Nabokov, Teleology, and Insect Mimicry

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1 Emergent Teleology and Nabokov's Aesthetics

Although Vladimir Nabokov may be better known for his outstanding literary achievements, he also had gift for science. While acting as curator at Harvard's Museum of Comparative Zoology in the 1940s, he became an expert on a group of butterflies popularly known as "Blues." He named one species and several have been named after him. He published nine articles on lepidoptery in prestigious scientific journals. During this time, he also developed compelling ideas about evolution. He argued that some instances of insect mimicry did not result from Darwinian survival strategies; that is, slight resemblances could not be furthered by the *function* or *purpose* they served, leading *gradually* to better resemblances. I contend that Nabokov's understanding of the origins of biological forms can be compared to recent work in evolutionary biology, namely structural evolution and neutral evolution. I also argue it was Nabokov's aesthetic interest in the mechanisms behind teleological phenomena that gave him the insight to construct a theory of mimicry that now appears quite progressive for its time.

This argument concerns recent advances in evolutionary biology and how they compare to Nabokov's scientific interests in accidental functionality, coincidental patterns, and mimicry; however, I would like to begin by mentioning the literary complement of these interests. One of the hallmarks of Nabokov's style is his use of coincidences to structure narrative events in such a way as to suggest intentionality or some form of teleological organization. According to the doctrine of teleology, natural events are determined not just by physical necessity but also by the functions they serve. How are coincidences related to the appearance of purpose? Mechanism can offer explanations for patterns that are generated according to physical laws (e.g., spiral shaped galaxies) but not patterns that are merely coincidental (e.g., the "big dipper" and the "little dipper"). If one believes that a recurring form is not merely mechanistic or a particular chance pattern is not merely coincidental, one might look for some inherent guiding principle, purpose, or intentional being behind the patterns. For instance, one might suppose that the stars are intentionally designed by a god with a partiality for patterns and a desire to entertain us mortals. Nabokov both appreciated and critiqued this tendency to see purpose, divine or otherwise, as a cause of a nonutilitarian resemblance formed by similar physical laws (like many spiral galaxies) or a mere coincidental resemblance (like the two dippers).

In *Pale Fire*, John Shade suffers a heart failure. When he recovers, he recalls having seen a fountain while on the other side. Although he had been a skeptic prior to this experience, he begins to suspect that he has seen evidence of an afterlife. Later, he becomes even more convinced when he reads in the paper of a Mrs. Z who also saw a fountain while clinically dead. He feels that this is too unlikely of a coincidence not to be meaningful. Shade travels to meet her and learns there had been a misprint in the article. She had seen a mountain, not a fountain. But ultimately Shade is not disappointed. He declares,

> …it dawned on me that *this*
> Was the real point, the contrapuntal theme;
> Just this: not text, but texture; not the dream
> But topsy-turvical coincidence,
> Not flimsy nonsense, but a web of sense. (342)

Some thing or someone seemed to be making "plexed artistry" or "ornaments/of accidents and possibilities." Apparently, whether or not there truly is a God or an afterlife is not as interesting to Nabokov as the fact that it is suggestive coincidences that give the impression life is like a novel with an omniscient and somewhat playful author.[1]

As an artist, Nabokov found teleology a natural mode of investigation. Teleology is, after all, derived from an analogy with intentional acts of creation. The term *telos* has been variously interpreted as end, purpose, function, utility, motive, intention, goal, or design. But it should not be understood, as it is so often today, as a predetermined "linear" mechanism.[2] In this paper, it is assumed that a teleological explanation is only necessary if a purpose is fulfilled in a way that could not have been predicted by analyzing the initial conditions, or the starting point that led to the goal. In retrospect, however, it appears as if each stage in the process was a precondition for the advantageous or more complex property, quality, or event that eventually emerged. This is the very situation that nonlinear dynamics theorists now refer to as "self-organization," the emergence of a directing, teleological "self" in systems that simply, albeit surprisingly, organize according to dynamical constraints. Scientists claim self-organizing systems are irreducible and hence unpredictable because effective factors (e.g., function or context) unaccounted for in the system's initial measure of energy are later generated by the dynamics, the interactions of the parts and the whole. Thus, one may say that these complex systems are capable of spontaneous increase in complexity or "progressive" behavior. At the same time, however, the degree of unpredictability is constrained by the dynamics that govern the system as a whole. Behavior, then, is directed as well as original. Only a nonlinear feedback situation could result in an act that could be considered intentional, that is, determined and yet free.[3]

Nabokov tends to be sympathetic to the teleologies of, say, 20th century vitalist Henri Bergson or the 19th century Kantian teleomechanists.[4] Like they, Nabokov recognizes telic behavior is not linear and involves mechanisms both for maintaining order and for discovering new order, which I call *directionality* and *originality,* respectively. Telic behavior can be compared to artistic behavior. To some degree, an artist must organize random information in a lawful or directed manner. But creative and original art must also involve essentially unpredictable activity that, while conforming to mechanistic laws, can transcend them. This might be done through (mis)interpretation or by making use of a chance analogy. The mechanisms of directionality and originality behind insect mimicry resonated deeply with Nabokov's interests in aesthetics and teleology. To put it simply, mimicry was for him a concrete exemplar both of art and of *telos*, as he understood these concepts.

Darwinism has its own relationship to the appearance of intentionality in the biological world. Natural Selection explains how a certain structure has evolved by pointing to the advantage it gives or the purpose it serves for increased reproduction. Although Darwin did away with the *Divine* Watchmaker,[5] as Richard Dawkins has argued, natural selection takes on the role of Creator as the *Blind* Watchmaker. In Dawkins' extreme interpretation, Darwinism actually encourages a kind of teleology as a mode of biological explanation. Nature may not fulfill a cosmic function, but nature is still determined by function (which is derived from increased rates of reproduction).

Contra the likes of Dawkins, in his work Nabokov tries to encourage lepidopterists to consider, on the one hand, the "nonutilitarian" mechanisms of physical and chemical constraints involved in wing pattern formation. These mechanisms can help explain, for example, the similarity between viceroy and monarch butterflies. Nabokov claims that neither species benefited from the resemblance, so it seemed a case of design without purpose. On the other hand, Nabokov's work also encourages lepidopterists to consider other "nonutilitarian" mechanisms behind the creation of a butterfly that looks like a dead leaf (fig. 1). As Nabokov regards this form of apparent mimicry it is something of a "statistically insane" coincidence,[6] not a useful representation of something in the species' environment.

According to Nabokov, both viceroy-monarch mimicry and dead-leaf mimicry involve elements of chance (resulting in the aspect of telic originality). They also involve nonutilitarian mechanisms that increase the probability of their occurrences (resulting in the aspect of telic directionality). In what follows I will offer examples of recent work in lepidoptery, which demonstrate that, despite the fundamentally random processes (e.g., mutation) involved in the evolution of separate species (such as the viceroy and monarch), non-inherited family resemblances do emerge, which indicate the existence of, what, in the literature of teleology, is called a *ground plan*. Enlarging upon this and other research in "nonutilitarian" evolution and developmental systems, I further argue that the origin of dead-leaf "mimics" should be attributed to selectively neutral mechanisms that happen to produce an unexpected coincidental similarity between two genetically unrelated organisms, an insect and a plant.

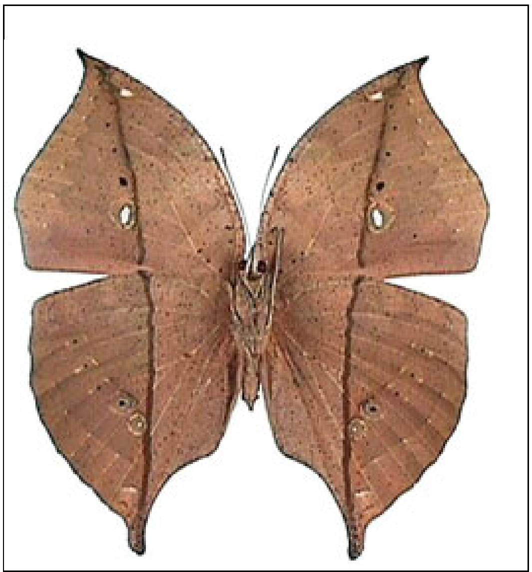

Figure 1: Kallima paraletka, a "dead-leaf butterfly." Pictured here are the undersides of the wings, which are dull brown. The upper sides are boldly colored bright blue, orange, and black. Photo by Yves-Pascal Dion, 1998. Used by permission.

Nabokov had a profound respect for coincidences *as* coincidences. One of his favorite examples of a selectively neutral instance of "mimicry" was a butterfly wing marking that looked like a drop of dew with light reflected in it. As he described it, a line along the wing edge running through the "dewdrop" was shifted in a perfect imitation of refraction—masterfully rendered, but a coincidence. It is difficult to imagine what function or advantage could be ascribed to an imitation of a dewdrop on, say, a Blue's wing. It must be admitted, then, that some forms of "mimicry" may be imposed by the lepidopterist's powers of interpretation. Since such cases of *false mimicry* conferred no reproductive advantage—they merely amused—Nabokov notes they "seemed to have been invented by some waggish artists precisely for the intelligent eyes of man" (*Nabokov's Butterflies* 178). The key word here is "seemed."

Although Nabokov was careful not to align himself with any particular philosopher, the ideas reflected here are Kantian. In Kant's *Critique of Judgment,* he argues that patterns in nature are typically appreciated in one of two ways, with the *aesthetic judgment* or with the *teleological judgment*. The former can appreciate nonutilitarian forms of spontaneous organization—beautiful geometric patterns on butterfly wings, for example. The latter can appreciate forms that exist because of the function they serve within a system—drab coloring on moth wings that makes them virtually invisible to predators, for example. Kant insisted that no empirical evidence could ever prove the existence of a transcendent intelligence that devised the aesthetic and telic laws of form and function. Aesthetic and teleological phenomena only *seem* to the reflective judgment to be indicative of a divine designer. Nabokov's attitude is Kantian when he writes in this oft-quoted passage on mimicry:

> The mysteries of mimicry had a special attraction for me. Its phenomena showed an artistic perfection usually associated with man-wrought things. Consider the imitation of oozing poison by bubblelike macules on a wing (complete with pseudo-refraction) or by glossy yellow knobs on a chrysalis ("Don't eat me – I have already been squashed, sampled and rejected"). Consider the tricks of an acrobatic caterpillar (of the Lobster Moth) which in infancy looks like bird's dung, but after moulting develops scrabbly hymenopteroid appendages and baroque characteristics, allowing the extraordinary fellow to play two parts at once … that of a writhing larva and that of a big ant seemingly harrowing it. When a certain moth resembles a certain wasp in shape and color, it also walks and moves its antennae in a waspish, unmothlike manner. When a butterfly has to look like a leaf, not only are all the details of a leaf beautifully rendered but markings mimicking grub-bored holes are generously thrown in. "Natural selection," in the Darwinian sense, could not explain the miraculous coincidence of imitative aspect and imitative behavior, nor could one appeal to the theory of "the struggle for life" when a protective device was carried to a point of mimetic subtlety, exuberance, and luxury far in excess of a predator's power of appreciation. I discovered in nature the non-utilitarian delights that I sought in art. Both were a form of magic, both were a game of intricate enchantment and deception. (*Nabokov's Butterflies* 85-86)

