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DNA, Nabokov, and Biogeography

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ABSTRACT: The authors examine the prehistory of Nabokov's surprising, controversial, and ultimately vindicated 1945 scenario for the dispersal of Polyommatini Blue butterflies across the Americas. This scenario produced one of the more poetic passages in Nabokov's scientific writings, referring to the "Wellsian time machine" a researcher might straddle to watch the various migrations of butterfly groups from Eurasia, across Beringia, to North and then South America. Due to their morphological peculiarities, Nabokov proposed that the butterfly groups came not in a single wave, later spreading and diversifying across the Americas from North to South, but rather in distinct waves that left the impression that modern North American species arrived more recently than those currently found in South America. The scenario could not be tested in Nabokov's time, but it gave rise to the well-known DNA-based study (Vila et al.), published in 2011, proving that Nabokov's proposal was exactly correct, and on that basis advancing a novel theory of thermal filtration across Beringia, utilizing genetic markers indicating ancient climate tolerances in different lineages. The present article asks a question that was passed over by Vila et al.: how did Nabokov arrive at his hypothesis—by luck, or by specific reliance on the data at hand? Piecing together phrases from two widely-separated articles, one on taxa from North America and the other on taxa from South America, the authors demonstrate the analytical method Nabokov used to derive his conclusion, which turns out to be factually derived from his transformation series illustrating the evolution of genitalic morphology. This transformation series allowed him to posit an "ancestral type" or "aspect" of the genera he worked on, and from this conclusion, he derived his surprisingly accurate dispersal scenario. These details of Nabokov's analytical process further anchor his legacy as a pioneer phylogenetic systematist.

Introduction

The significance of Vladimir Nabokov's achievements as a working scientist in the 1940s has been essentially settled since the follow-up studies of the 1980s and '90s, and especially the appearance in 2010-2011 of three articles confirming much of the previously unproved outer edges of his investigations (Gompert et al. 2010, Vila et al. 2011, Forister et al. 2011). Nabokov published five major revisions of New World Blues in the 1940s, resulting in new taxonomic categories and relationships.[1] Regarding Blues, Nabokov successfully recognized ten of the eleven natural groups (or genera) of the Polyommatine (Tribe Polyommatini) in the New World. Of these eleven groups, five still bear his original generic names from 1945. Two others were later replaced (because of technical rules of the modern International Code of Zoological Nomenclature [ICZN Code]). There was also one genus that, having seen no specimens, Nabokov was unaware of, and two for which he used older names incorrectly vis-à-vis the ICZN Code. For Old and New World Blues Nabokov also authored eight species or subspecies names, the statuses of which have since varied depending

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1 For a list and summary of all of Nabokov's scientific papers, see Dieter E. Zimmer, *Guide to Nabokov's Butterflies and Moths*, Online Edition (2012), section 4: http://www.d-e-zimmer.de/eGuide/SciPapers.htm.

on their usages in subsequent national and international taxonomic lists.[2] His classifications were greatly controversial at the time because, basing his views on internal, more than external morphology, Nabokov created additional groups, particularly in groups that were popular with amateurs and collectors using far more simplified classifications; this led some to accuse him of excessive "splitting."[3] The 2010-11 studies focused on areas of Nabokov's work that remained inconclusive in his lifetime: the species-status of the Karner Blue; the hybrid status of one of his rare finds; and his speculative proposal for the invasions of Blues into the New World. Those three studies were a decisive complement, with the new advantage of DNA analysis, to work that had been done following in Nabokov's footsteps by Kurt Johnson, Dubi Benyamini, and Zsolt Bálint, which had shown the value of Nabokov's groundwork toward establishing a sound phylogenetic classification for Neotropical Blues.

In this essay, we examine the prehistory of Nabokov's surprising, controversial, and ultimately vindicated 1945 scenario for the dispersal of Polyommatini Blue butterflies across the Americas. This scenario produced one of the more poetic passages in Nabokov's scientific writings, referring to the "Wellsian time machine" a researcher might straddle to watch the various migrations of butterfly groups from Eurasia, across Beringia, to North and then South America. Due to their morphological peculiarities, Nabokov proposed that the butterfly groups came not in a single wave, later spreading and diversifying across the Americas from North to South, but rather in distinct waves that left the impression that modern North American species arrived more recently than those currently found in South America. The scenario could not be tested in Nabokov's time, but it gave rise to the well-known DNA-based study (Vila et al., 2011) proving that Nabokov's proposal was exactly correct, and on that basis advancing a novel theory of thermal filtration across Beringia, utilizing genetic markers that indicate ancient climate tolerances in different lineages. The present article asks a question that was passed over by Vila et al.: how did Nabokov arrive at his hypothesis—by luck, or by specific reliance on the data at hand? Piecing together phrases from two widely-separated articles, one on taxa from North America and the other on taxa from South America, the authors demonstrate the analytical method Nabokov used to derive his conclusion, which turns out to be factually derived from his transformation series illustrating the evolution of genitalic morphology. This transformation series allowed him to posit an "ancestral type" or "aspect" of the genera he worked on, and from this conclusion, he derived his surprisingly accurate dispersal scenario.

In the introduction to our collection of Nabokov's scientific drawings *Fine Lines: Vladimir Nabokov's Scientific Art*, we attempted to put all of Nabokov's scientific work into historical perspective, with special attention to how he fit in with the ongoing (even tumultuous) changes in evolutionary theory in the 1940s. Nabokov wrote that he "accept[ed] evolution as a modal formula," but he was "not satisfied with any of the hypotheses advanced in regard to the way it works"[4] (Nabokov, 2000, 356). One of the most fascinating things to observe, and something we did not fully appreciate during our work toward *Fine Lines*, is the spectacle of Nabokov trying to turn the "elaborate sculptures" of butterflies' genitalia into a roadmap for their evolution. Far from being an opponent of Natural Selection or evolution as theories—an over-simplification that grew mainly from his non-scientific writings about butterflies—Nabokov actually spent his entire scientific career in the 1940s trying, as it were, to catch evolution by the scruff of the neck—to pin it up, caught in the act, for all to see. It was this effort that led to his novel sequential dispersal scenario.

In undertaking a new review and summary of Nabokov's contributions, we noticed some previously overlooked elements of this story that give us a clearer sense of how perceptive Nabokov's insights were. We are jumping ahead a little, but it was these insights, specifically, that enabled the ground-break-

2 More details can be found in Stephen H. Blackwell and Kurt Johnson (2016), "Introduction," in *Fine Lines: Vladimir Nabokov's Scientific Art* (New Haven: Yale University Press), 19.

3 On Nabokov's "splitter" and/or "lumper" status, see Kurt Johnson and Steve Coates (1999), *Nabokov's Blues: The Scientific Odyssey of a Literary Genius* (Boston: Zoland Books), 54 and 285.

4 Just above these lines, Nabokov wrote, "Adaptation to surroundings, to climate, altitude, etc., and hence 'natural selection' in its simplest sense, certainly had no direct action whatever on the moulding of the genital armature, and we know nothing of the physiological processes of which that elaborate sculpture is the structural overflow" (Nabokov, 1945, 6). See the two introductory essays in *Nabokov's Butterflies*, one each by Boyd and Pyle, for an overview of the state of scholarly perspectives on Nabokov's science in 2000.

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ing work of Vila et al. (2011). Kurt Johnson was one of that study's co-authors, and in fact, his 1999 book *Nabokov's Blue*s was the spark that set Naomi Pierce onto the task of putting the Vila et al. team in motion, resulting in their study's novel approach to studying waved dispersals from the Old World to the New, across what today is the Bering Strait, and used to be a land bridge scientists call "Beringia." Equally new and important, and just as dependent on Nabokov's preparations and hypotheses, was that study's successful devising and testing of a theory of "thermal filtration." Using DNA analysis, Pierce's team utilized genetic markers confirming the ancient thermal tolerances of each group of butterflies, and consequently establishing the details of a *thermal filter* in Beringia: specific climate conditions allowed particular species, possessing the needed tolerances, to disperse from Old World to New.

Work by scientists over the three decades before 2011 proved beyond doubt that Nabokov's scientific contributions were significant, and important, and set the stage for new research and discoveries. The 2011 Vila et al. paper was the one to synthesize all these elements and—more than simply proving Nabokov to be a highly successful taxonomist—build on his work in a manner that still today is moving science forward, even well beyond Nabokov's own narrow specialization on the New World "Blues."[5] In this historical retrospective, we want to explore why Nabokov's important work took so long to be accepted; how he achieved what he did and what was new about it; and how this work has led to subsequent new discoveries in larger areas of science as recently as 2011.

