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Notes on Eastern North American Lepidoptera.

parts by
Harry Pavulaan (editor), Annette Allor

ABSTRACT. New natural history elements and distribution records of several North American butterflies are reported. While diversity and distribution of butterflies in the eastern United States is commonly believed to be fully known, the findings presented here show that much is yet to be learned of our butterfly fauna.

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Celastrina ladon and *C. neglecta* (Lycaenidae: Polyommatinae) are distinct species differentiated primarily by a diagnostic wing scale structure, voltinism, and host tolerance of *Cornus florida*.

Harry Pavulaan
606 Hunton Place NE, Leesburg, VA, USA, 20176
intlepsurvey@gmail.com

ABSTRACT. With continued confusion of the two species by naturalists, *Celastrina neglecta* (W. H. Edwards) is here clarified as a distinct species, not a form or subspecies of fully sympatric *C. ladon* (Cramer). Each is characterized by distinct physiological characteristics, phenology, voltinism, host tolerance, and distribution. *C. ladon* is an obligate univoltine taxon, appearing in a single springtime flight throughout its range limited to the eastern United States, while *C. neglecta* produces multiple late-winter through early-fall broods over a much broader range, and may be represented by localized ecotypes or biotypes. *C. ladon* is distinguished from all other blue *Celastrina* species primarily by the presence of a unique male forewing scale structure found in no other *Celastrina* except for dorsally-black *C. nigra*.

Additional key words: Androconia, elongated overlapping scales, voltinism.

INTRODUCTION

Celastrina ladon and *C. neglecta* were each described as separate species, but have long been misunderstood, and subsequently treated as a single species consisting of a spring flight commonly referred to as form *violacea* ("Spring Azure") and subsequent summer flights commonly referred to as form *neglecta* ("Summer Azure"). William Henry Edwards studied and extensively documented the relationship of the North American *Celastrina*, in the process describing *L. violacea* (W. H. Edwards, 1866) (later synonymized under *C. ladon*), *L. neglecta* (W. H. Edwards, 1862), and "redescribed" *L. pseudargiolus* (W. H. Edwards, 1866, 1868-69) (what would eventually be known as *C. neglectamajor*), but ultimately confused their relationships. Edwards' confusion arose from his misunderstanding that any univoltine *Celastrina* will readily produce subsequent annual generations when reared under artificial (lab) conditions. No doubt confused by his own rearing results, he concluded his life's work on the genus in Vol. II of his Butterflies of North America (W. H. Edwards, 1884), exclaiming that all North American *Celastrina* comprised a single, highly variable and phenologically complex taxon: "...their history has come to be thoroughly known, and it is found that they…constitute one polymorphic species, which has possession of the broad continent…" Virtually all subsequent taxonomic treatments through the end of the 20th century followed Edwards' faulty conclusion, with few authors actually performing necessary study to support their own assumptions.

Furthermore, several authors have treated North American *Celastrina* populations as subspecies of Eurasian *C. argiolus* (dos Passos, 1964; Howe, 1975; Eliot & Kawazoe, 1983; Scott, 1986; Ferris, 1989). The present paper clearly demonstrates that *C. ladon* is uniquely different from *C. argiolus* by the dorsal forewing scale structure of males (Ômura *et. al.*, 2015) (**Fig. 3A & 3M**). *C. neglecta* and *C. argiolus* both have typical *Celastrina* androconia (**Fig. 3A & K**), yet they differ primarily by phenotypical characters. They are also broadly allopatric, with *C. argiolus* confined to Eurasia, and *C. neglecta* confined to eastern North America.

The purpose of the present paper is to present joint findings with my research associate David M. Wright, resulting from 38 years of fieldwork, rearing, and detailed examination of specimens. Our work on the *Celastrina* set aside over a century of erroneous presumptions by authors and commenced with a fresh look.

COMPARISON OF DIAGNOSTIC PHENOTYPICAL CHARACTERS

Despite the superficial similarity of both species in their spring flight periods; their similar blue dorsal surfaces and gray ventral surfaces displaying the same general pattern of black markings; the primary difference between both species is in the structure of the male dorsal forewing scale alignment (**Figs. 1-3**). Understanding of this morphological character and recognition of this difference in both *ladon* and winter/spring brood *neglecta* is critical to proper identification of both species.

Dorsal forewing scale structure in males

C. neglecta: Males of all broods have typical *Celastrina* forewing scale structure in which the blue scales are arranged in neatly-aligned rows and underlain by androconia (**Figs. 1 black arrow & 3K**) which are also arranged in neat rows, best described as appearing like shingles on a roof. The dorsal side of the forewings of the winter/spring form has a "metallic" luster.