More than a few commentators have supposed that Nabokov's rejection of natural selection as an explanation for the origin of mimicry was motivated by a belief in a metaphysical intelligent force, creator, or predetermined telic principle of organization. Brian Boyd refers to Nabokov's theory of mimicry evolution as his "dearly held metaphysical speculations" (*Nabokov's Butterflies* 20). He claims Nabokov

> thought that mimicry could be so complex, perfect and beyond predators' powers of perception as to pose a challenge for natural selection and almost an implicit proof that the design in nature could only be accounted for by some form of intelligence. The very depth of his attraction to this idea, for metaphysical reasons, made him interested in challenging explanations for mimicry through natural selection, but also made him disinclined to think seriously about how science might be able to explain mimicry one day. His position has proved to be wrong… whether near-perfect or not, mimicry nevertheless increases survival rates of the mimics; … the perceptual systems of the predators are better than he had assumed… we have reason to infer he didn't think nearly as seriously or scientifically about naturalistic explanations for mimicry as he might have, had he not had a powerful commitment to a non-naturalistic explanation. (Boyd)

Boyd may feel that Nabokov's comment about predators' limited powers of appreciation is central to his objection to Darwinian gradualism as an explanation for the origin of mimicry, but the focus of the passage is on the "excess" of the pattern, not the "power" of the predator. Nabokov is comparing the "mimic" to a work of art, like, for example, stone carvings in Gothic cathedrals that are placed so high and out of the way that no one would reasonably expect a person to ever see them. This is artistic excess. The assumption about this art is that it was done for the pleasure of a higher intelligence. Similarly, Nabokov is implying that the artistic excess of the "mimic" does not serve the function of fooling predators (since they would be fooled by less) but seems to imply an audience of higher intelligence. Nabokov is exploring the origins of the anthropomorphic principle in this passage, not predator-prey relations. His noting the "perfection" of mimic forms does not necessarily indicate a belief in an intelligent or intentional force as cause of the perfection. It seems rather more likely that he is noting the fantastic improbability of the perfection. Nabokov was keenly aware that it is too coincidental coincidences that inspire belief in supernatural intention. Like Kant, he seems more interested in the epistemology of belief than arguing for the objective existence of the object of belief itself. With all due respect to Boyd's excellent knowledge of Nabokov's life and work, I believe it was uncanny chance that excited Nabokov's imagination, not metaphysics. If there is a godlike force for Nabokov, from the human perspective its actions would be more or less identical with the ordering (and disordering) tendencies of chance.[7] Furthermore, Nabokov could not have been particularly interested in the question of predator-prey relations because he does not pursue this line of argument in his scientific work. He knew better, since the task of objectively assessing a predator's powers of appreciation would be insanely complex. The enormous amount of literature on the subject attests to its lack of consensus. Nabokov's argument against Darwinian gradualism does not depend upon disproving natural selection, but in offering a much more elegant explanation instead.

Stephen Jay Gould has implied that Nabokov's view of Darwinism is quaint and old-fashioned. He does admit, however, he does not "understand Nabokov's psyche or his ontogeny well enough to speculate about his conservative approach to theoretical questions, or his disinclination to grapple with general issues in evolutionary biology" (110). Despite his being aware of his limitations, Gould does speculate to the extent that he assumes Nabokov's approach *was* conservative and that he *was* disinclined to address general issues in evolutionary biology. Gould's own specific interest in the important role of environmental contingencies in the evolutionary process made him less interested in what captured Nabokov's scientific imagination: the search for inherent laws of biological form.

Lepidopterist Charles Remington claims that it was Nabokov's lack of mathematical training that prevented him from realizing how quickly a singular reproductively fit mutation can spread throughout a population. However, Nabokov had no quarrel with the basic principles of natural selection, generally speaking. He accepted Darwinian evolution as an explanation for many of nature forms. For example, Nabokov presumed that vivid line patterns on the upper sides of butterfly wings tend to flash and dazzle birds, thereby helping them avoid predation. As he writes in "The Nearctic Members of the Genus *Lycaeides* Hüber (lycaenidae, Lepidoptera)," "the zebroid patterns…suggest specialized protective adaptation" (*Nabokov's Butterflies* 414). Elsewhere Nabokov discusses the reproductive advantage of other forms of disruptive coloring, "A bird comes and wonders for a second. Is it two bugs? Where is the head? Which side is which? In that split second the butterfly is gone. That second saves that individual and that species" (*Nabokov's Butterflies* 530). Nabokov simply thought fitness selection did not create so-called mimicry. He insisted that, in addition to reproductive fitness, there were other mechanisms that drive and shape evolution.

In *Nabokov's Blues* (1999), Kurt Johnson and Steve Coates describe the thoroughness and reliability of Nabokov's research at Harvard. They give a detailed description of Nabokov's controversial method of classification, which was based more on internal anatomical structure than external appearance; importantly, they do not discuss the fact that his interest in the *symmetrical* nature of certain structures derives from his interests in teleology and its search for the laws of biological form. One of Nabokov's specialties was describing the relative shapes and sizes of butterfly reproductive organs, the basic shape of which is triangular. Aberrant members of a species tend to be less symmetrical, but the "main peaks of speciation" argued Nabokov, exhibit a "convenient constant in the structural proportions," conforming to an equilateral triangle (*Nabokov's Butterflies* 321). It seemed *as if* symmetry were a goal toward which species strive. Rather than ignore this apparent directedness, Nabokov chose to search for the laws of biological form that might explain it. Such was the approach of the morphologist-teleomechanists in the 19th century. Johnson and Coates do not specifically note Nabokov's general tendency throughout his lepidoptery toward theoretical biology, a pre-Darwinian scientific focus. (Johnson has since indicated that he did think these interests were unusual when he first encountered them and is happy to consider teleology as their possible source.)[8]

Nabokov's Blues started an interest in Nabokov's lepidoptery, which was quickly intensified by *Nabokov's Butterflies* (2000), edited by Brian Boyd and Robert Pyle. This valuable work collects Nabokov's many scattered references to lepidoptery and includes a significant previously unpublished piece involving evolution and the so-called argument from design entitled "Father's Butterflies." However, in their commentary, the editors chose not to attempt to unpack Nabokov's theory of mimicry. This is what I intend to do here.

First of all, for any reader to assume that Nabokov's argument against Darwinian gradualism as the cause of the origin of "mimicry" reflected a belief in creationism is to jump to the wrong conclusion, since there are several well-known neutral (or "nonutilitarian," in Nabokov's terms) evolutionary mechanisms that assist fitness selection.[9] These include the mechanisms that involve varieties of selection that are not based on reproductive fitness, random drift, various "laws" of biological form, and spontaneous pattern formation. Secular forms of teleology focused on these kinds of phenomena and did not seek to prove the existence of a creator, but rather sought to understand the principles that govern biological form and activity. Judging from Nabokov's scientific work, one may conclude that he was convinced that most of nature's patterns are primarily spontaneous and produced by largely deterministic processes; most were shaped somewhat by natural selection; and a rare few patterns (specifically, *resemblances*) were purely coincidental.

If a resemblance does not appear to have any use, like the dewdrop marking on a Blue's wing described above, it is often either written off to chance or attributed to an intentional being with a sense of humor. This kind of situation is so often played out in Nabokov's fiction it is clear that examples of "nonutilitarian" insect mimicry helped Nabokov define his concept of art. Nabokov's aesthetic theory can be summarized as the answer to the question: What makes an object a work of art, as opposed to an object produced merely by spontaneous mechanistic causes? or an object produced by random chance? It is the suggestion of intentionality. A similar argument was used by teleologists to define telic systems in nature. What makes an object telic, as opposed to an object produced merely by spontaneous mechanistic causes? or an object produced by random chance? Again, it is the suggestion of intentionality.

The insights Nabokov gleaned from teleology demonstrate that the value of a theory may not lie in the specific answers it provides but in the way it identifies a particular problem. Teleologists from Aristotle, to Kant, to Bergson have noted that nature seems to develop in a limited *direction* toward more complex and organized forms than can be predicted by reductive analyses. They also noted that nature often creates *original* systems that seem to anticipate unpredictable future needs by reinterpreting old tools for new uses. Therefore, teleological phenomena were considered analogous to, *though categorically different from*, products of human intention. They concluded that some rational guiding principle must inhere in the order and arrangement of the components of complex systems.

Throughout history, the debate over teleological phenomena has divided into two distinct interpretations, which I will refer to as Kantian teleology and Providence.

These distinctions are also relevant to Nabokov's science and art. Kantian teleologists argue that inherent design (i.e., pattern/orderliness) in biological systems or in the universe as a whole is created by internal automatic principles. A nonphysical cosmic intention is believed to be immanent in physical interactions of the parts of the system itself. They posit an *internal* set of constraints, implying not a rational Creator but a rational universe. True to his interests in Kantian teleology, Nabokov focused much of his scientific work on morphology and the ways in which butterfly wing patterns are shaped not by their fitness vis-à-vis contingencies in the external environment but by internal chemical and mechanical constraints. Nabokov sought to understand a pattern as a whole in order to determine how the organization and activities of individual parts are related to the whole. Such internal processes are lawful and lend themselves to rational description. If morphogenetic constraints could account for the similarity between the monarch and the viceroy, then any additional explanation such as natural selection would be superfluous.

Providence is similar to teleology insofar as it also depends upon a notion of reverse cause: events are thought to be caused by the purposes they eventually serve. (Kantian teleology approaches the notion of "reverse cause" with a different emphasis: the behavior of any part is shaped by the irreducible context in which it functions; the preexisting laws that guide functional relationship determine this interaction, and thus determine the parts.) However, Providence (as defined here) relies upon external, unnatural, or supernatural intervention, which can be quite arbitrary or unpredictable. In *Physics,* Aristotle gives the example of a debtee who runs into his debtor at an opportune moment and is able to collect the money he is owed. Superstitious people often suppose such lucky events are purposeful. Unlike teleology, Providence operates beyond time and space, thus it is not constrained by the laws of physics (it may not break the laws, but it is indifferent to them). Its ways are mysterious to those existing in linear time who cannot understand how the end could affect the beginning. Natural selection can seem Providential if we look at it this way: An observer (a bird) can (mis)interpret one object (a butterfly) as another (a leaf) by means of a false analogy or coincidental resemblance. Thus, the observer redefines the object, causing it to have an effect (or ascribing to it an effect) that cannot be attributed to the object itself. If the effect of a resemblance can be said to have some use to the object, it may seem *caused by* its utility, which leads to a somewhat different mode of teleological explanation than Kantian teleology. Here we have two separate systems interacting, an observer and an object observed. Here effects are not internally constrained by a natural relationship between the parts and the whole. Rules are transcended rather than followed. This is akin to the idea of a "special" Providence form of teleology that posited a divine artist who brings about coincidences for the sake of the functions that they serve. True to his artistic fondness for Providence as teleology (which is really pseudo-teleology since it involves a constantly intervening and intrusive force: telic laws are by definition inherent), Nabokov's literary work involves the role of uncanny coincidence in the evolution of meaning.