In the 1980s, a time of emergent scientific focus on the global relationships of organisms and threats to their biodiversity, Kurt Johnson and his future collaborators set about deciding which areas of butterfly taxonomy were most in need of, or most ready for, productive work. Among various possibilities, Nabokov's groups stood out because he had done foundational work on extremely complicated groups, and there was still much work to be done. The complexities of the groups on which Nabokov had specialized included multiple small, look-alike, "Blue butterflies" which taxonomists over the decades had placed into drastically varied classifications, mostly depending on their personal calculi concerning wing pattern characteristics. Adding to this confusion were enigmatic and inconsistent data sets concerning what entities were viewed as interbreeding with each other (or not) and thus key to defining actual or "biological" species. To this, Nabokov added seminal work on the genitalic anatomy of these butterflies, introducing entirely new data sets shedding abundant light onto the understanding of what was, or was not, a species in these Blues. Moreover, Nabokov's foundational work grappled with the relationships of organisms across continental and plate tectonic boundaries, making them a textbook subject for biogeographical study and an examination of the meaning of the "Genus" taxonomic rank among these confusing butterflies. Controversially, Nabokov had introduced nine new generic names in his foundational work on Blues (five of these remained valid after revisions in the 1980s by Johnson et al.).[6]

Adding to their attraction, Nabokov's study groups also seemed small enough (deceptively, as time would eventually prove) that they could be essentially completed, and moreover, many of the actual specimens and other study materials he worked with were preserved in the collections of the institutions immediately available to Johnson and his co-workers (Harvard's Museum of Comparative Zoology [MCZ] and Nabokov's collection at the American Museum of Natural History in New York City). Further, between Johnson, Bálint, and Benyamini, access to important collections in Europe and South America was also readily available, and the three were planning new fieldwork in Latin America.

It seems safe to say that, without all these components in

5 Plebejinae when ranked as a Subfamily, Polyommatini when ranked as a Tribe. The former was the usage in Nabokov's time; "higher classification" has changed over time, particularly following DNA and other bases for recognizing actual lineages or also placing them by geologic time-frames. For a modern study see Talavera et al. (2012).

6 Two (Icaricia* and Plebulina*) in Nabokov (1944); seven (*Cyclargus, Echinargus, Parachilades*, Pseudochrysops, Paralycaeides, Pseudolucia, Pseudothecla**) in Nabokov (1945). He also restored one non-Blues genus (*Carterocephalus*) in Nabokov (1941). [* = no longer valid]. If the addition of generic names made Nabokov look like a "splitter," his 1949 work showed him actively "lumping": as Dieter E. Zimmer writes, "using the methods devised in [Nabokov (1944)], Nabokov studied wings and genitalia in about 2,000 specimens. He reduced the North American representatives of the genus to two species, *argyrognomon* and *melissa*" (Zimmer, 2012; V. Nabokov (1949); it is noteworthy that one subspecies in this group which he had identified and named in Nabokov (1943), *L. melissa samuelis* Nabokov, was promoted to species status in 2011 (Forister et al. [2011]).

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place, it is unlikely that Nabokov's Blues would have been further studied for many years, perhaps not until the DNA-mapping era two decades later. His work was already held in general ill-regard by lepidopterists not wanting to engage in the degree of detail in his work, especially regarding painstaking dissection of genitalia. However, a few specialists (like John C. Downey in the United States and John N. Eliot in the United Kingdom) knew that Nabokov had been onto something and Johnson, Bálint, and Benyamini had each already, from their own preliminary work and communications, ascertained that the denigration and dismissal of Nabokov's results by so many lepidopterists were simply incorrect.

Of course, completion of work on these Blues could also have been accomplished sooner, even by Nabokov himself, had he remained active in professional Lepidoptery longer, or if field workers had, sooner than the 1980s, recognized the value and promise of his work. In any event, the work of Johnson, Bálint, and Benyamini, published in fourteen papers from 1986 to 1997, completed the major portions of basic taxonomic work in this area and returned Nabokov's generic and species nomenclatures to general use in the global, continental and regional nomenclatorial lists employed daily by entomologists, both professional and amateur.[7] Along with a non-Polyommatine Latin American Blue genus (*Leptotes* Scudder 1876) in which other workers have named butterflies after Nabokov, in common parlance, these Blues make up the Latin American component of "Nabokov's Blues." This scientific recognition of Nabokov's successes brought new international attention to the significance of his scientific mind and accomplishments.[8]

As a simple matter of bringing order to a disordered area of taxonomy, this work represents a significant accomplishment for the seven or so years Nabokov spent focused on the task. He dissected at least 1500 butterflies' genitalia, and examined thousands more externally (wing patterns, primarily), all while teaching Russian language and literature at Wellesley College and writing a novel, stories, memoirs, translations, and works of literary criticism. His work days were long, often with sixteen hours spent at the dissecting bench.

Nabokov's work on the Blues was significant but long overlooked—sometimes in questionable ways that left his clearly valid taxa out of some of the most widely-used guides and summaries of the state of the field in the decades following his work. This situation probably came about due in part to traditions within the field (inertia); in part to the age of some workers conducting the comprehensive overview work; and also in part to personal relationships that may have caused some taxa that would have been "sunk" by Nabokov's discoveries to be, instead, preserved in the popular and overview literature. In all likelihood, this unfortunate (for science) situation arose because Nabokov effectively left scientific work in 1949 (when his last extensive paper was published; more precisely, in the fall of 1948, when he was hired full-time to teach and research literature at Cornell). His departure had other consequences, too, but certainly, the absence of his name from regularly appearing journals would have made it much easier for his work to fade in memories, and to seem less important to cite (for active workers) than that of other, also active lepidopterists with whom publishing scientists had ongoing relationships. Nabokov had about twelve scientific publications of varying length between 1942 and 1949,[9] and it is not hard to imagine how different that community would have looked (and how it would have looked at him) had he continued publishing at that pace.

However, the reawakened attention to Nabokov's scientific work in the 1980s was not without further controversy. After so many years of dismissal or denigration, especially by prominent lepidopterists (albeit not specialists), a nagging question lingered: could new taxonomic work based again on traditional methods—albeit enhanced by hundreds of additional dissections and other new data—change the mind of the average lepidopterist or butterfly enthusiast? The scientific community seemed to wonder, "Could the new work be trusted?" After all, nothing changed the salient fact that all the little Blue butter-

7 For a complete list of these publications, see Johnson and Coates (1999), *Nabokov's Blues*, 348.

8 Historical counts of "genera" for Nabokov's Blues may vary from our numbers here if one includes (i) some old generic usages far prior to Nabokov's work (especially for South America) like *Lycaena* Fabricius 1807 and (ii) how many times one counts a name like *Itylos* Draudt 1921 which early taxonomists applied to quite different groups of Blues. See also: "Genera, Species and Subspecies Named by Nabokov," in Zimmer (2012).

9 All summarized in Zimmer (2012) at: *Guide*, "Summaries of Nabokov's Lepidopterological Papers," http://www.d-e-zimmer.de/eGuide/SciPapers.htm

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flies, externally, look so much alike.

Before too long, this work came to the attention of additional professionals armed with even newer forensic tools, eager to look again at Nabokov's basic taxonomic work and evaluate some of his most audacious (and previously untestable) hypotheses. This resulted in the key publications of 2010 and 2011, which used DNA analyses. We'll turn to that story now.

Nabokov's groups after the DNA-based studies

It seems fair to state that the whole kerfuffle surrounding the Vila et al. research and publication was unexpected, and even unimagined by Johnson, Bálint, and Benyamini, when they wrapped up their work. Nabokov himself probably could not have dreamed of it, even with his rather prodigious powers of imagination.