C. ladon: Males possess a unique forewing scale structure different from males of *C. neglecta* and all other *Celastrina* except the black *C. nigra* which also has this unique structure. A layer of clear elongated scales (**Fig. 2 black arrow & 3M**) overlays the layer of blue scales beneath, replacing the rows of androconial scales that are found in other *Celastrina* with the exception of *C. nigra*. The appearance of these overlaying scales gives a haphazard appearance under magnification. The dorsal side of the forewings has a distinct "greasy film" sheen in sunlight.

Dorsal characters of males

C. neglecta: Males of the winter/spring brood tend to be uniformly bright metallic blue dorsally (**Fig. 4**). The outer fringe of the hindwings is normally clear white. Striking white wing veins highlight the leading edge of the forewing; sometimes white veins appear in the center of the forewing. Males of the subsequent summer broods (**Fig. 4**) tend to be a lighter violet blue and the secondaries display a distinct arrangement of white coloration within the wing cells, appearing as white rays extending out from the base.

C. ladon: Males tend to be uniformly violet-blue dorsally (**Fig. 4**). The outer wing fringes are normally gray or somewhat "checkered" with alternating gray and white. The leading edge of the forewing has a subdued shade of lightened scales.

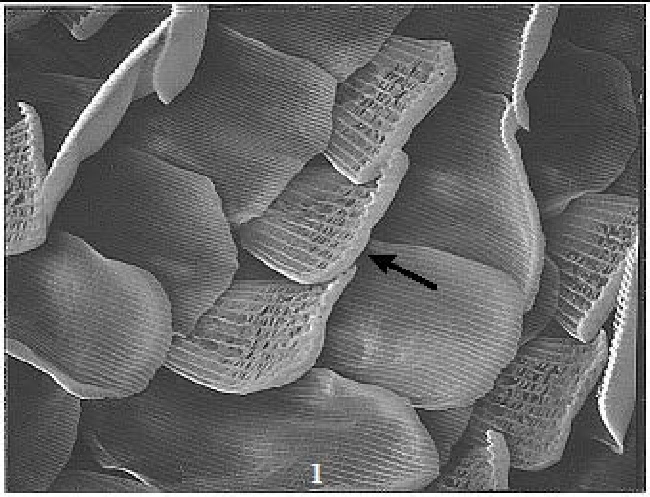


Fig. 1: *C. neglecta* wing scales and androconia.

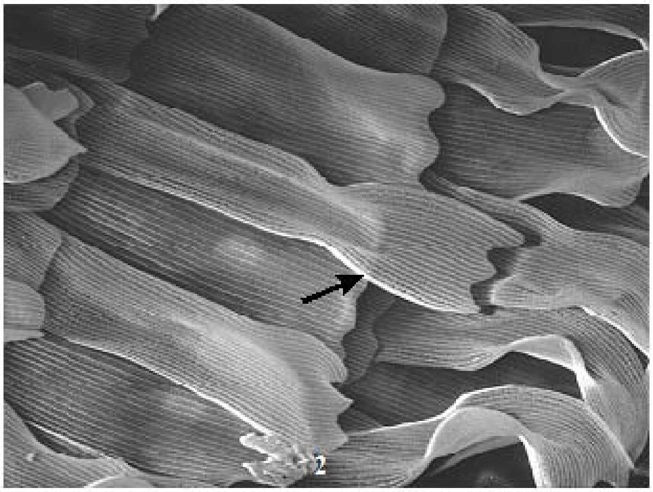


Fig. 2: *C. ladon* overlay scales, covering blue scales.