Despite our current discomfort with teleological explanations, teleology has made significant contributions to scientific progress. As historian of science Timothy Lenoir explains, many 19th century Kantian teleomechanists were not mystics in any sense.[10] They simply sought to investigate how in biology a

> functional whole gets assembled and why it is organized in one way rather than another ... [They believed] the whole determines the organization of the parts, [but] in so doing it never violates physical laws. On the contrary, the very existence of the [whole system] depends on the most efficient organization of the parts. The end ... determines organization ... by establishing the parameters of possible physical solutions. (179)

The teleomechanists worked in embryology, rational and functional morphology, and cell theory. If one traces the history of teleology through Aristotle and the Kantian teleomechanists, one sees that it eventually led to an investigation of the laws of biological form and pattern formation, anticipating the work of 20th century scientists, such as D'Arcy Wentworth Thompson, Alan M. Turing, and Brian Goodwin, as well as lepidopterist H. Frederik Nijhout, who have offered alternatives to an exclusively adaptationist evolutionary program. Thompson insists that biological form was to be explained in terms of physical and chemical processes. Turing claims the task of the biologist was to discover the set of forms that are likely to appear. Only then is it worth asking which of them will be selected. Goodwin proposes expansions and alternatives to the modern synthesis of Darwinism and twentieth-century genetics. Nijhout has examined butterfly wing patterns using nonlinear dynamics and theories of spontaneous pattern formation.

A likely source for Nabokov's ideas about mimicry is a Russian evolutionary theorist and explorer, Lev S. Berg, whose book *Nomogenesis* (published in Russian in 1922 and in English in 1926) takes a strong position against an exclusively Darwinian evolutionary paradigm.[11] According to Berg, frequently "the utility of mimicry is problematic," and "the explanation of the *origin* of mimicry by means of the struggle for life is inadequate. But when mimicry has arisen, it may, of course, be beneficial to the organism" (324). Berg, relying in part on teleomechanist von Baer, argues that the process of evolution is lawful insofar as relationships between parts and whole are concerned. He takes what is now described as a "developmental systems approach" to evolution. He considers how the actual life of an individual may affect its development, and therefore its phenotype, and therefore its chances of being selected, and therefore the overall genetic frequency of a species' gene pool. Berg relies upon theoretical biology to argue, for example, "the potential power of mimicry in some forms is present before a problematical selection can assume its sway" (323). Each of Berg's foci entails considerations of the notion of (apparently) "purposive" adaptation or directionality in evolution. Significantly, Berg uses butterfly "mimicry" as a key counter-example to evolutionary adaptation determined by reproductive fitness. The English version of *Nomogenesis* includes a forward by D'Arcy Thompson, and so if it is Nabokov's source, it provides a link between Nabokov's ideas about mimicry, contemporary structural evolution, and the theoretical biology of the Kantian teleomechanists.

Although Nabokov had a critical understanding of a number of different kinds of teleology, his own idea of *telos,* or "agent X" as he called it,[12] seems most influenced by Henri Bergson. Evolution, in Bergson's view, is creative, not fixedly mechanistic.[13] As he writes in 1907, if teleology implied

> that things and beings merely realize a programme previously arranged …. As in the mechanistic hypothesis, here again it [would be] supposed that *all is given.* Finalism thus understood is only inverted mechanism. (39)

Bergson argued that functions, dependent as they are on interpretation (or *perception*, to use his term) can have an unpredictable effect on the direction of evolution. In this view, *telos* includes the aspect of originality and must be *emergent*, not prespecified.

We can find examples of emergent *telos* or intentionality in *The Real Life of Sebastian Knight.* Knight's biographer is his half-brother, who is simply called "V." While V is conducting his research, his habitual, and often eccentric, modes of perception sometimes happen to resonate poetically with situations that do not demand them. He recognizes that the use of such *stochastic resonances*, as it were, is a way of creating a new order, or an original work of art. He decides, therefore, to abandon the traditional mode of biographical research and to employ this artistic mode instead. V continues to gather information in a haphazard fashion, accumulating an excessive amount of irrelevant detail, but he remembers and pays more attention to those details that happen to form some aesthetically interesting coincidental patterns. For example, while V unsuccessfully searches for the last woman to break Sebastian's heart, he stumbles upon a woman who had given Sebastian his first heartbreak. V uses the coincidence to organize his narrative. He explains,

> A more systematic mind than mine would have placed [the first heartbreak] at the beginning of the book, but my quest had developed its own magic and logic and though I sometimes cannot help believing that it had actually grown into a dream, that quest, using the pattern of reality for the weaving of its own fancies, I am forced to recognise that I was being led right, and that in striving to render Sebastian's life I must now follow the same rhythmical interlacements.
>
> There seems to have been a law of some strange harmony in the placing of a meeting relating to Sebastian's first adolescent romance in such close proximity to the echoes of his last dark love. (137)

When other interpretable situations arise that cause coincidences to make a kind of literary sense, V thinks that the resultant complex and harmonious structure seems to have been purposefully made available (from a retrospective point of view, that is). What V ends up with is a biography that beautifully and uncannily seems to *mimic* the life of Sebastian Knight.

The "real" and the actual lives of Sebastian represent two separately evolved narratives, which nevertheless develop similar themes. One might compare this to what in evolutionary biology is called *convergence.* In the case of a hummingbird and a hummingbird moth, the bird and the insect traveled separate evolutionary pathways; nevertheless, each has been shaped by a similar niche (see fig. 2). Thus, they resemble each other. To my knowledge, no sensible person has bothered to make the argument that the resemblance itself confers a reproductive advantage. The hummingbird moth is *not* a mimic of the hummingbird. Neither the moth nor the bird required the other as a model on which to base its appearance. Similarly, in *The Real Life of Sebastian Knight,* V does not make much use of the facts of Sebastian's life to model the biography. Rather, he focuses on *his own* pathway, his own recollections and feelings, as well as the coincidental patterns he encounters in his research.

Figure 2: A Hummingbird Moth, also called a White-lined Sphinx Moth (*Hyles lineata*), of the family sphingidae. Photo by Thomas H. Hogan, 1986. Used by permission.

In the end V feels the biography is a more interesting achievement than the actual life because it does somehow ring true, and such near perfect convergence is so unlikely as to seem, perhaps, supernaturally contrived. The reader realizes the irony, however, knowing that two individuals toiling in a similar niche will inevitably encounter and be influenced by similar circumstances, which may very well result in a "law of some strange harmony."

To summarize, this paper has so far been concerned with three types of resemblances in nature, none of which can be properly called mimicry. The first is the nonutilitarian viceroy-monarch resemblance, which, as I demonstrate below, can be attributed to their both being formed according to similar morphogenetic, chemical, and energetic constraints. The second is the resemblance between a dead-leaf and a particular butterfly, which, as I also demonstrate below, probably arose suddenly by coincidence, not by the gradual refining powers of natural selection. The third, which I only mention in passing, is the resemblance between hummingbird and hummingbird moth. These similar morphologies were created independently by natural selection, but the resemblance itself does not serve a purpose. In each case, the resemblance is incidental, that is, it does not exist because of the function it serves. Resemblance then is something of coincidence.

Although Nabokov was charmed by coincidences, there is no reason to believe he did not have an appreciation of the laws of probability. It is rather straightforward to understand that samples drawn at random may not be without some coincidental order. In his fiction, Nabokov often notes that people commonly think they have found evidence of supernatural intention in apparently improbable events, good or bad luck, and even funny coincidences. It is important to realize that, as Michael Wood has noted, Nabokov himself never interpreted or assigned symbolic meanings to coincidences, though his characters frequently did. In "The Vane Sisters," Sibyl Vane and her friends tend to assume that random systems should show no regularity at all; therefore, if *any* kind of pattern is detected, they believe it could not have arisen by chance, and they assume that patterns without any other cause must have a patterner.

It is trivial to say that any one *unspecified* member of the 12,000 or so species of butterflies will *by chance* resemble another unspecified member of a different species or some unspecified object in nature. Similarly, it would also be trivial to predict that *someone's* lottery ticket will match the winning number in a given drawing without saying who will win.[14] Although there is nothing magical about winning the lottery, every winner cannot help but feel a bit favored by the gods of fortune. This is because, as far as the lottery winner is concerned, he or she did prespecify the winning number. What seems odd about mimicry is that the advantageous form toward which natural selection must work seems prespecified. For example, the viceroy species is said to have evolved toward, not just any advantageous form selection could find for it, but one particular form, the monarch species. This kind of adaptation would be very different from a more straightforward form of adaptation such as camouflage. Moths, whose color blends with tree bark, are excellent examples of Darwinian natural selection favoring a nonspecific unpredetermined pattern. Moth wings are patterned, naturally having dots and lines, which makes them more regular than tree bark. The wing patterns that are least noticeable against tree bark are those that are busy. A simple bold wing pattern of dots and lines would stand out against bark. However, busy wing patterns and bark fool the eye and blend together. Because wing patterns are less random than background, the amount of information in the wing pattern must be relatively higher if camouflage is to work. The wing pattern must also be of a drab color, but, as Nijhout points out, "there is no requirement that the elements of the pattern be of a specific shape" ("Development" 236). The important point to understand is that camouflage wing patterns do not resemble bark in pattern or shape. Camouflage is not mimicry. Because any busy wing pattern of various configurations of dots and lines may be selected as camouflage, natural selection might very easily and gradually evolve a large number of various kinds of complicated wing patterns that might function as camouflage.

If natural selection had only one pattern that it could select for fitness, for example a pattern that looked like the wing pattern of another insect, then the chance that natural selection would find it would be relatively low, just as the odds that a *particular* lottery ticket will win are low. Since non-inherited resemblances do occur frequently, there must be some other mechanism that is causing this. An explanation might assume one of two things. First, all numbers are not equally probable, that is, the nature's lottery is biased. It is argued that this is the case in the viceroy-monarch relation. Second, the resemblance only seems to be prespecified, as it does to the individual lottery winner who feels especially favored by fortune. I argue this may well be the case with the dead-leaf butterfly.