When Kurt Johnson and Steve Coates wrote *Nabokov's Blues* (1999), they thought they had summarized everything interesting Nabokov said in his scientific work, and everything valuable that grew out of it in the 1980s and '90s. This book, however, was read by Naomi Pierce of the Museum of Comparative Zoology and she noticed in it the following quotation from Nabokov's ambitious 1945 article, "Notes on Neotropical Plebejinae." In that work, Nabokov wrote,

> "One can assume, I think, that there was a certain point in time when both Americas were entirely devoid of *Plebejinae* [sic] but were on the very eve of receiving an invasion of them from Asia where they had been already evolved. Going back still further, a modern taxonomist straddling a Wellsian time machine with the purpose of exploring the Cenozoic era in a 'downward' direction would reach a point—presumably in the early Miocene—where he still might find Asiatic butterflies classifiable on modern structural grounds as Lycaenids, but would not be able to discover among them anything definitely referable to the structural group he now diagnoses as *Plebejinae*. On his return journey, however, he would notice at some point a confuse adumbration, then a tentative 'fade-in' of familiar shapes (among other, gradually vanishing ones) and at last would find *Chilades*-like and *Aricia*-like structures in the Palearctic region."[10] (Nabokov, 1945, 44)

At the time of the work by Johnson and others, even in the 1980s and '90s, a narrative of this sort had the whiff of an old-timey "dispersal scenario," just a whimsical, if informed, fantasy about what might have happened. Adding to the tendency to overlook this passage, if not dismiss it, was the fact that nothing it said was testable; accessible DNA sequencing was far in the future, and, to top it all off, the "Wellsian time machine" made it all seem too literary and non-scientific: not something that scientists following up on the very real and concrete contributions Nabokov made needed to worry about. (Nabokov was prone to such moments of metaphorical levity, even in his scientific writing and on his research note cards.) Naomi Pierce, though, upon reading the passage in *Nabokov's Blues* in the early 2000s, had a very different reaction: "We can test this" (Zimmer, 2011). Her response was made possible by the fact that finally, economical DNA sequencing, and accompanying statistical tools, *were* now available, and she assembled the team to do the work.

What Nabokov had proposed was this: that the Blues had not simply spread across to the new world and, once established, diversified, but, instead, they arrived in five distinct events of dispersion from Asia, spread over a period of ten million years. He was suggesting that the South American Blues had been "local" for longer than the North American Blues, and this was counter-intuitive since he believed that the only likely route of dispersion was across Beringia (as turned out to be true in this case). This scenario raised important questions that he could state but not address scientifically: why were there, from morphological study, no apparent "close relatives" of the Neotropical Blues in North America? Science, most likely, is only as good as the questions it asks, especially if it can answer them. These were very good questions, but there was no way, in Nabokov's or even his first followers' days, to even imagine how they might be tackled scientifically. Nabokov was posing scientific questions—based on his observed data—that had to wait over fifty-five years before they could be studied.

In the paragraph after the one quoted above, Nabokov lays out the precise sequence of the waves' arrival in the New World:

> "*Plebejinae* arrived first, made it to South America, and all traces of this invasion vanished from North America by modern times;
>
> *Icaricia*, *Plebulina*, and the species *Plebejus saepiolus* arrived next;

10 In this article, Nabokov erected seven new genera (six still valid) and fully revised two others that were in disarray (*Hemiargus* and *Itylos*)—all based on a mere one hundred and twenty dissections, a very small sample.

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Later, in sequence, came three *Holarctic* species:
Lycaeides argyrognomon[11]
Agriades glandon
Vacciniina optilete"

This precise sequencing was what provided the template for the work initiated by Pierce, which became the Vila et al. paper. But that article did more than simply prove that Nabokov had the sequencing exactly right (simply based on his extensive and systematic study of the diverse "sculptures" within all these butterflies, on which more below): it used Nabokov's hypothesis as a foundation on which to (i) build a modern model for verifying "dispersal biogeography" scenarios such as this one, and (ii) generated a new hypothesis regarding *why* these taxa migrated when they did (thermal tolerances), proposed and proved the existence of a *molecular clock aligned with thermal tolerances* in these taxa, and finally, by coordinating these results with verifiable climate data over the millions of years under study, proposed and proved the existence of a *thermal filter* in Beringia, where the specific climate conditions allowed only certain species to disperse from Old World to New at a given time. Nabokov could not have imagined these kinds of scientific innovations or experiments, and yet it is also true that without his groundwork, these hypotheses, studies, and conclusions would not have happened. These very modern advances in paleo-climate study, paleoecological study, and the utilization of molecular clocks in establishing time-specific thermal tolerances are very much built on the foundations that Nabokov created in the 1940s.

As we reconsidered this history, we became curious about that dispersal scenario of Nabokov's: it was not immediately apparent, from the 1945 article itself or our review of his laboratory drawings leading up to *Fine Lines*, whether his proposed sequence was essentially a lucky guess (he was, after all, right), or was instead based on his understanding of the data at his disposal (consisting of both morphological shapes, and specific sizes and ratios, often in the form of what he called among friends "magic triangles"). *If* it had turned out to be luck, then Nabokov's responsibility for the important work that emerged recently would be relatively small; but if it was based on his precise, scientific evaluations of the data, and his sequence of invasions was fully justified by his interpretation of the evidence, then his responsibility would be much larger. We decided to push hard on this question, and what we found reveals a surprising hidden thread buried within his work, with traces in two unrelated articles, demonstrating that he was working on a fully empirical basis.

Even in *Fine Lines*, we were already aware that Nabokov's great strength as a scientist—one who had theoretical insights, in addition to "simple" taxonomic ones about what species exist, and in what genera—derived from the fact that he had, it seems, an extraordinary visual memory, and likely had near-instant mental access to all of the structural forms he had dissected and drawn. He could choose the ones he wanted to think about, most likely, and run them together like a primitive film or zoetrope, noticing how forms seem to shift and grade one into another, a process he at one point calls "the shadow of a phylogenetic tree on a plane surface," because he had taken the synchronic as an analogy, and a clue, for the diachronic (Nabokov, 1943, 88). And he could then look at his notes and calculations to see how these forms all related to one another, numerically. Sometimes, in his lab work or even in published papers, he figured large groups of these forms in what are known as "transformation series," implying the diversification of related forms over the years and eras. This richness of vision is what enabled him to create such robust new groupings, so many of which have survived subsequent analysis. But, again, it is one thing to notice "good" species and group them into genera. It's something else entirely to propose how, across eons, the present diversity took shape in the New World.

To get a sense of whether Nabokov had a solid foundation for his dispersal scenario, we realized that a detailed look at the variety and distribution (taxonomic and geographical) of Nabokov's genitalic dissections was needed. Accordingly, in the following figure (See Fig. 1 below, borrowed and adapted from Vila et al.), we have marked with an asterisk each node of the DNA phylogeny within which Nabokov performed multiple dissections (not exclusively for the 1945 paper). We also looked through his scientific notes (in the published and unpublished cards from the Berg Collection), finding the assemblages about which he made relevant comments; we marked these nodes with the "@" symbol. Finally, we took a careful new look at the language in his scientific publications for clues to how he made the heuristic decisions that led to his multi-wave Beringian scenario. Again, if we had found nothing clear or systematic in his evolutionary treatment of these forms, there would have been a