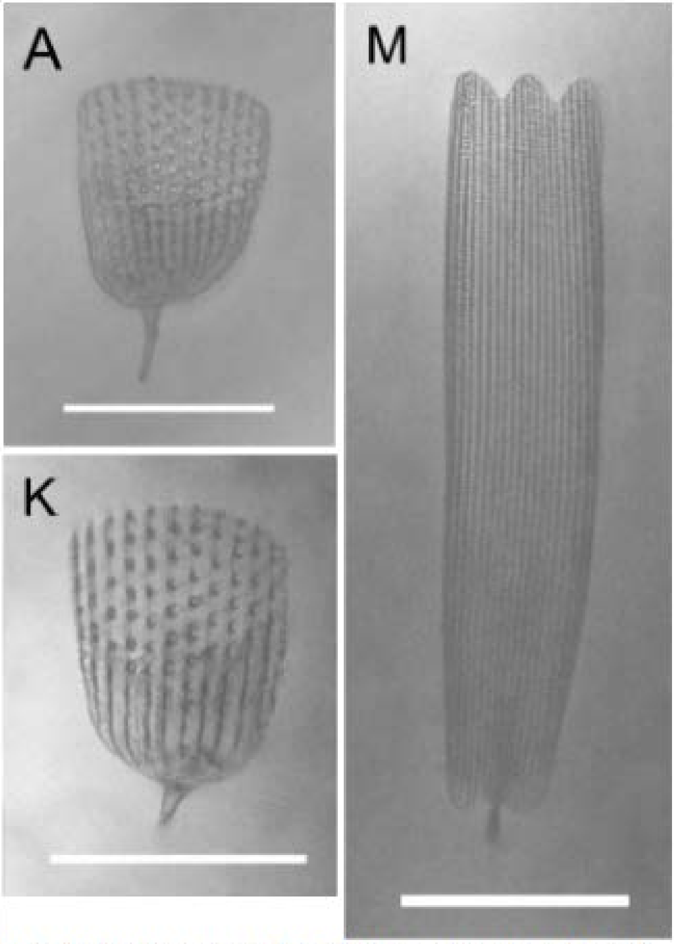


Fig. 3: Androconia of *Celastrina argiolus* (A) and *Celastrina neglecta* (K), and elongated scale of *Celastrina ladon* (M) from Ômura, *et. al.* (2015).

Figs. 1 & 2 from Wright & Pavulaan (1999).

Dorsal characters of females

C. neglecta: Females of the winter/spring brood tend to be uniformly brilliant blue dorsally with a distinct metallic sheen (**Fig. 4**). The outer wing fringes of the hindwings are normally clear white. Striking white wing veins highlight the leading edge of the forewing; sometimes white veins appear in the center of the forewing. Females of the subsequent summer broods (**Fig. 4**) tend to be a paler blue in the forewings with a cloud of gray/white scales centered in the disk. The hindwings display white coloration within the wing cells similar to the males, appearing as white rays extending out from the base, often extending over the entire wing, giving the secondaries an almost completely white appearance.

C. ladon: Females tend to be uniformly deep violet-blue dorsally (**Fig. 4**). The outer wing fringes are normally gray or somewhat "checkered" with alternating gray and white.

Ventral characters of males and females

C. neglecta: Adults of the winter/spring brood tend to be whitish-gray ventrally (**Figs. 4, 5**), and have been described as having a white or light "steel-gray" appearance. The wing outer fringes are normally clear white. The spot pattern on the hindwing can be highly variable (as variable as in *ladon*). The spots can be quite enlarged or very reduced, often appearing like the summer form beneath. Individuals with darkened margins or discal patches occur, though rarely. In neglecta, these markings are characteristically black-pigmented. The summer form is much whiter beneath, with a greatly reduced spot pattern (**Fig. 4**).

C. ladon: Adults tend to be medium gray ventrally (**Figs. 4, 6**). The outer wing fringes are normally gray or somewhat "checkered" with alternating gray and white. The spot pattern on the hindwing is variable but the spots tend to be more enlarged than in winter/spring form *neglecta*. The form with a darkened margin along the outer edge of the hindwing (form "*marginata*" of authors) (**Fig.** 7) is frequently encountered, but mainly in the northern tier and in the Appalachian Mountain region. Both spotted-venter and dark-margined forms tend to have these markings more brown-pigmented.

Fig. 4. Comparison of *Celastrina* phenotypes. Top row, left to right: *C. ladon* male female; underside. Middle row, left to right: *C. neglecta* winter/spring form male; female; underside. Bottom row, left to right: *C. neglecta* summer form male; female; underside. All specimens taken by the author in Loudoun County, VA.

Fig. 5. *C. neglecta* spring form. Photo courtesy Matt Orsie.

Fig. 6. *C. ladon*. Photo courtesy Lydia Fravel.

Fig. 7. *C. ladon*, margined form. Photo courtesy Annette Allor.

DIAPAUSE, VOLTINISM AND PRESENCE OF ECOTYPES AND BIOTYPES

C. ladon is an obligate univoltine butterfly. After 38 years of rearing *C. ladon* from both wild-collected and lab-obtained ova and larvae, it is clearly evident that *C. ladon* is strictly obligate-univoltine, and does not produce multiple annual generations. It is important to realize that larvae reared under artificial conditions (a regimen of unnatural day length and steady temperature) will almost always produce a false "summer" brood of an unnatural phenotype. This lab-reared false generation of *ladon* displays the same unique male forewing scale structure present in the natural parental adults, at a rate of 100%. The unique *ladon* forewing scale structure is not subject to variation. Only by rearing larvae in natural (outdoor) conditions of normal day length and fluctuating day/night temperatures, can one reasonably expect pupae to go into diapause, thus confirming the univoltine nature of *ladon*. Natural broods were produced from *C. ladon* females collected in Maryland, Pennsylvania, Virginia, and West Virginia. Artificially produced "second-generation" broods with the unique wing scale structure were produced from *C. ladon* females collected in Maryland, Missouri, Pennsylvania, Virginia, and West Virginia. Among thousands of *Celastrina* specimens examined from the eastern U.S., in various institutional and private collections, individuals possessing the unique wing scale structure appeared only in the spring.