Natural selection alone could not *create* a mimetic form by gradual fine-tuning. The form would have to appear suddenly as a definite resemblance since a non-resemblance that was an earlier stage for the resemblance would not be selected because of what it would eventually resemble. This, I argue, is the crux of Nabokov's dispute with the Darwinists of his day. Nabokov accepted the fact that a fortuitous resemblance might confer a reproductive advantage through predator evasion once it was already in existence. The question Nabokov posed about "mimicry" was: How do resemblances *arise*? gradually, by natural selection? or somewhat suddenly, by chance?

2 Structural Evolution: How Dynamical Constraints Govern Chance

If one wanted to argue that the viceroy-monarch relation arose "by chance," one would have to discover limiting mechanisms that would make this resemblance probable. Today the goal of structural evolutionary theorists, like that of the 19th century Kantian teleomechanists, is to elucidate the "principles of organization" that result in the appearance of similar patterns in nature. They study the energetic, mechanical, and morphogenetic constraints that limit the range of possibility in biological forms. Like the teleologists, structural evolutionary theorists contend that these constraints result in a relatively small number of structural archetypes considering the multi-dimensional space in which they evolve. Thus, if the Earth's history could be set back to a more or less similar initial position and run again, many of the forms we know today would reappear.[15] The task of biologists today, then, is to discover which forms are likely to appear. Only then is it worth attempting to estimate which of them will have a differential fitness significant enough to confer a reproductive advantage.

Structural archetypes occur throughout nature. They are sometimes referred to as *structural attractors* and compared to Platonic solids because they exist, as concepts, *prior to* their appearance in natural processes. The constraints underlying attractors are the kinds of mechanisms that Nabokov thought were behind mimetic forms, not selection for reproductive fitness. Nabokov argued that all butterfly patterns are "variations on a theme," which was a favorite phrase of teleomechanists. To lepidopterists in the 1940s, this usually meant a variation on the *nymphalid ground plan* (fig. 3), which was conceived independently in the 1920s by both B. N. Schwanwitsch and F. Süffert. The ground plan was thought to be a Platonic ideal from which all possible wing patterns were derived through the distortion of individual elements. The existence of such a template would mean a wing is not a blank sheet on which any design can be developed if it happens to confer a reproductive advantage. Moreover, it would also mean that one need not posit a Darwinian primitive ancestor from which species diverged in order to explain similarities between families and species. The ground plan fits the Kantian idea of a teleological principle as a heuristic device, and it can be used to make predictions about evolution because some patterns are more likely to occur than others, regardless of utility (Nijhout, "Development" 221).

Nabokov did not regard the ground plan as a primitive form whose individual elements were variously distorted in later descendants. He regarded the ground plan as the initial conditions and set of constraints that limit the otherwise stochastic process of pigment diffusion across a wing surface.

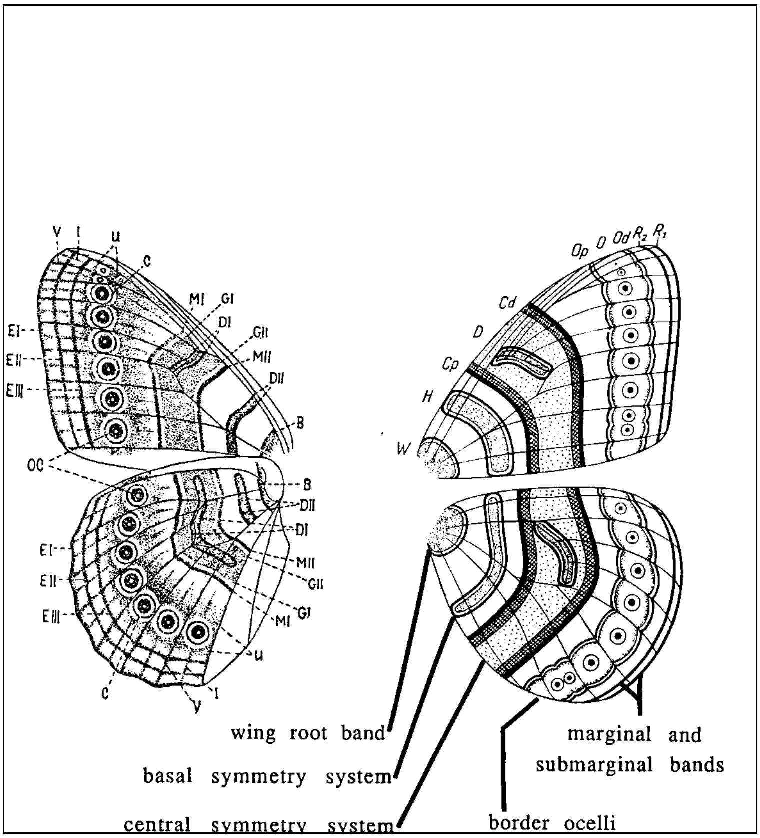

Figure 3: The nymphalid ground plan. The spoke-like sections are *wing cells*. Within each cell, pigment can diffuse in various ways, creating up to five distinct line segments (as in the marginal bands), spots (as in the ocelli), smudges (not shown) or other shapes (such as scalloped lines, around the border ocelli). This illustration represents two alterative expressions of all possible elements. (Left from Schwanwitsch, 1924; Right from Süffert, 1927.)

Nijhout has recently explained the origins of the ground plan using a reaction-diffusion model developed by H. Meinhardt in 1982. Nijhout applied the model to a domain that resembles an individual spoke-like section of a butterfly wing (see fig. 3). The proper term for this spoke-like section is a *wing cell.* Nijhout's model of pattern formation within a wing cell starts with a rectangular field with the bottom side open (see fig. 4), where that part of the wing cell would attach to the insect's body.

Meinhardt's model assumes the existence of two substances, an activator and an inhibitor, distributed equally throughout a rectangular shape. The activator is so-named because its by-products (i.e., its syntheses) tend to increase their own production. The inhibitor is so-named because it neutralizes the activator's by-product.[16] Thus, only if the inhibitor is present in the right amount will a homogenous steady state throughout the rectangular field be maintained.

Nijhout found that if the activator is slightly increased along three of the edges, where the wing veins are, a reaction-diffusion process occurs that gives rise to dynamically stable patterns. (The steady-state behavior might go out of balance along the edges because these areas do not get the same balancing feedback from all neighboring regions as other areas do. In this way, a sudden increase in activation might occur spontaneously.[17]) Soon after increased activator appears at the edges, it diffuses toward the center. A line of activator forms in the center then retreats toward the open edge. In the concentrated areas at the end of the receding line, activation increases even further. Then these areas are finally pinched off by surrounding areas of inhibitor, leaving traces of activator production behind. These traces, together with any traces that may have been left on the edges, form areas of greater or lesser density. This difference in density is metaphorically referred to as the "topography" of the wing cell, which in turn affects the diffusion of pigment. Individual pattern elements of the ground plan (see "major themes" in fig. 5) are determined according to whether or not the topography "attracts" or "repels" pigment, condensing or stretching it into various shapes.

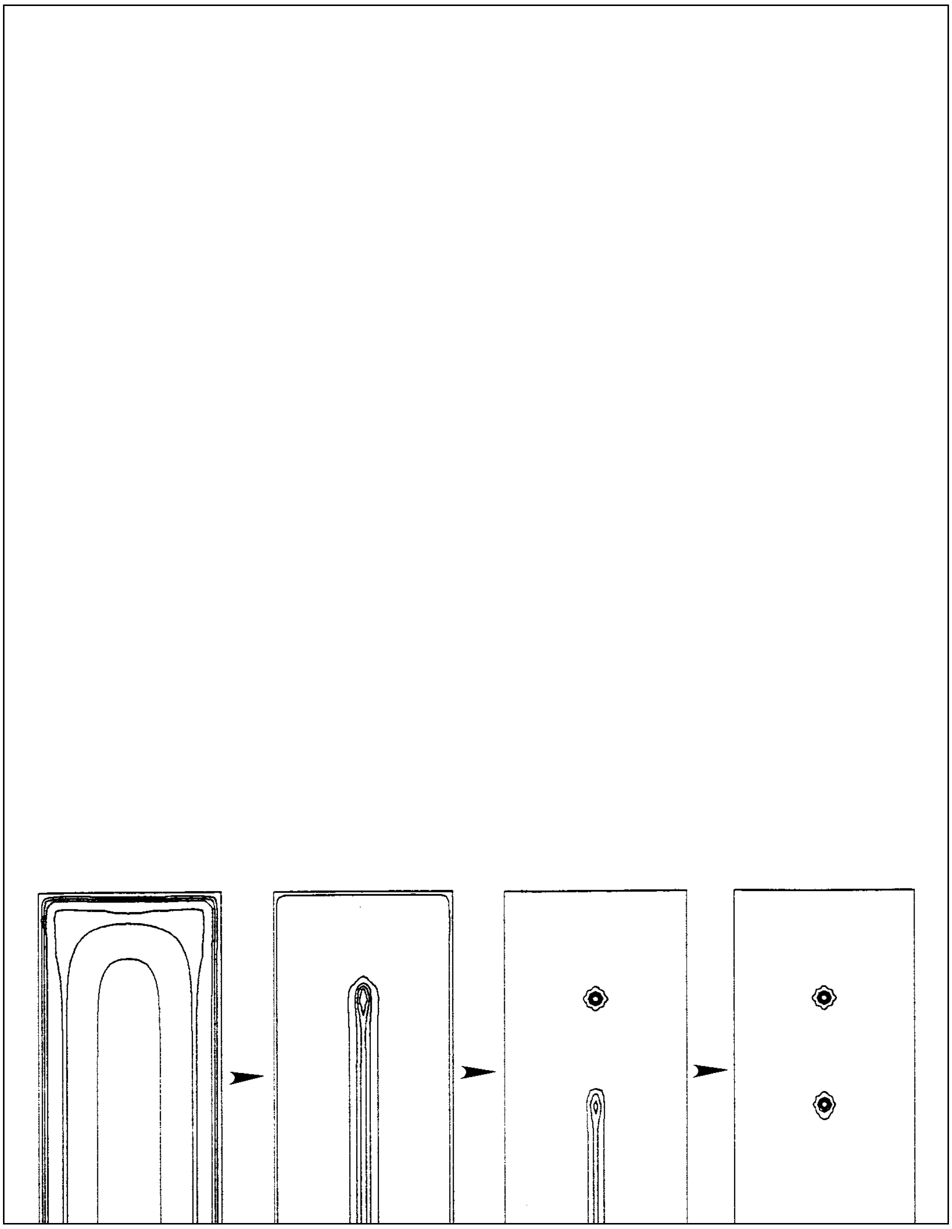

Figure 4: Nijhout's model of pattern formation within a wing cell. Activation is increased along three sides (left, top, right). Activator gradually flows toward the center. A line of activator forms then retreats toward the open edge (bottom), like a stream of water leaving droplets behind. Depending on the initial and boundary conditions, different patterns arise. For example, activator may or may not be left

behind on the edges, or an additional point may or may not be left behind in the center. (Adapted from Nijhout "Development." Used by permission.)