11 This species he later revised, in Nabokov (1949).

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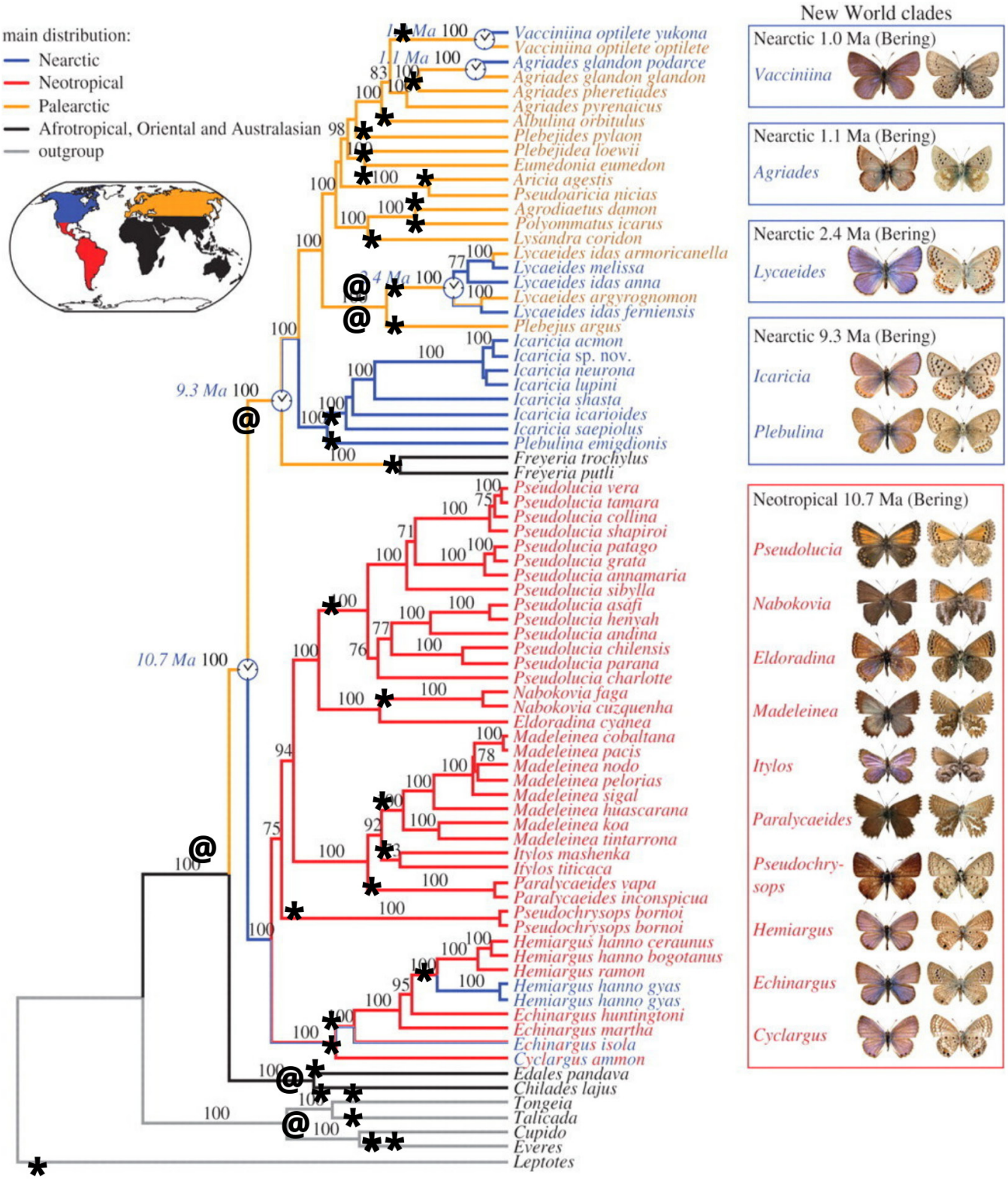

Figure 1. DNA Phylogeny of New World Blues, showing Nabokov's specific working points. * = dissection, @ = lab notes/commentary. Adapted, with permission, from Vila et al. (2011).

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strong chance that Nabokov's proposal was a matter of luck. But that's not what we found at all.

Figure 1, above, is Figure 3 from Vila et al., showing all the species under study, grouped into genera and higher groups, and color-coded by broad geographical region (Nearctic, etc.). The chart also indicates at which nodal point an ancestor is believed to have invaded the New World, and lists the estimated time of that invasion. The black symbols we have overlaid on the chart give a sense of exactly where Nabokov's labwork (*), and his commentary (@), interacted with the broad diversity of these fauna as it is known today. (Many of the included species were not yet discovered in Nabokov's time.) The chart makes clear that Nabokov dissected broadly across all these taxa, and he made analytical notes about most of the groups.

Nabokov's Deduction

A close rereading of the articles led us to the evident explanation. Nabokov wasn't hiding it, really, but he wasn't foregrounding it either: at that time, *discovering the actual evolutionary relationships of species was a new, even just-emerging element in taxonomy*, with the result that while he was making evolutionary statements, whose truth seemed obvious to him, he was not highlighting the novelty of his claims. We had to look for and identify such novelties. Additionally, his papers' real scientific goal and upshot was the revision of the taxonomy of the present, not the establishment of evolutionary history. Therefore, later scientists, including one of us (KJ), Bálint, and Benyamini, were not paying particular attention to these evolutionary statements, offered by Nabokov almost in passing, amidst much larger amounts of information showing the present-day morphological situation and the taxonomic entities and divisions this situation drove him to establish. Additionally, this team was concerned with the South American Blues, whereas Nabokov's breadcrumbs begin in the North. The first hint of this quest to determine real evolutionary relationships appears in his 1944 paper, "Notes on the Morphology of the Genus *Lycaeides*,"[12] in a chart giving a transformation series within the genus, labeled "Evolution and Speciation of Uncus in *Lycaeides*" (See Fig. 2).

We see the following annotation to the triangle in the upper-left corner: "X—hypothetical ancestor; FHU = 0.25 +0.22 + 0.22 = 0.69 mm." Now, if the researchers of the 1980s and '90s had been working on North American groups, or if they had a special interest in teasing out evolutionary relationships, they might have been drawn back to this figure and thought about it.

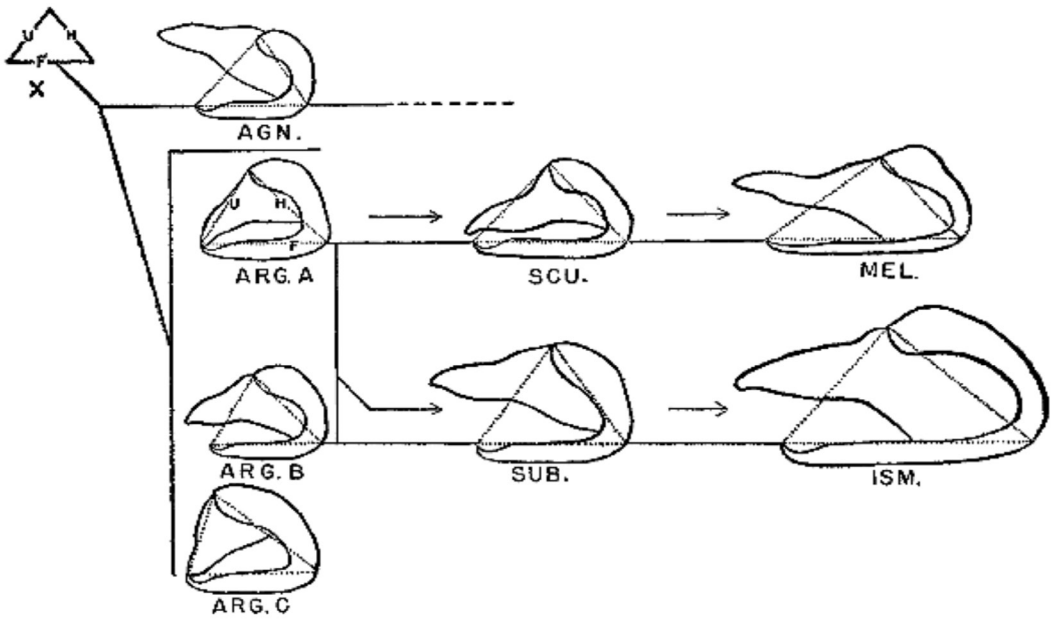

Figure 2. Nabokov's transformation series, "Evolution and Speciation of Uncus in Lycaeides," given as "Figure 1" in his "Notes on Morphology of the Genus Lycaeides" (1944)

12 Chart is from p. 109. Nabokov's relationship to the early history of phylogenetics is discussed in H. Blackwell and K. Johnson (2016), "Introduction," in *Fine Lines: Vladimir Nabokov's Scientific Art* (New Haven: Yale University Press), esp. 6-19.

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But their goals were different; they were centering on the building out of the Latin America diversity of Nabokov's Blues, which in the longer run grew from Nabokov's originally noted seventeen species (as of 1954) to about a hundred today. Further, with this burgeoning diversity, they also had to account for the validity and status of the seven generic names that Nabokov had proposed for the Latin American fauna and grapple with nomenclatorial issues that arose with the International Code of Zoological Nomenclature which, in its current form, did not exist in Nabokov's time.

At the time of *Fine Lines*, we were of course aware of this diagram, but we did not ask ourselves if there was evidence in Nabokov's work about how he had gotten there. He had presented the scenario in about 150 words, and none of them involved claims or assertions about character states. As we have said, before the compelling results of the DNA studies, a brief dispersal scenario was easily dismissed as "old-timey" stuff that old-time taxonomists used to do. It was only when we sat down to this new stock-taking that we posed the question: was there evidence about how, exactly, Nabokov had derived his remarkably concise dispersal scenario? The answer, it turns out, was not easy to find, because it was broken into two parts, in two quite unrelated articles, one of which concerned his work on North American species (which had not been the subject of Johnson, Bálint and Benyamini's years of research).

Below we will trace the discovery of these references in Nabokov's published scientific work and, for the sake of brevity here, describe the structures, with appropriate detail, in the captions to Figure 3 in the essay's epilogue.

