Whitman sided with the Darwinian camp. This is best indicated by several of his students. One was quoted as remembering:

As the result of long continued investigation, Dr. Whitman's attitude toward evolution was selectionist, and he severely opposed the mutation theory of de Vries. He considered that variation occurred in nature in various ways and that nature selected certain ones among various ones.⁴⁶

Another recalled Whitman himself saying,

I cannot believe that mutation theory of de Vries; the cause that makes the species vary is selection. Nothing but selection can explain the cause of variation. It is professor Weismann who completely

44) Charles O. Whitman, "Hybrids from Wild Species of Pigeons, Crossed inter se and with Domestic Races," *Biological Bulletin* 6 (1905), p. 316.

45) Whitman, "Origin of Species" (1906), pp. 11, 13.

46) Morse, "Whitman," *National Academy of Science Biographical Memoir* (1912), p. 282.

beat the mutation theory. It is professor Weismann who completely confirmed that the selection theory is true.⁴⁷⁾

Reading these passages, I believe that Whitman's orthogenesis implies a force such as the so-called "ortho-selection" force, in which selective force helped variations to proceed in definite directions. Whitman wrote that:

Natural selection may enter at any stage of orthogenetic variation, preserve and modify in various directions the results over which it may have had no previous control.... Natural selection waits for opportunities, to be supported, not by multifarious variation or orderless mutation, but by continuous evolutionary processes advancing in definite directions.⁴⁸⁾

It seems that Whitman implicated Darwinian selection in inducing orthogenetic change in evolution, but he did not clearly explain how. Nevertheless, we could still see rhetorical evidence of Darwinian selection when Whitman critically read the Lamarckian orthogenesisist from Germany, Theodor Eimer, who was actively engaged in controversy with Weismann's neo-Darwinian stance. In the debate between Eimer and Weismann, Whitman showed that his concept of orthogenesis might be compatible with the Darwinian camp. Whitman wrote that Eimer argued for:

complete proof of definitely directed variation, as the result of the inheritance of acquired characters, and as showing the utter impotence of natural selection.... Eimer's intemperate ferocity toward the views of Darwin and Weismann, coupled with an equally intemperate advocacy of the notion that organic evolution depends upon the inheritance of acquired characters, was enough to prejudice the whole case of orthogenesis. Moreover, the controversial setting given to the idea of definitely directed variation, without the aid of utility

47) *Ibid.*, p. 282.

48) Whitman, *Posthumous Works*, vol. 1, p. 11.

and natural selection, made it difficult to escape the conclusion that orthogenesis was only a new form of the old teleology, from the paralyzing domination of which Darwin and [his] followers had rescued science. Thus handicapped, [Eimer's] theory of orthogenesis has found little favor outside the circle of Eimer's pupils.⁴⁹⁾

Being critical of Eimer's theory of orthogenesis, Whitman claimed that his own theory of orthogenesis should not be seen as "teleological." Orthogenesisists were criticized for reinstating a teleological order in the science of evolution because of their claims for the strictly predetermined course of evolution, but Whitman fought against teleology. He used the Darwinian method, which he viewed as contrasting with teleological processes. Indeed, Whitman avoided the dismissal of orthogenesis as teleological that prevailed among evolutionary scientists. He wrote:

I venture to assert that variation is sometimes orderly and at other times rather disorderly, and that the one is just as free from teleology as the other.... If a designer sets limits to variation in order to reach a definite end, the direction of events is teleological; but if organization and the law of development exclude some lines of variation and favor others, there is certainly nothing supernatural in this.⁵⁰⁾

All in all, it seems that Whitman grafted the Darwinian notion of evolution onto his theory of orthogenesis. He wrote, for example,

Orthogenesis and natural selection appear to present fundamental contradistinctions, but I believe that each stands for truth, and that reconciliation is not distant.... That variation does issue a new species, and that natural selection is a factor, though not the only factor, in determining results, is, in my opinion, as certain as that grass grows although we cannot see it grow, I have found indubitable evidence

49) *Ibid.*, p. 9.

50) Whitman, *Posthumous Works*, vol. 1, p. 11.

of species-forming variation advancing in a definite direction (orthogenesis),
and likewise of variations in various directions (amphigenesis)...
If I am not mistaken in this, the reconciliation for natural
selection and orthogenesis is at hand.⁵¹⁾

The rise of orthogenesis represented an important challenge to Darwin's theory of evolution. In particular, Whitman's theory provides an opportunity to see a larger context of turn-of-the-century evolutionism, in which orthogenesis interacted with the other competing theories of evolution, and to seek a relaxation of the distinction between orthogenesis and the Darwinian theory of evolution that historians have made. After studying variation, heredity, and development, Whitman reconstructed his premises concerning these problems to be consistent with his observation concerning pigeon evolution. Although it should not be assumed that Whitman's theory of orthogenesis did not have its own drawbacks, it had significant merit before the ascendance of Mendelian genetics. Whatever the value of his theory of evolution in pigeons, Whitman was able to work out a mechanism by which variations and evolution occurred in definite directions.

Conclusion

A leading biologist at the turn of the century in America, Whitman conducted research on all aspects of pigeons—breeding, behavior, natural history, and evolution. Throughout the decades of his research on the coloration of pigeons, Whitman established himself as a theorist of evolution by orthogenesis. A variety of factors—his work on cell lineage, his views on development, and his work on pigeons—enabled him to reject teleology and to formulate an evolutionary mechanism of orthogenesis, or directed evolution. Comparing various varieties and species of pigeon, Whitman found that the pigeon variations tended always to occur in a definite

51) *Ibid.*, p. 10.

direction, moving from a chequered to a barred color pattern. Reconstructing a developmental mechanism based on germ cell continuity and recapitulation and developing a theory of orthogenesis, Whitman criticized the neo-Lamarckian idea of inheritance of acquired characters and completely denied de Vries's mutation theory. But Whitman favored Darwinian evolution, by utilizing continuous nature of variation scientifically and natural selection rhetorically in his formulation of orthogenesis. Since historians of evolutionary biology deal little with these factors and neglect Whitman's reaction to the other competing theories (e.g., Lamarckism and mutationism) they somewhat misrepresent Whitman in terms of a larger context of evolutionism at the turn of the century. Whitman's theory of orthogenesis cannot be fit into a mere dichotomy between Darwinian and non-Darwinian evolutionary theories.