Both Nijhout and Nabokov describe overall pattern formation in terms of individual wing cells. They both realized the significance of the fact that each wing cell is separated by veins, preventing communication (diffusion) between wing cells and providing a frame that shapes the reaction-diffusion process. This was not generally acknowledged in Nabokov's day. He noted that sometimes one wave of pigment in a given wing cell might happen to reach a threshold at about the same time as the waves in its neighbors, giving the impression of a band running across several wing cells. See, for example, the marginal bands and the symmetry bands in the ground plan (fig. 3). However, Nabokov argued, the bands are merely "pseudo lines," "manmade" lines, or macules in "linear disguise." He was quite adamant about this because he recognized it as key to understanding pattern formation in butterfly wings. In "The Nearctic Forms of *Lycaeides* Hüb. (Lycænidæ, Lepidoptera)," Nabokov writes,

> What we see as a transverse, more or less sinuous, "line" or "row" of spots seems to me to be the outcome of two unrelated phylogenetic phenomena. The "upper" part of the "row" … is formed by spots having radiated fanwise … owing to an apicoid extension of the wing texture; the "lower" part … [has] been pulled out … presumably by a cabitoid extension … This is why the classical conception of a row of ocelli [eyecells] as the result of a statically placed line or band having broken up into spots seems to me absolutely irrelevant to the understanding of the Lycænidæ pattern. Insofar as spots have been evolved in this family, they occupy different positions in different species or genera, and what we see is [sic] not the remnants of a definite band in a definite place, but this or that stage of a more or less coordinated longitudinal movement of spots … (certain comet-tail traces of this progress are sometimes caught and fixed aberrationally). In a word it is not a row of squares on a chessboard, but a shifting line of attacking pawns. (*Nabokov's Butterflies* 282)

In "Notes on the Morphology of the Genus *Lycaeides*," Nabokov further explains how spots and "pseudo lines" emerge when progressively shorter waves of pigment reach a limit and a gradual deepening and concentration of the pigment occurs, forming a spot. Then the whole process is repeated again in a second wave down the length of the wing cell. If the process happens to be activated earlier than normal in development (by, say, some extreme temperature), an additional spot may occur. Pattern, Nabokov concludes, is the "*result* of those processes and not a 'primitive' line which Mother Nature automatically traced with her brush" (*Nabokov's Butterflies* 327-329). Patterns are not genetically fixed: stability is as determined by developmental context and dynamical constraints as by genes. Fitness selection of genes is not required to drive nature in this direction; the tendency is already inherent in the laws of biological form. Although Nabokov's obsession with the dynamical nature of patterns may have seemed eccentric to other lepidopterists in the 1940s, it is now clear that Nabokov was beginning to sketch out a theory of spontaneous pattern formation that was not fully articulated until the 1950s when Alan Turing published "The Chemical Basis for Morphogenesis." One might compare Nijhout's understanding of the effect of wing cell topography on pigment diffusion to Nabokov's observation that pigment seemed to be "pulled out" during development by wing "texture," diffusing from high density to low density areas. In significant ways, Nijhout's research recalls Nabokov's. Both describe pattern formation as that which, in Nijhout's words, is "not specified by a detailed genetic program or blueprint, but [as] emergent properties of relatively simple processes occurring in particular physical or chemical context" ("Pattern" 2). Nabokov's Bergsonian notion of emergent teleology would have made him sensitive to the existence of spontaneously formed patterns which *seemed to* but *do not require a predetermined program*.

According to Nijhout, a rather simple model "can generate virtually the entire diversity of patterns found in nature" ("Development" 211, 218). (One must simply allow, first, that the relative values of the two diffusion coefficients or of the decay constants in the lateral inhibition model can be varied and, second, that the activator along the wing cell edges will naturally diminish as it flows toward the open end.) The range of spontaneously generated patterns includes "eyespots." Indeed the prevalence of eye-like macules is expected given that there commonly is found a single point trace in the center of the wing cell (see fig. 5). Pigment will tend to diffuse from the point, leaving a relatively lighter center behind.

As Peter Godfrey-Smith has noted in the context of teleological arguments, "properties due to constraint" should not be considered functional because whatever *accidental functionality* they may come to have does not explain *why* they exist. One must be careful to distinguish between "fortuitous benefit and genuine adaptation" (196). It should be possible to design an experiment to see whether or not eyespots are any more common in nature than would be predicted by Nijhout's model regardless of whether or not they might more reproductively fit. Another experiment might be designed to test how likely it would be that the ground plan constraints might spontaneously generate two separate species that exhibit a kind of family resemblance, such as the viceroy (Nymphalidae Limenitis *archippus*) and the monarch (Nymphalidae Danainae Danaini Danaus *plexippus*).

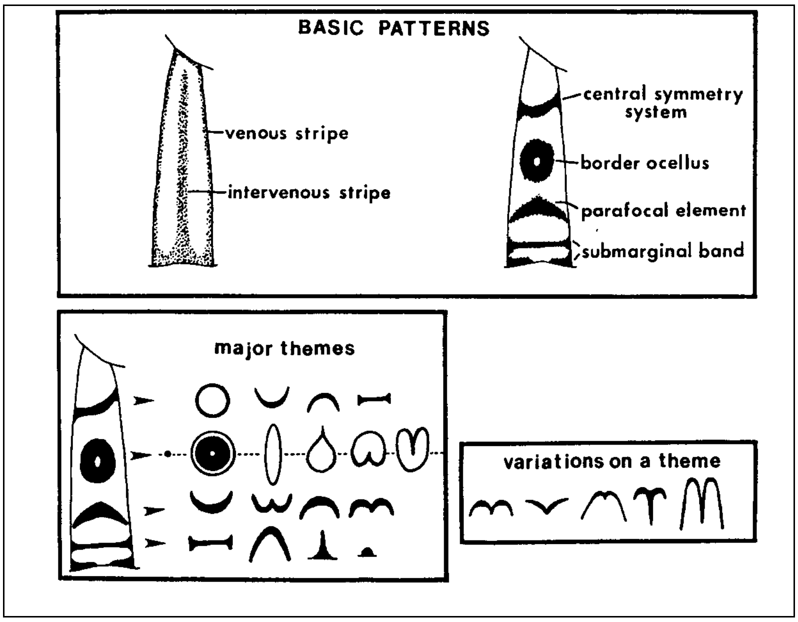

Figure 5: There are two, mutually exclusive, major themes in wing patterns, the intervenous stripe (top left), and the ground plan (top right). Major variations of the ground plan elements are shown in the lower left. Further variations on one of the elements are shown lower right. Variations can be attributed to differences in the reaction-diffusion process during individual development or across species. (From Nijhout "Development." Used by Permission.)

While Nabokov was working at the Museum of Comparative Zoology in the 1940s, it was believed that the viceroy and the monarch had traveled two different evolutionary pathways, the viceroy driven to an unlikely form by natural selection alone, the monarch frozen in a state of genetic equilibrium. The two species were said to exemplify convergence. Yet, unlike the convergence involving hummingbird moth and the hummingbird, for example, the viceroy was said to have been shaped by the function of its resemblance to the monarch, not by their similar environmental niches. According to Batesian mimicry, the fact that the viceroy looks like the unpalatable monarch makes it less likely to be preyed on by birds that have sampled monarchs. Therefore, a resemblance might be reproductively advantageous to viceroy butterflies as they would be preferentially selected. Nabokov tasted both the viceroy and monarch himself and reported that they *both* were unpalatable (*Nabokov's Butterflies* 535). Credulous Darwinists continued to believe the Batesian mimicry story without testing it themselves. Finally years later, a study by Lincoln Brower and David Ritland (using birds to do the taste test) found that indeed the viceroy is also "bitter," and they concluded that "the viceroy butterfly is not a Batesian mimic" (497). After Brower and Ritland discredited the Batesian theory as an explanation for the viceroy-monarch relation, the Müllerian theory of mimicry took its place.[18] According to this theory, different species of butterflies, each unpalatable, mutually reinforce the association between appearance and bitter taste. But as R. I. Vane-Wright notes, "Because, in addition to sharing the same warning signal, all members of a Müllerian group are well-protected, it has been argued that no deception is involved and, therefore, they are not really mimics at all" (460).

There is more to this mimicry mystery. A 1984 study by J. R. G. Turner provides some support for Nabokov's argument (in "Father's Butterflies," see below) that natural selection may not have gradually and painstakingly shaped resemblances between different species of butterflies, such as the viceroy and monarch. Turner concludes that Müllerian mimics and their models have *not* traveled long and unique pathways. Turner shows that because butterflies share a common *toolbox* (e.g., laws guiding reaction-diffusion processes) for forming patterns, a single mutation leads to a large change in appearance, bringing one species reasonably close to another. Turner's findings are consistent with Nabokov's view of pattern formation. Nabokov supposed that the resemblance between similar species was the product of similar mechanistic, temporal, or chemical constraints. Nabokov never denied that functionality *might* help stabilize the resemblance between "mimics" once it is already in existence, but the initial cause of the resemblance must be sought in some ahistorical limiting principles, such as the ground plan constraints, which have nothing to do with survival or increased reproduction. One can still argue against Brower, Ritland, Van-Wright, and Turner if one likes (as Boyd insists, Nabokov's "position [on mimicry] has proved to be wrong"), but there is no denying that Nabokov's comments against viceroy-monarch mimicry receive compelling support from these scientists.

Nabokov argued against Darwin's idea of gradual adaptation toward increasing reproductive fitness, which, in its extreme interpretation, requires each new mutation to be functional if it is to survive and replicate. This is an absurd Panglossian notion. Not everything in nature is due to function. It is improbable that the viceroy species was gradually driven nearer to a likeness with the monarch species while the monarch population was randomly mutating in some other direction. One must suppose that the monarch remained in a state of genetic equilibrium. This is not impossible, but not particularly likely, unless a neutral form of selection is introduced to help explain the equilibrium. In which case, one might as well argue that the same kind of neutral mechanisms that found and continue to stabilize the monarch pattern also work for the viceroy pattern, and thus, it would not be necessary to bring in the concept of reproductive fitness to explain the similarity. In "Father's Butterflies" (written in 1939), Nabokov considers this and ridicules the logic behind Batesian mimicry. Selection according to function could only result in Batesian mimicry if the mimic were pursuing this goal consciously, having conferred beforehand with the model and determined that the latter, during the full number of centuries required by the toiler at evolution toward a gradual attainment of resemblance, would remain unchanged (in the kind immobility that a painter demands of his model). The process would accelerate further if the model just as consciously indulged the imitator by mutating part way in proportion to the mime's mutations, or if the very goal of the imitator were to change concomitantly with the evolutionary metamorphoses of the model, in the same way a painter, having begun a nude of a young female model, might strive for a likeness with such ardor that, as he tirelessly recorded every trait, he would, in the end, find that he was depicting the old woman into which the model had evolved during her plurennial pose. Yet the concept of evolution in no way presupposes either the existence of a conscious and focused will within a developing creature, or a coordination of actions between two creatures or between a creature and its environment. As for the presumption that nature mesmerizes subjects selected for mimetic study, influencing them to perform specific roles, that notion must be relegated to fantasy, for where are the anchor points for the cobweb of hypnosis? The same variations that might result from a blind struggle for survival, no matter how credible their results may *appear …* endlessly retard the putative course of a given evolutionary process, for it is here that the element of happenstance reappears. (*Nabokov's Butterflies* 225)

Since Motoo Kimura first introduced *The Neutral Theory of Molecular Evolution* in the 1960s, research in evolutionary dynamics has recognized a number of nonadaptive forms of evolution, which can occur in a variety of evolutionary settings, one of which is a fluctuating environment. Nabokov's description of the difficulties that a bug-artist would have in representing an ever-changing model refers to such an environment. Darwinian natural selection cannot maintain consistent pressure in a particular evolutionary direction if the contexts in which natural selection makes its interpretation of fitness are constantly in flux.