In the 1945 study of Latin America blues, Nabokov states:

> "Paralycaeides n.g. (figs, INC, pl. 6). Type and only species known *Itylos inconspicua* Draudt 1921 . . . One male investigated . . . ex coll W. P. Comstock, . . . Amer Mus. Nat. Hist. Extremely close to *Lycaeides*, in the falx, furca and valve, and considered here as retaining an **ancestral aspect** of that genus."

And of the triangulate falx/furca measurements of this specimen, Nabokov wrote,

> "These figures come rather close to the dimensions (0.25+0.22+0.22=0.69) of the **hypothetical ancestor** of *Lycaeides* as worked out (1944, l.c.) prior to the discovery of the structure of *inconspicua*." (Nabokov, 1945, 36-37) [Bold emphasis added in both quotations.]

On Plate 6 (p. 59), at INC 2, Nabokov illustrates this triangulation, about which, in the Plate Caption (p. 52, at "2—") he says "the method of measurement for *Lycaeides* has been applied." However, there is an obvious misprint referring to the Plate element as "VAP 2", not INC 2 as on the published Plate.

Regarding his 1949 article on Nearctic *Lycaeides*, Nabokov told Robert H. Boyle, "This work took me several years and undermined my health for quite a while. . . . This is my favorite work." (Nabokov and Boyle, 1959). In this study, he wrote:

> "An **ancestral type** of *Lycaeides* male armature was deduced by me from a preliminary study of the variation in the genitalia of the palearctic and nearctic forms (1945, Psyche for 1944, 51, p. 109), and was later discovered to have survived in a butterfly still inhabiting the mountains of Peru (*Paralycaeides* Nabokov, 1945, Psyche, 52, p. 36)." (Nabokov, 1949, 480) [Bold emphasis added.]

These fleeting, but exceedingly important, mentions of two "ancestral aspects" (in the valve and the falx/furca) occur only in these two, short statements, intellectually connected but widely sundered, written to sound almost like afterthoughts or asides. Noticing their combined significance required a thorough comparative reading of his Neotropical Plebejinae and North American *Lycaeides* works aimed at determining what anatomical characteristics he had in mind while envisioning his Beringian dispersal scenario.

And so, as it turns out, even as late as 2016, modern science had not had occasion to explore the depth of Nabokov's interest in "ancestral types" or in his visions of evolution *in action*. In fact, this is where the interdisciplinary part of this essay, and of *Fine Lines*, comes in handy: to the literary scholar, or perhaps any avid re-reader of his fiction and memoirs, Nabokov's interest in the way time threads through life and nature is obvious. Knowing how Nabokov's mind approached the world in his art, it is completely predictable that, confronted with a series of forms displayed across a diverse group of related species, he would inevitably be drawn to seek and find in them traces of the way their anatomical details and "sculptures" have been shaped, through time, by the forces of evolution. The various species, to Nabokov, are points in a larger pattern; he could never resist a pattern.

Let's return to the key sentences from 1945 and 1949 for a moment. These are the ones that give us the first clues to how Nabokov, as Harvard's Dr. Naomi Pierce later said, "got every

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one right" (Zimmer, 2011). In isolation, to a person studying not Nabokov's full career but only a subset of the butterflies he worked on, these asides appear as anecdotal commentary and are easy to overlook. But from a broader perspective, attempting to provide a comprehensive overview of Nabokov's contributions to science, his "deduction" appears in a new light. In both of these statements, Nabokov proclaimed that in these anatomical structures, he was seeing "the ancestral character state" as "retained" in two modern contemporaneous species—one in the large assemblage of the Blues he studied from Europe & Asia (in the genus *Lycaeides* Hübner) and one in the large assemblage of Blues he examined from Latin America (in the genus *Paralycaeides*), and this was his precise reason for creating this new generic name. In other words, he was looking at modern forms, and seeing deep time at work on their anatomy.

It is the distribution of these two character states (illustrated and described as the "bilobed" and "triangle" "silhouettes" in Figure 3 in our epilogue) that Nabokov observed, firstly, in contemporaneous species (shown at the diagram's top) and, secondly, inferred as the "ancestral state" at the diagram's bottom. Since these character states embrace some seventy-one of the seventy-eight taxa (species and subspecies) in the diagram—these were likely the initial anchor for his process of thinking through the eventual detailed sequence that he proposed. Recognizing in contemporaneous taxa that these two character states occurred in both the (i) Latin American (Neotropical) assemblages and (ii) the Asian-North American (Holarctic) assemblages of these Blues likely gave him confidence that these two large assemblages were "sister groups" (as indeed they appear in the DNA analysis as sister groups joined at the node now dated to 10.7 Ma.).

To further confirm his vision of these ancient groups, Nabokov added an extra nuance. He not only noted "ancestral" conditions in the male valve and the triangulate measures of the male's falx/furca structures (see Figure 2), he also commented (still in Nabokov 1945) on an ancestral state he suspected in the male's penis (aedeagus), as it occurred in only some taxa from these groups:

> "The general *Hemiargus—Echinargus—Cyclargus* type of aedeagus is not found in the Old World and apparently represents a very ancient type retained and developed in the neotropics, but extinct or unrecognizably altered elsewhere." (Nabokov, 1945, 43)

As with previous character references, we further describe the structures themselves in the epilogue's caption to Figure 3.

This inference—because this condition in the male aedeagus is uniquely characteristic of the Neotropical assemblage—allowed him to have further confidence that the two major Neotropical and Holarctic groups of Figures 1 and 3 are distinctive "sister groups" (as was proven by Vila et al.).

To these diagnostic tools he added a further observation, one concerning the occurrence of "the differential/extremely rare/otherwise unseen occurrence of a sheath around the aedeagus" (which Nabokov named the "sagum") of which he says (p. 45, in several sentences) that, given its differential occurrence in Latin American taxa but not elsewhere in the world, was a likely primitive (ancestral) character that was subsequently lost in many other groups of these Blues. (For additional details, see caption discussion in the epilogue).

Inferences drawn from these two further morphological characteristics—the overall shape of the aedeagus and the differential occurrence of the sagum—occurring in some Neotropical Blues allowed Nabokov to further buttress his synthetic view of the distinctness, admixture, and relative phylogenetic position of the Neotropical elements in this wider, global, assemblage of Blues.

Indeed, these major clusters, as described by Nabokov, are faithfully represented in the DNA lineage sequence (phylogeny) as determined by Vila et al. in 2011. In the illustration below (Fig. 3), we have added symbols for each of these character states that Nabokov evidently relied on in his mental process determining his phylogenetic, and Beringean dispersal, sequence. The figure also shows the taxa in which these character states occur.

Of further note, one of these characteristics, the structure Nabokov himself named the "sagum," is also notorious for having produced controversy for decades, because it forced Nabokov to separate some members of a long-used ("sacred cow") genus, *Hemiargus*, whose species were well known to amateurs and hobbyists in the USA, from one of his new genera, *Cyclargus*. Due to entrenched, but fundamentally unscientific, resistance to Nabokov's new *Cyclargus*, the faulty taxonomy lingered in popular guidebooks and even at Wikipedia as late as 2015 (Blackwell & Johnson, 2016, 27, fn 50).

Essentially, once Nabokov had confidence in his deduced evolutionary placement of the main and basic ancient groups that would *anchor* an evolutionary dispersal sequence of these

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global Blues, it would have been relatively easy for him to add the more recently evolved elements of the larger group, by considering what is well known of their current diagnostics and geographical distributions. The difficulty is in deducing the ancient assemblages since there is no *current* extant knowledge of them and their diagnostics. All that Nabokov had to go on was the "ancestral state" as he deduced it; everything else was presumed to be derived, and inferred, from the deduced existence of that character state.

A colloquial way of considering what Nabokov deduced—with a nod to his "Wellsian time machine" fantasy—is to see how he considered these perceived morphological transformations as evidence of a kind of evolutionary time travel. Waking up from the very deep past, rather like a Rip Van Winkle, he envisions certain characteristics as having survived, as if preserved in amber and now many thousands of miles away from their starting points, while faded away elsewhere in the present day. These butterflies of South America were, in that light, a time capsule for him, from which to also draw conclusions about "lost traits" in the present. And yet, his sequence was the same as that drawn from the modern DNA analysis.

Evidence vs. Luck

We must pause to elaborate something important further here before we close. From what we have said above, two things are obvious:

- First, as Dr. Naomi Pierce verified by her surprise at the actual accuracy of Nabokov's evolutionary sequence, Nabokov knew enough to "get every one right."
- Second, as we have said, in looking at these characteristics and inferring relationships from them, Nabokov was evidently running them through his mind like a "zoetrope," envisioning how structures and taxa had evolved through time. A taxonomic method elaborating such inferences about structural change is called a "transformation series"; we see one of these in Nabokov's 1944 chart (Figure 2, above). Among lepidopterists, Nabokov was an early adopter of this method, which was an important precursor to current-day techniques of phylogenetic analysis, of which DNA forensics are a part.

What is important to note here, and prompted a next step in our own investigation, is the fact that there are limitations to the accuracy of information derivable from inferred transformation series.

As we discuss fully in *Fine Lines*, of the three schools of taxonomic methodology competing in Nabokov's active days in science, the one that describes his work is "phylogenetics," the approach that was looking for a truly reliable method for reconstructing evolutionary lineages. Eventually, the matter was laid to rest, long after Nabokov's active tenure in science, when DNA analyses could corroborate or falsify views of evolutionary lineages that had been generated by the conventional, earlier methods. The taxonomic school that won the day was phylogenetic systematics (or cladistics), from the now-celebrated work of German systematist Willi Hennig, first published in English in 1966 (Hennig, 1966).

This comprehensive method utilized the concept of transformation series but required demonstrating *successive nested sets of shared derived characteristics* at each sequential node of a diagram of evolutionary relationships. Such rigor at every successive node of a proposed evolutionary diagram (each node offering the options "corroborate/not-corroborate" or "verify/falsify") provides a high level of confidence. This system, compared to the smattering of pieces of the puzzle that Nabokov inevitably had, is more like driving with both hands, whereas Nabokov was, in a way, driving with just one. His inferences were not validated at every node within a larger taxonomic array or diagram. Regarding exactness, there were some risks involved with his speculative inferences.

Awareness of these risks led us to a further step in our analysis of Nabokov's employment of transformation series in devising his Beringian scenario. Helpfully, some general patterns in the appearances and relationships of anatomical characteristics (especially the sclerotized ones of insects) across long-term evolution are evident when one looks at many highly corroborated phylogenetic analyses. These patterns offer no guarantees, but they are illuminating.

It is often the case that primitive (and thus ancestral) anatomical conditions are relatively simple, unelaborate structures, like the ones marked with silhouettes in Figure 3. Consequently, in the highly corroborated lineages produced by Phylogenetic Systematics, and their related "transformation series" (or paths of transformation over time and space), it is often—but not always—seen that such transformations proceed *from* **more simple**, less structurally complex and less structurally elaborate characteristics, *to* **more structurally complex**, more structurally elaborate characteristics. Nabokov himself illustrated this in his "transformation series" of characters in *Lycaeides*,

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seen above in Figure 2.

This rule of thumb facilitated a further question regarding the five character states illustrated and tracked in our Figure 3: were Nabokov's inferences also consistent with this general pattern?

Indeed if one generally examines the anatomical states of the many taxa presented and laid out in Figure 3, the ones that are not tagged as bearing the ancestral forms are generally *all more structurally complex and more structurally elaborate*, compared to those manifesting what Nabokov took to be the "ancestral" state (that is, the ones marked with various silhouettes in the figure). Because the number of these other taxa is quite large, we cannot list here all the relevant illustrations corroborating this statement but one can easily see the generality by scanning Plates 1-6 in "Notes on Neotropical Plebejinae."[13]

Conversely, had Nabokov's clusterings of the major ancestral groups within this massive assemblage of Blues been *incorrect*, and *not* matched the DNA phylogeny shown in Figures 1 and 3, there would be no parallel coherence in the relative simplicity or complexity of structures across the remaining taxa. But there *is* coherence. Not only was Nakokov's view of the evolution of these Blues confirmed in the DNA phylogeny, but it was also consistent with certain generalities, established *after* his time as an active worker, often seen regarding relative characteristics of insect anatomy's simplicity or complexity across the diagram.

Obviously, Nabokov's inferences, drawn as we've portrayed above, served him well. If this were not the case, we would *not see* any consistency between Nabokov's stated views and the morphology of anatomical features across all these Blue butterflies, including ones he did not know, and the DNA evidence of the actual relationships and evolution of these taxa, known or unknown to Nabokov in his day. Their "character states" would appear without any particular pattern (or with a contradictory one), and Nabokov's success at sequencing the invasion waves accurately, with confirmation by DNA analysis, would have likely just been a matter of luck.

Nabokov's Conclusions

This essay gave us the occasion to explore the motivations behind Nabokov's "Wellsian time machine" thought experiment, which unexpectedly presented a final coda to the story of Nabokov's impact as a working scientist. Previously, it seems, all workers who addressed Nabokov's scenario for Beringian dispersal ignored the question of whether it was devised on the basis of precise reference to taxonomic characteristics, but even so, Naomi Pierce and her team found it to be worth testing. Now, with these fleeting clues to the character states grounding his vision brought into better focus, one finds further valuable material hidden in the "Conclusions" sections of his various published scientific works.

Because the main goal of Nabokov's publications was to produce valid and useful taxonomic classificatory work, useful for understanding the groupings of modern extant species, subsequent researchers, building from that work, had similar priorities. They were not attending to *the evolutionary story Nabokov*

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13 Nabokov (1945) can be viewed as a PDF (https://www.hindawi.com/journals/psyche/1945/065236/). Some examples of this generality in Plates 1-6 include those below. Note, however, that the Plates, their captions, and the related species descriptions are each in different sections of his paper. As noted in *Fine Lines*, this complexity historically caused confusion in interpreting Nabokov's results. Examples below thus cite the Plate numbers, page numbers, and (in quotations) the places in the species descriptions that Nabokov described particular traits.

Relevant general trends in morphological transformation (elongation, complexification and additional components) are especially noticeable among more species-rich groups, like *Cyclargus* (as in Plate 3, p. 56 [Explanation of Plate, p. 50], bottom half of Plate, degree of valve's rostellum length and its terminal "coxcomb" (p. 16) and, in *Hemiargus* (Plate 4, p. 57 [Explanation of Plate, pp. 50-51]), in Plate's left and right columns of valve structures— degrees of (i) "bluntly tapering tip" (pp. 21-22) of the rostellum, and in Plate center (ii) aedeagus length, comparably "aedeagus very long..." (p. 21).

Also in less speciose groups, *Echinargus* (Plate 5, p. 58 [Explanation of Plate, p. 51]), Plate's top third, sagum "armed with set of teeth...along whole of the margin" (p. 28); *Pseudolucia* (Plate 5, p. 58 [Explanation of Plate, p. 51]), Plate's center-right valve figures, degree of tapering of rostellum (p. 33) and "comb of valve" (Plate 5, 3-5, and "CHI 4"); *Paralycaeides* (Plate 6, p. 59 [Explanation of Plate, p. 52]), Plate's top half, degree of tapering of rostellum and "comb" "at the tip" (p. 37 & p. 52 [Plate 6, 3-4]); and *Madeleinea* (Nabokov's "Itylos") (Plate 6, p. 59 [Explanation of Plate, p. 52]), Plate's bottom half, condition of rostellum and terminal comb.

More related visualizations and detailed commentaries on their significance can be found in Blackwell and Johnson (2016), 73-107, 158-161.

Complex as they may seem, these, and numerous others not specifically illustrated by Nabokov, were the morphological conditions Nabokov was looking at to draw his conclusions.

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was working to tell (and, to repeat, he told it rather telegraphically). Perhaps because in those days evolutionary scenarios were often not taken seriously, Nabokov downplayed that part of his work, too. But now, it reveals itself to the seeking eye, and in fact, in a lecture to his Wellesley College students, from 1946, Nabokov is quite explicit about his ambitions as an evolutionary theorist. Speaking of a child who merely collects butterflies enthusiastically, he reports to his audience the fascinating things the child will not notice:

> "He will not even suspect the fascinating variety of inner organs, the varying shapes of which allow the scientist not only unerringly to classify them, often giving the lie to the seeming resemblance of wing patterns, but also to trace the origin and development and relationship of the genera and species, the history of the migration of their ancestors, the varying influence of the environments on the developments of the species and forms, etc. etc. etc." (Nabokov, 2000, 399).