Even in a fluctuating environment, a species can remain stable. In the 1940s it was widely believed in biology that, without Darwinian selection to favor some forms over others, most structures (in freely breeding populations of ample size) would have no ultimate power against the tendency to disorder, enshrined, for example, in the second law of thermodynamics, resulting in a perfectly random distribution of hugely diverse forms. Nabokov realized that this was not the case. In fact, the existence of fluctuating environments (which render natural selection ineffective) allowed him to see more clearly the evidence of other mechanisms maintaining order in the face of constant random mutations.

By considering the effects of spontaneous organization of reaction-diffusion processes and the limits illustrated by the ground plan, one can better understand the likelihood that the viceroy and monarch wing patterns might arise without the help of external agents or environmental conditions consistently favoring one form over others.

Above I have referred to the viceroy-monarch relation as a case of apparent design in nature without purpose. Thus, in Kantian terms this phenomenon is valid for the aesthetic judgment but not the teleological judgment. The common occurrence of this type of resemblance (it can hardly be referred to as mimicry) is attributed to the mechanisms of spontaneous pattern formation, not to fitness. In the next section, I will consider another type of resemblance, the dead-leaf "mimic," that would appear to be valid for the teleological judgment: the resemblance's apparent function would seem to be the cause of its existence. However, as I will show, the butterfly's resemblance to a leaf may only occasionally serve an *accidental functionality*, which does not explain why the resemblance came to exist.

3 Neutral Evolution: How Diversity Allows for Useful Coincidence

Now I will illustrate how a coincidentally useful form such as a dead-leaf butterfly might have emerged, not gradually through selection of ever-increasing reproductive fitness, but suddenly with the aid of neutral evolutionary mechanisms working with the ground plan. This illustration will also parallel the fact that the fossil record indicates that evolution often proceeds in sudden jumps, not by Darwinian-style gradual adaptation.[19]

Karl Ernst von Baer, one of the most prestigious teleomechanists and father of modern embryology, may have been one of the first biologists to take notice of the effects of what is now known as neutral evolution. It is plausible that Nabokov was aware of von Baer. The last great effort made by teleomechanists against gradualism in Darwinian evolution took place in Nabokov's home of St. Petersburg just decades before Nabokov's birth. Von Baer, who had moved to St. Petersburg and was active there until 1876, was one of the first explorers to visit Nova Zembla. Von Baer published two articles "Sketch of animal life in Nova Zembla" and "On the recent Russian expeditions to Novaia Zemlia." (The latter emphasizes the colorlessness of the air that far North, pointing to the unreliability of Kinbote, who emphasizes a very blue Zemblan sky.) Von Baer was concerned with mechanisms for stasis and the maintenance of biological order. He discovered that the early stages of embryological development are both very conservative and restrictive of later development. 20th century research has shown that because the developmental process is integrated (as von Baer argued), mutations in the genotype will not necessarily result in phenotypic difference.

According to Kimura's theory of neutral evolution, when different genotypes result in a single phenotype, natural selection has no way of favoring one phenotypically equivalent genotype over another. Under such conditions, random mutations in the genotype accumulate unchecked for long periods of time. This results in a great amount of diversity in the gene pool, all of which is selectively neutral.

To illustrate the concept of many-to-one genotype to phenotype mappings more concretely, let's say there is a species of butterfly whose genotype for a typical kind of wing pattern formation (see fig. 3) can be designated as sm***s. The letters and asterisks illustrate (in a very simplified manner) a genetic sequence. The asterisks are *wildcard* genes. Only the first two and the last letters have to be set in a particular way (s, m, and s, respectively) for normal sm***s forms to be produced. Therefore, the four butterflies with the following distinct genotypes are virtually identical in appearance:

smokes smells smiths smiles

Despite the genetic differences in these four genotypes, they all result in essentially the same wing pattern phenotype. The final s represents a regulator gene than can inhibit or excite the activity of the wildcard genes in such a way that the pattern produced is the same in every case. By definition, Darwinian natural selection cannot see or differentiate wildcard variability. This results in long periods of species stasis, which are inevitably followed by sudden appearances of new species.

It turns out that several 19th century teleologists were aware of the phenomenon of sudden speciation or what James P. Crutchfield calls "epochal evolution."[20] While von Baer investigated mechanisms underlying genotype diversity and *phenotype stasis* (herein considered directionality) as described above, another teleologist Etienne Geoffroy Saint-Hilaire investigated phenotypic change and *sudden speciation* (herein considered originality). Geoffroy Saint-Hilaire studied *teratology*, that is, aberrations in morphological development that led to phenotypically unique individuals. Based on this work, he developed a theory of evolution suggesting that morphological change was not slow or gradual but dramatic, occurring when distortions in the universal ground plan were suffered by the developing embryo. 20th century research later confirmed this work, showing that large errors in the early embryonic stages set the stage for further development. The effect of an error may be replicated causing serious aberrations in form, often leading to spontaneous abortion but sometimes leading to what Geoffroy Saint-Hilaire considered "monsters" and what we call mutants today. Given his interest in teleology, Nabokov was probably familiar with this well-known research. He, like Geoffroy Saint-Hilaire, also conceived of speciation as a sudden event, which he compared to the bursting of a bubble (*Nabokov's Butterflies* 218).

In the 1960s and 1970s, Nabokov was more absorbed with his literary career than with butterflies. He missed the opportunity to compare Kimura's newly articulated theory of neutrality to von Baer's or Geoffroy Saint-Hilaire's writings. Nevertheless, we can assume that he would have been able to do so. Even Nabokov's literary works involve the kind of conceptual framework needed to understand evolutionary neutrality and sudden speciation. Just as a population can accumulate a large amount of irrelevant genetic diversity (wildcards), a writer might accumulate a large amount of irrelevant and diverse detail awaiting some turn of events that might make them relevant. As "V" discovered in *The Real Life of Sebastian Knight*, the more diversity one accumulates, the greater the chance that something useful might be found.

In biological realm, the question to be considered then is: How does this hidden genetic diversity ever get expressed, allowing selection to "use" it? What constraints might limit the diversity such that natural selection may be more effective? A possible answer involves the effects of environmental conditions on the developmental process.

It so happens that butterfly wing pattern development is particularly sensitive to climatic conditions. Many species have wildly different summer and winter or wet- and dry- season forms. In fact, the dry-season form of *Precis almana* looks a bit like dead-leaf mimic although the wet-season form does not (fig. 6). Studies have shown that near-lethal high or low temperatures temporarily disrupt the activity of certain genes during development (Nijhout, "Development" 130). (This might have been the kind of thing that Geoffroy Saint-Hilaire was investigating.) When this happens to an entire population, the previously hidden wildcard diversity can be suddenly revealed, and, in turn, natural selection can act on it.

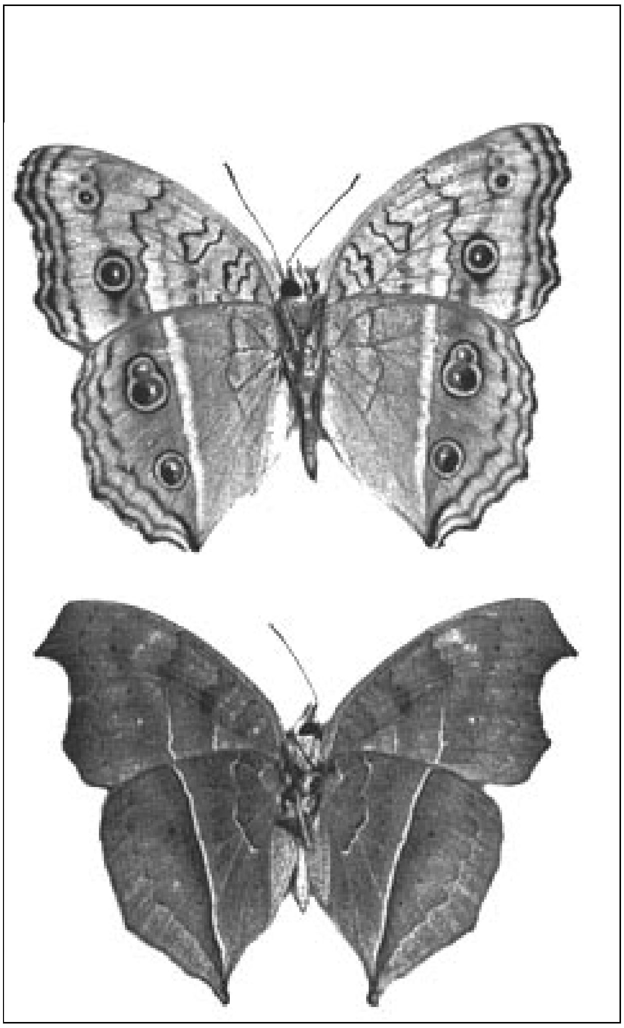

Figure 6: The wet-season form (top) and the dry-season form (bottom) of *Precis almana*, both showing the under sides of the wings. The dry-season form is conventionally called a dead-leaf mimic, although it does not look very much like a dead leaf. It does, however, resemble a related species called the *Kallima* (fig. 1), which is a fairly convincing leaf mimic. (From Nijhout "Development." Used by permission.)

There is, therefore, a relationship between how individual butterflies within a species can differ depending on environmental conditions during development and how new species evolve and differentiate from each other. Such issues are now studied as the developmental systems approach to evolution. It is worth noting here that many 19th century teleologists investigated a possible relationship between the developmental process (ontogeny) and the evolutionary process (phylogeny).