In contrast to this imaginary child—Nabokov's own younger self in reminiscence—the later Nabokov knew the fascinating variety, "unerringly" classified them, contradicted wing patterns, traced the origins and relationships of genera and species, and—what Vila et al. finally unpacked in 2011—charted the history of the transcontinental migrations and invasions of species from the Old World to the New. The "thermal filter" of Beringia, and the genetic markers of thermal tolerances, constitute part of the "etc. etc. etc.," unimaginable to Nabokov in specifics, but implied in his work as a future path of scientific discovery, to researchers with the right tools: Naomi Pierce and her team.

Demonstrating this insight in his "Conclusions" sections, Nabokov often made additional comments relative to his sense of ancestral vs. derived states, sometimes regarding small assemblages, sometimes concerning larger ones. A pertinent example, synthesizing elements we have presented above, is his short closing paragraph from 1945's "Notes on Neotropical Plebejinae," which demonstrates how these discovered traits helped him distinguish the evolutionary relationships of these Blues worldwide, especially in the context of his Beringian dispersal scenario. He wrote:

> "The following general remarks may be added. Of the nine neotropical genera none occur elsewhere. Three, namely *Parachilades*, *Paralycaeides* and *Itylos*, have **retained** in the Andes . . . structural shapes closely similar to such structures from which *Chilades*, *Lycaeides* and *Aricia*, respectively, **can be easily imagined to have been derived** in their Old World homes. Three, namely *Pseudochrysops*, *Hemiargus* and *Echinargus* reveal certain characters of the paleotropical *Freyeria* (the first) and *Chilades*, but have become strongly differentiated in the neotropics. Still more remote is the relationship between *Cyclargus*, *Pseudothecla* and *Pseudolucia* on one side and Old World forms on the other. It is to be noted however that *Cyclargus* and *Hemiargus* are allied to *Aricia* and *Itylos* in the falx. The general *Hemiargus—Echinargus-Cyclargus* type of aedeagus is not found in the Old World and apparently represents a very ancient type retained and developed in the neotropics, but extinct or unrecognizably altered elsewhere." (Nabokov, 1945, 43) [Bold emphasis added.]

Here, we find extremely wide-ranging content, densely presented, and whose significance comes to light only in the context of other short comments, scattered elsewhere in this same paper and in Nabokov's publications on (North American) *Lycaeides*.

As a historical matter, highlighting these types of summaries also helps us come to understand the many instances in which Nabokov's work was ill-understood, often, it appears—oddly enough—simply because of its level of profuse and dense detail. To mention only a few cases that are well documented: *Nabokov's Blues* and *Nabokov's Butterflies* both described instances of his contemporaries considering his scientific papers dense or hard to decipher (Johnson and Coates, 1999, 310-11; Boyd, 2000, 22-25); *Nabokov's Blues* presented the example of his entire Latin American Blues classification not finding general usage for decades because the British Museum's celebrated lepidopterist Norman D. Riley—apparently not comprehending, or referencing, the unmistakable data in the complex Plates and Plate Captions in Nabokov (1945)—left Nabokov's superior classifications out of his "authoritative" works on the region (Johnson and Coates, 1999, 91-92, 100-102); and here too, in the current case, where it had been concluded, or assumed, that Nabokov had not developed his evolutionary and Beringian dispersal scenario for Blues on the basis of particular taxonomic characteristics.

Yet it was this same level of detail in this work that captivated Nabokov. Such immersion was essential to the personal delight he expressed about the entomological pursuit. There are many examples of course, but one that is especially memorable is his comment to his sister, Elena Sikorski, on Nov 26, 1945: "To know that no one before you has seen an organ you

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are examining, to trace relationships that have occurred to *no one* before, to immerse yourself in the wondrous crystalline world of the microscope . . . . all this is so enticing that I cannot describe it" (Nabokov, 2000, 387). These secrets of evolution became dearer to him than the discovery of "new" species in the wild—something he had regularly wished for in childhood and as an amateur lepidopterist, but which faded in importance as his understanding of the deeper mechanisms of evolution grew throughout the 1940s.

Epilogue: Phylogenetic locations of key morphological traits

We present our discoveries about the bases for Nabokov's discernments and taxonomic revisions in Figure 3, indicating on which branches in the phylogenetic tree each feature occurs. We also briefly describe each of the anatomical structures that Nabokov inferred as "ancestral" and are represented in the figure by certain symbols.

(1) the bilobed silhouette—the superior and inferior processes of the male armature (a.k.a "clasper", "valve") [inferred as ancestral by Nabokov 1944 and 1945, as cited and quoted previously]. The sclerotized armature's two lobes are unelaborate, of somewhat equal length, and with relatively simple termini (not ones with elaborated or highly sculptured structures). This is consistent with simple, unelaborate, unsculptured structures often being substantiated as primitive (or ancestral) states in the context of specific highly corroborated phylogenies (though, of course, this is not always the case). Accordingly, in relatively derived character states of the armature, the lobes are likely of varying relative size and length and likely terminate with elaborate and/or variously sculptured termini.

(2) the triangle silhouette—the "triangle" formed by selected measurements of elements of the falx, furca, gnathos etc. (a.k.a. Nabokov's "Magic Triangles") [viewed as ancestral by Nabokov (1945)]. The triangulation data of the falx, furca, gnathos etc. is that generally typifying a more equilateral triangle, a relatively simple configuration of these structures. Accordingly, sculptural derivations of these structures are likely to produce triangulation data generally typifying (even radically) non-equilateral triangles of all kinds.

(3) the rodlike silhouette—conditions of the male's penis (a.k.a. aedeagus), inferred as ancestral by Nabokov (1945) (as quoted previously). As illustrated in Nabokov (1945) Plates 3-5, a rather parenthesis-shaped, sclerotized, rodlike structure with a variously spikey terminus but blunter anterior end and (as noted in 4 below) sometimes centrally wrapped with a sclerotized sheath which often shows additional components like spines or other dentate elements. As we have quoted directly, previously (from Nabokov [1945], p. 43), Nabokov viewed this general structural configuration of the penis as distinctive from other varied conformations in Blues and interpreted it as "ancient" and thereafter lost or unrecognizable in other Blues.

(4) the square silhouette—the occurrence of a structure in the male genitalia Nabokov named the "sagum" (from the name of a Roman military cloak that was wrapped around the body) (Nabokov, 1949, 480; Nabokov, 1944, 109; Nabokov, 1945, 52). A sclerotized sheath-like structure, variously wrapped around the penis and sometimes covered with additional components like spines or other dentate elements. The differential occurrence of this structure was used by Nabokov, at the time controversially, to separate, as distinct genera, some Latin American Blues previously long considered to be the same. Nabokov considered the sagum to be a differentially occurring, relatively more primitive, characteristic lost in taxa he viewed as exhibiting more derived character states (like those we summarize in our Footnote 22). He devoted a detailed paragraph to this interpretation on Nabokov (1945, 45) which (added to his statements about the sagum in taxon descriptions [pp. 11-19, 27-37]) portrayed the sagum as also appearing in "rudimentary" form in (i) some other Neotropical Plebejinae taxa and (ii) some more distant outgroup blues elsewhere in the world. This indicates that his determination of the ancestral nature of this character state arose from both (i) his view of generalities about apparently more derived character states (Footnote 22) and (ii) outgroup comparison. How far afield one can go with outgroup comparison is complicated, of course, by possibly not knowing what structures are homologous (actually the same in evolutionary origin) or analogous (simply looking alike), something Nabokov himself warned about in his own opening remarks (p. 4) regarding "false resemblances" and "false dissimilarities."

We note (1) and (2) above both:

(i), at the **right** of the Figure, where they occur in modern-day contemporaneous species (and where Nabokov inferred such conditions as retained ancestral characters) and

(ii) at the **left** of the diagram of the Figure, marking the node which would contain the various species Nabokov was inferring

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had more "derived" states of these primitive anatomical features.

Also, it is important to note these further generalities regarding the taxonomic value of the Blue butterflies' genitalic characteristics. The chapter in *Fine Lines* by Pierce et al. enumerated evolutionary factors aiding the taxonomic value of genitalic characteristics. "There are several good evolutionary reasons for this focus on the morphology of genitalia," they say (Pierce et al., 2016). "Rapid evolution is useful for the taxonomist because it permits closely related species to be distinguished," a perfect description of Nabokov's taxonomic practice. Further, both rapid evolution and stabilizing selection (as in the wing patterns of Blues also studied in minute detail by Nabokov) add to the value of genitalic characters. They summarize: "A group of closely related butterflies may thus have identical wing coloration but distinct yet related genitalic morphologies" and all of this "results in evolutionary change that may be useful to the taxonomist" (Pierce et al., 2016, 286-7).