The experimental disruption of specific genes during development is now widely used to study how new butterfly species arise because it simulates the effects of natural mutation. According to Nijhout, "temperature shock could thus mimic an alteration [a mutation] in a mechanism that regulates gene expression during pattern development, and the [aberrations] that develop would reveal the consequences of small quantitative differences in the cellular mechanisms of gene regulation" ("Development"130). Whereas mutational events are typically unique to individuals, wide-spread disruption of pattern formation caused by environmental conditions (extreme temperatures, for example) might affect large numbers in a population. In such a situation, if regulator genes happened to be knocked out, natural selection would have the opportunity to act on a generous sample of previously hidden genetic diversity, thereby increasing the likelihood of the aberrational forms becoming favored and established.

To illustrate more concretely how wildcard variability can be expressed, we return to our thought experiment that represents genetic sequences with words. Now let's say our population of butterflies with the genotype sm***s is exposed to near-lethal high temperatures during development. The trauma temporarily knocks out the final *s* gene during development, as indicated in italics, producing four aberrations, which are all different phenotypes.

smoke*s* smell*s* smith*s* smile*s.*

In these forms, the final *s*, a regulator gene, does not function. Hidden genomic variability in the wildcards is now revealed because their activity is no longer limited by the regulator gene.

Generally speaking, in most temperature-shock studies, a number of distinct aberrations appear, though on the whole, most tend to be duller in color and have smaller eyespots than the parent. The double bands of the central symmetry system (see fig. 3) tend to merge and shift toward the axis of symmetry. Marginal and submarginal pattern elements (see fig. 3) tend to be lost (Nijhout, "Development" 122). In sum, compared to their parents temperature-shock aberrations are more drab in color and their markings contrast less with wing background.

The remarkable result is that some aberrations closely resemble other species. These imposters are called "pheno*copies.*"[21] Phenocopies look like other species, but they still have the genotype of their parents. In our thought experiment, a phenocopy is still an sm***s butterfly even though it does not express the original wing pattern. Moreover, it still produces normal offspring, like its parent.

Taking our thought experiment one step further, let's say that a temperature-shock damaged smile*s* happens to look very much like a dead leaf (whose genotype we designate with the sequence of letters: toiler) even though smile*s*' parents look nothing like leaves whatsoever. It is not as unlikely as it may seem that offspring could differ so much from their parents. As Nijhout has noted, each individual pattern element in the ground plan tends to be controlled by one or very few genes ("Development" 243-244). Moreover, in 1927 Süffert deduced that only two modifications of the ground plan account for the main characteristics of the dead-leaf pattern: the distal half of the central symmetry system is aligned with the outer band of the ocelli border, forming a single line down the center of the wing (like a midline leaf vein), and most other pattern elements are muted (fig. 7). Therefore, one might easily conclude that the first dead-leaf forms, perhaps even the *Kallima* (figs. 1 and 7), could have arisen as phenocopies produced by trauma that knocked out one or two genes. Perhaps it is not incidental that *Kallimas* tend to occur in hot climates.

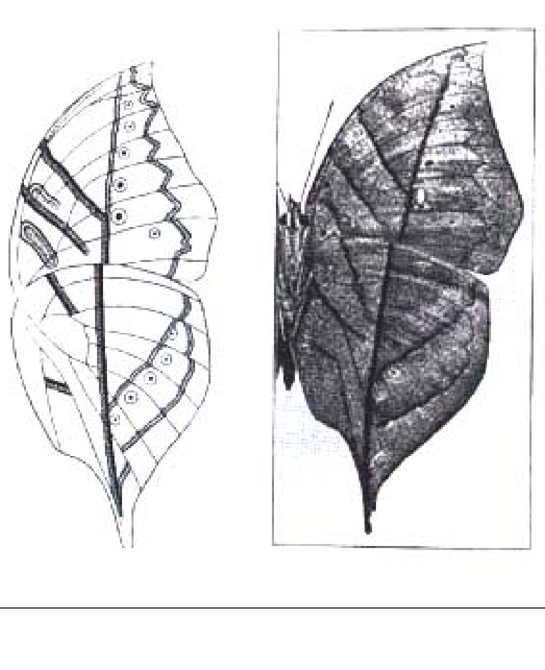

Figure 7: The form of a dead-leaf butterfly (Lepidoptera: Ditrysia: Papilionoidea: Nymphalidae: Nymphalinae *Kallima inachis*) is achieved with relatively few modifications of the elements of the ground plan (fig. 3). In the upper wing, reduced eyecells (ocelli) and the left half of the ocelli border have moved to the center, connecting with a merged version of the central symmetry system. Together the ocelli border and the symmetry system form a single line down the center, which looks like a leaf vein. (From Süffert, 1927.)

It is important to keep in mind, however, that the first dead-leaf phenocopy, if such an animal ever existed, would still have been a member of its original species. Even though it looked like the dead-leaf species with the toiler genotype, it would still have had the genotype sm***s. Despite the distortions suffered during its own development, any heat-shock aberration will still produce normal offspring like its parent. However, it has been shown that if only one particular kind of aberration is selected and interbred for many generations, eventually offspring begin to produce the aberrant forms *without* being exposed to temperature shock during development (Waddington). This process is known as *genetic assimilation*.

In the 1950s, it seemed as if Lamarckian evolutionary theory involving the inheritance of acquired characteristics might apply here, but this is not the case (Nijhout "Development" 122). Genetic assimilation can be explained if one demonstrates how the probability of a given mutation is increased by segregation. For example, if smiles phenocopies (which look like dead leaves) tended to segregate themselves,[22] the probability that part of the population might successfully mutate into, say, an individual with a toiler sequence (which produces dead leaf forms without temperature shock) is higher than it would be in a freely interbreeding population with more genetic diversity. In a population of, say, interbreeding smokes, smells, smiths, and smiles butterflies, only one forth of the genes are properly set, as indicated in bold face font, to create a toiler phenocopy if the regulator gene is disabled. In a pure smiles population, half the genes are properly set, as indicated in bold face font, to produce toiler phenocopies.

So then let's assume that extreme temperatures continue to cause trauma during development, and butterflies with the genotype smiles all appear as phenocopies of toiler and segregate themselves from other sm***s that are not phenocopies of toiler. How many generations of mutational events would it take for a population made entirely of phenocopies with the genetic sequence smiles to get to toiler? And what kinds of constraint does nature put on the mutation process? To investigate these questions, I will make use of a favorite game of Nabokov's, which he called "word golf." In this game, one starts with an English word (for example, smiles) and changes one letter at a time until one arrives at a target word (for example, toiler). Each letter change along the way must result in an English word.

The game happens be remarkably suited to illustrating how evolutionary change works: just as word golf does not allow the use of nonsense letter combinations, nature aborts deleterious forms. For example, imiles is prevented from getting into the evolutionary game. Desirable mutations (smiler, for instance, in generation one, and soiler, in generation two) only have to compete against other *viable* forms (smiles, smiley, and stiles, for instance), not all possible forms. One should also note that there are fewer possible viable forms in an all smiles population than in the mixed population. In the mixed population, the first generation of viable mutations might yield: stokes, spokes, smoker, smoked, smalls, shells, stiles, and smiler. In a pure smiles population, there are only three possible viable mutations in the first generation, stiles, smiley, and smiler. The possible viable mutations in succeeding generations would be:

stiles smiley soiled boiled

boiler

smiles smiler soiler toiler

A butterfly with the genotype smiles can produce a stiles, smiley, or a smiler mutant. A stiles, in turn, can produce a smiles mutant. A smiler can produce a soiler or a smiley mutant. A smiley can produce a smiles or a smiler. A soiler can produce a soiled, boiled, or toiler mutant. A soiled can produce a soiler or a boiled. A boiled can produce a boiler or a soiler. This illustration shows that even if a mutation goes in an undesired direction, for example soiler to boiler, in the next generation a mutation in the desired direction (to toiler) may occur. Therefore, there are a number of routes, several indirect and one direct, to the desired form of toiler.

In a population of smiles, there is a thirty-three percent chance that a viable mutation will result in the desired direction, smiler. In the next generation within the smiler group, there is a thirty-three percent chance that a mutation will occur in the desired direction, soiler. Within the third generation soiler group, there is a twenty-five percent chance that a mutation will occur in the desired direction, this time to toiler. Thus, true toiler species might be produced in just three generations. This will happen with the probability of 1/36 if trauma and segregation of phenocopies continues throughout the generations. It is also interesting to note that some viable mutations that go in an *undesired* direction may have descendents that return to an earlier form, thereby opening up the possibility of additional desired mutations.

This thought experiment presents a picture of the way in which genetic assimilation could work. Although the game of word golf as a model for evolutionary processes is very simple, it does illustrate how the random mutational process might be internally constrained, as well as historically contingent.

Although aberrant forms might be *stabilized* through selection, neutral mechanisms allow the mutation process to diffuse through a wide range of genotypes with various wildcard configurations. Therefore, it is neutral mechanisms that have the power to *create* diverse genotypes, which natural selection may later "see" and "use." At the same time, structural evolutionary constraints limit the diversity and improve the possible effectiveness of natural selection. Peter Schuster and colleagues' research on RNA sequences, the evolution of which is simulated by computer, demonstrates how such constraints work. Schuster's experiment starts with a homogeneous initial population. After replications involving mutations, a number of what he calls *final structures* or *target structures* (in an apparent use of teleological language) evolve from the initial sequences. Typically, there emerge relatively few different kinds of common structures and a wide diversity of rare ones. However, the total number of common structures drastically outnumbers the rare. In one series of experiments, for example, more than 93% of all RNA sequences folded into common structures that represented only 10.4% of all structures. Overall, the most common structures were of comparable frequency and usually closely related to the parent structure, while the distribution of the rare structures was random and fulfilled a power law distribution. The common structures were found again and again, in numerous experimental runs.

The key point that Nabokov makes about the dead-leaf "mimic" is that it was not produced gradually by natural selection. It might have appeared suddenly, in a developmental response to heat shock, for example, and only later, if ever, realized an advantage by fooling predators. Structural and neutral evolutionary theories do not deny that Darwinian evolutionary mechanisms exist. They supplement Darwinism by explaining the mechanisms, which either limit diversity or enable diversity, and which increase the probability that a structure may be found, that is coincidentally close enough to a form with potentially higher (or at least different) fitness, and then eventually proliferate in a population.[23]

Since dead-leaf mimicry cannot be explained as a kind of family resemblance in the way that the viceroy-monarch relation can, it is simply coincidental or "false," and as Nabokov explains,

> i.e. attained by essentially different means. Such false resemblances are extremely rare and the number of characters involved is small, and this is as it should be, since such 'convergence' depends upon the mathematics of chance. False dissimilarities also occur (and are also rare), i.e. the striking difference between one type and another is seen, when analysed, to be due to a simple and brief process of evolution in an unusual direction. (*Nabokov's Butterflies* 354)

The more we study Nabokov's lepidoptery writings, the clearer it becomes that his arguments against Darwin in regards to mimicry were not conservative, as for example Gould suggests, but innovative. In fact, Nabokov was not against Darwinism properly understood. He simply had something more radical to add.

In his fiction, Nabokov satirizes the tendency to see utility as a *cause* of coincidental resemblance. For example, in "The Vane Sisters," a man is obsessed with typographical errors. He pours through books in search of misprints such as "Hitler" for "Hither." If such typos happen to alter the sentence in a way that make sense, conferring a new, perhaps more clever, function, and it might seem as if someone had intended the new meaning. Nabokov claims such typos were illustrative of "the chance that mimics choice, the flaw that looks like a flower" (622). Nabokov calls attention to the fact that we have a very strong, and sometimes irrational, tendency to perceive coincidences as functional products of an agent's intention. The agent we posit may be an artist, a supernatural intelligence, or a duped mockingbird.

Among Nabokov's readers it is well-known that he intended to write a book-length study of insect mimicry that would offer an addendum or correction to the theories of evolution that were current in the 1940s. Although he never attempted that book, hints of it appear in *Ada, or Adore,* "Father's Butterflies," *The Gift, Pale Fire,* and *Speak, Memory*. And although Nabokov never wrote specifically about mimicry to the extent that he wished, the teleomechanistic bent that pervades all of his lepidoptery is evidence enough of his argument against an exclusively Darwinian evolutionary program. A similar bent also infuses his literary work and further elucidates his theory of intentionality. Nabokov's two worlds of art and science were very interactive. As a writer, he knew that coincidental patterns often form unintentionally in narratives. He also knew that they could appear intentional/functional if they could be interpreted as such. He supposed that a similar situation could occur in nature.

When Nabokov writes that he "discovered in nature the non-utilitarian delights that [he] sought in art," he is referring to beauty created accidentally and spontaneously, not to beauty created by a supernatural artist with a predetermined plan. Although some commentators have supposed Nabokov's argument against

Darwinism indicated a belief in creationism, this is inconsistent with Nabokov's aesthetics, as well as the fact that he frequently expressed a lack of interest in religion. Moreover, Nabokov's choice of the term "agent X" for a teleological force indicates a departure from the then-popular notion of teleology, namely that of the 19th century philosopher Herbert Spencer, whose pernicious interpretations of Darwin tried to justify what have come to be known as social Darwinism. According to that argument, natural selection becomes a substitution for a supernatural purposeful creator, and evolution progresses inevitably toward more perfect forms, superior races eliminating inferior ones in accordance with the laws of nature. Nabokov reacted against this idea. He clearly felt that it is often the merely lucky, not necessarily the best strategists, who survive.

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[1] Michael Wood makes a similar argument in *The Magician's Doubts: Nabokov and the Risks of Fiction* (Princeton: Princeton University Press, 1994). See pages 190-191.

[2] In *Ariadne's Thread: Story Lines* (New Haven: Yale University Press, 1992), J. Hillis Miller claims a linear narrative "tends to organize itself or to be organized in a causal chain" and follows an "inevitable sequence," according to a "*telos*, *arche*, or ground" (18). Miller's ideas are derived from Derrida, who critiques the notion of telic order insofar as it derives from "a linked chain of determinations from the center." He equates the "center" with both *arche* and *telos.* See his1966 lecture, "Structure, Sign, and Play in the Discourse of the Human Sciences," trans. Richard Macksey and Eugenio Donato in *The Critical Tradition: Classic Texts and Contemporary Trend*s, ed. David H. Richter (Boston: Bedford Book, 1989), 959-971. The *arche* or "primal matter" should be understood as coincidental regularities that appear as fluctuations around equilibrium (produced by chance) in a highly entropic system. Thus, the *arche* or "the beginning" (chance structures) is a distinct concept from *telos* or "the end" (the dynamical constraints and physical laws that emerge out of stochastic interactions of chance structures). Given that contemporary understandings of teleology contradict the way teleologists have thought of their own work and the way that self-organizing behavior is understood today in physics, some clarifications must be made so there is no confusion about my use of this concept. While teleology is partly concerned with developmental stages of increasing complexity, the transition from one stage to the next is not linear. Each new stage is surprisingly more complex than reductive analyses of the initial conditions imply. The idea that teleological or goal-directed activity is linear may derive from late 19th and 20th century analytic philosophers who, in direct contrast to early 19th century teleologists, tried to fit telic behavior into a reductionist paradigm. As Lowell Nissen has demonstrated analyzing the seminal literature, this cannot be done. See his *Teleological Language in the Life Sciences* (New York: Rowan & Littlefield, 1997). For further analysis of teleology as a nonreductive science, see Timothy Lenoir, *The Strategy of Life: Teleology and Mechanics in Nineteenth Century German Biology* (Chicago: University of Chicago Press, 1989).

[3] See Victoria N. Alexander, "Narrative *Telos*: The Ordering Tendencies of Chance," (Ph.D. diss., Graduate Center, CUNY, 2002).

[4] Nabokov may have become familiar with the teleomechanists through E. S. Russell's *Form and Function: A Contribution to the History of Animal Morphology*,

published in London in 1916 and New York in 1917. Russell was well-known during Nabokov's day as an opponent of "merely mechanistic" biology. He argued that feedback effects that occur during the life of an individual organism affect the direction of evolution. His position may be compared to the contemporary developmental systems approach to evolution.

[5] The divine watchmaker idea is associated with the "argument from design" found, for example, in William Paley's *Natural Theology: Or Evidence of the Existence and Attributes of the Deity Collected form the Appearance of Nature* (1802). It is this kind of (pseudo)teleology that is critiqued by Aristotle, Descartes, Hume, Kant and contemporary complexity scientists.

[6] As Nabokov called such chance events in "The Vane Sisters," *The Stories of Vladimir Nabokov* (1959: New York: Knopf, 1995), 615-627.

[7] Such (anti)metaphysics are not unknown. See, for example, C. S. Peirce, "Design and Chance," in *The Essential Peirce: Selected Philosophical Writings*. eds. Nathan Houser and Christian Kloesel. Vol. 1. (Indianapolis: Indiana University Press, 1992).

[8] Personal communication.

[9] For an overview, see James P. Crutchfield, "When Evolution is Revolution: Origins of Innovation," *Evolutionary Dynamics: Exploring the Interplay of Selection, Neutrality, Accident, and Function*, eds. J. P. Crutchfield and P. Schuster (New York: Oxford University Press, 2002), 101-134.

[10] Teleomechanists Karl Ernst von Baer, Johannes Müller, Carl Bergmann, and Lotze Leuchart are to be distinguished from Romantic natural philosophers. Geoffroy Saint-Hilaire in France and Schelling in Germany who led the Romantics in transcendental morphology, which relied on mathematical mysticism. They sharply contrasted with teleomechanists, who investigated how forces, interrelated processes, and pattern formation contributed to the formation of animal types. See Timothy Lenoir, *The Strategy of Life: Teleology and Mechanics in Nineteenth-Century German Biology* (Chicago: University of Chicago Press, 1989), 147.

[11] I have Michael Golubovsky to thank for informing me of the possible link between Nabokov and Berg. Golubovsky is Professor of Population and Evolutionary Genetics at the Institute of Science History and Technology of the Russian Academy of Sciences and currently a Visiting Professor at Duke University.

[12] According to Nabokov, "Three forces make and mold a human being: heredity, environment, and the unknown agent X. Of these the second, environment, is by far the least important, while the last, agent X, is by far the most influential." Nabokov's renaming of *telos* as "agent X" signals a felt departure from typical conceptions. See Vladimir Nabokov, "Madame Bovary," *Lectures on Literature* (Ithaca: Cornell, 1982), 126.

[13] Bergson's term "mechanism" refers to 18th century reductive determinism, which understood causality as a physically continuous series of events. In this view, each event would be entirely predictable if one had sufficient knowledge of initial conditions.

[14] According to Persi Diaconis, "our intuitive grasp of the odds is far off. We are often surprised by things that turn out to be fairly likely occurrences." See Persi Diaconis and Fredrick Mosteller, "Methods for Studying Coincidences," *Journal of American Statistical Association* 84 (1989): 854.

[15] See W. Fontana and L. Buss, "What Would be Conserved if the Tape were Played Twice?" *Proc. Nat. Acad. Sci.* USA 91 (1994): 757-761.

[16] This type of process is described by Meinhardt's *lateral inhibition* model, a special case of reaction-diffusion models. See H. Meinhardt, *Models of Biological Pattern Formation* (New York: Academic Press, 1982).

[17] For a general description of spontaneous symmetry breaking, see Ilya Prigogine and Isabelle Stengers, *The End of Certainty: Time, Chaos, and the New Laws of Nature* (New York: Free Press, 1991).

[18] See F. Müller "Ituna and Thyridia: a remarkable case of mimicry in butterflies," *Proc. Entomol. Soc.* (London: 1879), 20-29.
[19] See Niles Eldredge and Stephen J. Gould, "Punctuated Equilibria: An Alternative to Phyletic Gradualism," *Models In Paleobiology* (San Francisco: Freeman, Cooper 1972).
[20] Crutchfield's theory describing the underlying mechanisms responsible for stasis and change differs from Eldredge and Gould's "punctuated" evolution. As Crutchfield stresses, "long periods of stasis and sudden change need not be driven by external forces. They are the product of the many-to-one mappings from genotype [i.e., parameter values] to phenotype [i.e., resultant structure] and phenotype to fitness." Small changes in the parameter values may have no effect in the resultant structure. A number of different parameter values can make the system fall into the same attractor basin. This situation gives rise to the phenomenon of directionality. If the number and/or degree of changes in parameter values are/is large enough, there may be a sudden jump to a new structural archetype (without moving through intermediary stages). Crutchfield's theory may soon offer the first testable theory of adaptation in its method of quantifying the changes in structural complexity from one level to the next. See James P. Crutchfield, "When Evolution is Revolution: Origins of Innovation," *Evolutionary Dynamics: Exploring the Interplay of Selection, Neutrality, Accident, and Function*, eds. J. P. Crutchfield and P. Schuster (New York: Oxford University Press, 2002), 101-134.
[21] "Phenocopy" is a term coined by Goldschmidt in his temperature shock study of *Drosophila.* See "Gen und Auszeneigenschaft (Untersuchungen an *Drosophila*)," I: *Zeitschrift für Induktieve Abstammungs – und Vererbungslehre* 69 (1935): 38-69 and "Gen und Auszeneigenschaft (Untersuchungen an *Drosophila*)," 2: *Zeitschrift für Induktieve Abstammungs – und Vererbungslehre* 69 (1935): 70-131.
[22] Through, say, sexual, rather than fitness selection. See Charles Darwin, *The Descent of Man, and Selection in Relation to Sex* (London: J. Murray, 1871).
[23] Neutral evolution has also been shown to work faster than adaptive evolution. See E. van Nimwegen and J. P. Crutchfield, "Metastable Evolutionary Dynamics: Crossing Fitness Barriers or Escaping via Neutral Paths?" *Bull. Math. Bio.* 62 (2000): 799-848.