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References:

Blackwell, S. H. and Johnson, K. (2016). Introduction. In Blackwell and Johnson (Eds.), *Fine Lines: Vladimir Nabokov's Scientific Art* (pp. 1-28) Yale University Press.

Boyd, B. Nabokov. (2000). Nabokov, Literature, Lepidoptera. In V. Nabokov, *Nabokov's Butterflies* (pp. 1-31).

Forister, M. L., Gompert, Z., Fordyce, J. A., & Nice, C. C. (2011). After 60 years, an answer to the question: what is the Karner blue butterfly?. *Biology Letters*, 7(3), 399-402.

Gompert, Z., Lucas, L. K., Fordyce, J. A., Forister, M. L., & Nice, C. C. (2010). Secondary contact between *Lycaeides idas* and *L. melissa* in the Rocky Mountains: extensive admixture and a patchy hybrid zone. *Molecular Ecology*, 19(15), 3171-3192.

Hennig, W. (1966). *Phylogenetic Systematics*. Translated by D. Davis and R. Zangerl. University of Illinois Press.

Johnson, K. and Coates, S. (1999). *Nabokov's Blues: The Scientific Odyssey of a Literary Genius*. Zoland Books.

Nabokov, V. (1941). On some Asiatic species of Carterocephalus, *Journal of the New York Entomological Society* 49 (3), 221–223.

Nabokov, V. (1943). The Nearctic forms of *Lycaeides* Hüb. (Lycaenidae, Lepidoptera). *Psyche: A Journal of Entomology*, 50, 87-99.

Nabokov, V. (1944). Notes on the Morphology of the Genus *Lycaeides* (Lycaenidæ, Lepidoptera), *Psyche: A Journal of Entomology*, 51 (3–4), Sep–Dec, 104–138.

Nabokov, V. (1945). Notes on Neotropical Plebejinae (Lycaenidae, Lepidoptera). *Psyche: A Journal of Entomology*, 52, 1-61.

Nabokov, V. (1949). Nearctic Members of the Genus *Lycaeides* Hübner (L,L), *Bulletin of the Museum of Comparative Zoology*, 101 (4), 477–541,

Nabokov, V. and Boyle, R. (1959). An absence of Wood Nymphs. *Sports Illustrated*, 14 Sept, 1959, E5-E8. Reprinted in V. Nabokov, *Nabokov's Butterflies* (pp. 528-537).

Nabokov, V. (2000). *Nabokov's Butterflies*. B. Boyd and R.M. Pyle (Eds). Beacon Press.

Pierce, N. E., Vila, R., Eastwood, R. G, Berry, A. J., Dai, T (2016). Nabokov's notes and labels from the Museum of Comparative Zoology: Boon for a recondite biographer, or data for a serious systematist? In Blackwell and Johnson (Eds.), *Fine Lines* (pp. 285-294). Yale University Press.

Talavera, G., Lukhtanov, V., Pierce, N. E., Vila, R. (2012). Establishing criteria for higher-level classification using molecular data: The systematics of *Polyommatus* blue butterflies (Lepidoptera, Lycaenidae). *Cladistics* 29(2) (June 2012):166-192. DOI:10.1111/j.1096-0031.2012.00421.

Vila, R., Bell, C. D., Macniven, R., Goldman-Huertas, B., Ree, R. H., Marshall, C. R., Bálint, Z., Johnson, K., Benyamini, D. & Pierce, N. E. (2011). Phylogeny and palaeoecology of *Polyommatus* blue butterflies show Beringia was a climate-regulated gateway to the New World. *Proceedings of the Royal Society B: Biological Sciences*, 278(1719), 2737-2744.

Zimmer, C. (2011, January 25). Nonfiction: Nabokov Theory on Butterfly Evolution Is Vindicated, *The New York Times*. https://www.nytimes.com/2011/02/01/science/01butterfly.html

Zimmer, D. E. (2012). Genera, species and subspecies named by Nabokov. In D. E. Zimmer, *Guide to Nabokov's Butterflies and Moths*. Web Edition. http://www.d-e-zimmer.de/eGuide/Lep1.htm#Lep1.1

Zimmer, D. E. *Guide to Nabokov's Butterflies and Moths*, Online Edition (2012). http://www.d-e-zimmer.de/eGuide/

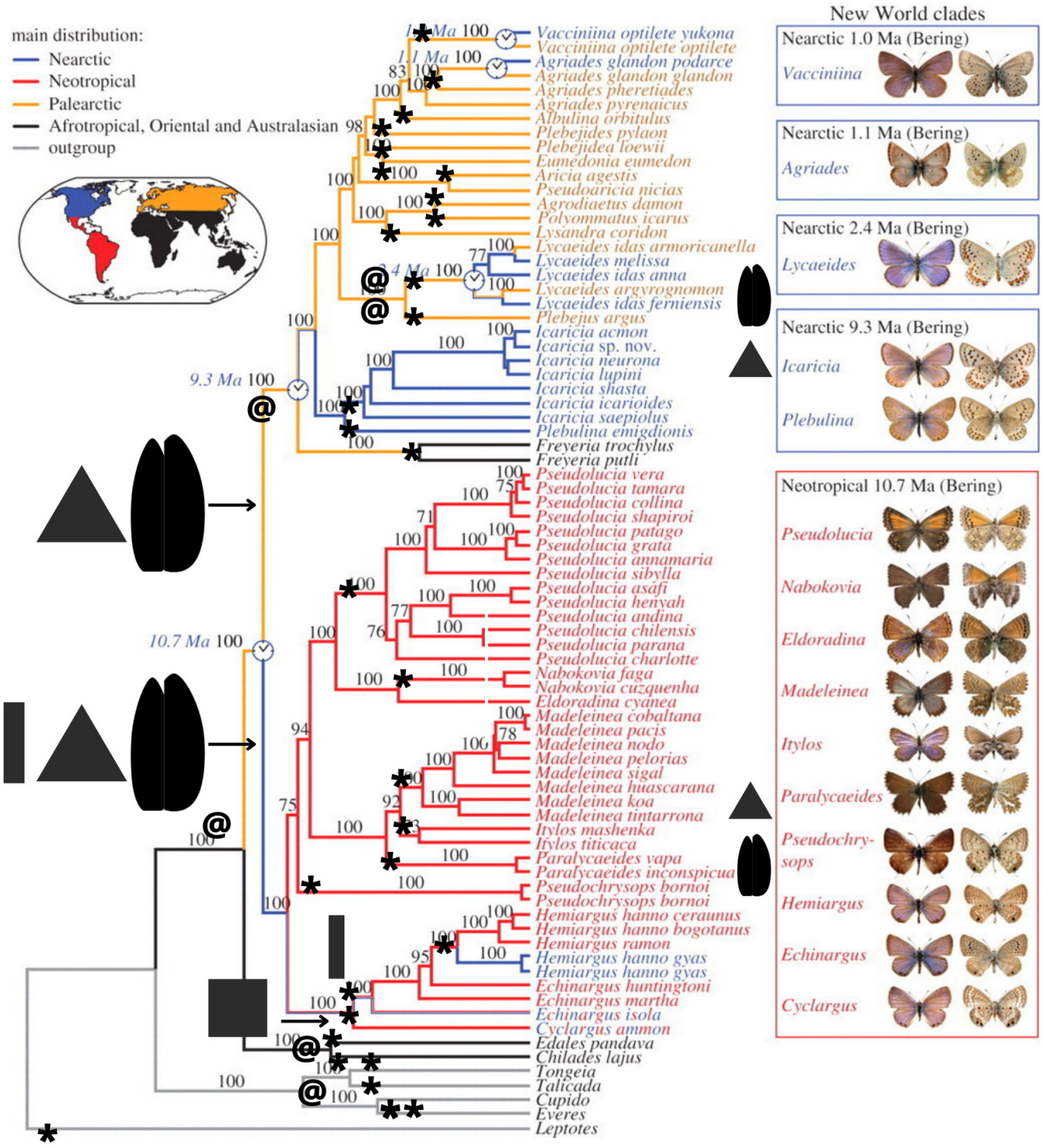

Figure 3. The Vila et al. DNA Phylogeny diagram, with silhouettes indicating branches with diagnotic features Nabokov used to establish key distinctions among species and genera. See epilogue text for description of each silhouette's meaning.

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