C. neglecta, on the other hand, produces multiple annual generations. In northern Virginia and central Maryland, adults have been found to emerge as early as February. Larvae reared both under natural conditions of spring and early summer, and artificial (laboratory) conditions, will always produce the typical summer phenotype (**Fig. 4**). Ova and larvae collected in late-summer and early-fall and reared under natural conditions will undergo diapause and hibernate until the following year, and will produce the natural winter/spring phenotype.

An interesting topic is the highly adaptable nature of regional and localized populations of *C. neglecta*, fine-tuning their flights to coincide with and to take advantage of the pre-bloom budding period of select hostplants. Several apparent ecotypes or biotypes of *C. neglecta* have been identified (this will be addressed in greater depth in subsequent papers currently in work). Most populations in the northern Piedmont region will produce a late-winter/early spring brood of the winter/spring form, followed by multiple annual broods of the summer form which commence in mid-May. I refer to this fully multivoltine entity as ***C. neglecta* type-1** in research. Type-1 is exceptionally common along the Potomac River immediately west of Washington D.C. and at sites along the foothills of the Blue Ridge.

In some isolated sites, a population or localized colony will actually skip the winter/spring flight, and first emerge during the second generation of type-1 that flies in surrounding areas in mid-May, thus producing the summer phenotype as the first brood at that location. This has been observed annually in a marsh habitat study area in Herndon, VA for several decades. In some locations in the Appalachian Mountains, there is a delayed-emergence bivoltine *neglecta* that first emerges in June, after the May flight of *neglecta* type-1. It will produce a second brood in August. Generally, it flies between broods of type-1 and consists of only the summer form. I refer to this as ***C. neglecta* type-2** in research. The overlapping broods of types 1 and 2 give the appearance of a continually-brooded species in areas where both occur.

Whether these represent ecotypes, biotypes, consistent host races, or cryptic sibling species remains under intensive study. For the purposes of this paper, the *C. neglecta* type-1 populations are of greatest importance in comparisons to *C. ladon*, since the late-winter/early-spring brood and phenotype of *neglecta* has long been confused with *C. ladon*, prior to our discovery of the unique male wing scale structure of *ladon*.

HOSTPLANT SELECTION OF *C. ladon* AND SPRING BROOD *C. neglecta*

Due to overwhelming confusion over which names applied to the various *Celastrina* in the literature, previous hostplant listings are unreliable and inaccurate at best. Both *C. ladon* and *C. neglecta* have varied host choices during spring. For the purposes of this paper, I am primarily only concerned with hosts selected by *ladon* and the sympatric winter/spring brood of *neglecta* type-1. Rearing larvae to maturity or photographing larvae on certain hostplants is essential to our understanding of which species is present.

Hostplants only of the early winter/spring brood of *C. neglecta* are listed here to help define the distinction between the two fully sympatric taxa. *C. ladon* has been documented/confirmed on the following hosts in Virginia, West Virginia and central Maryland: *Cornus florida* (regionwide), *Prunus serotina* flower buds and eriophyid mite leaf galls (Frederick Co., VA.; Allegheny Co., MD.), *Viburnum prunifolium* (Loudoun Co., VA.), *Ilex opaca* (Westmoreland Co., VA., Anne Arundel Co., MD.). Winter/spring brood *C. neglecta* has been documented/confirmed on following hosts in Virginia and central Maryland: *Ilex opaca* (Fairfax and Westmoreland Co's., VA.; Anne Arundel Co., MD.), *Prunus serotina* flower buds and eriophyid mite leaf galls (Frederick Co., MD.; Frederick Co., VA.), and *Viburnum prunifolium* (Loudoun Co., VA.). Additional hosts are used elsewhere.

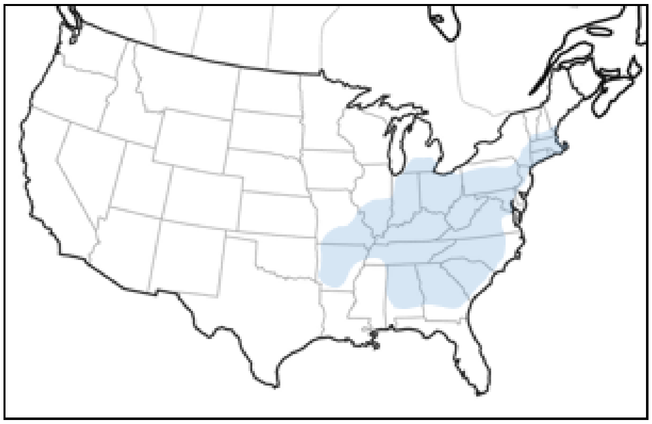
A CRITICAL FINDING OF HOSTPLANT ACCEPTANCE

In a previous study (Pavulaan, 2014), it was noted that spring *Celastrina neglecta* females will not oviposit on, and neonate *C. neglecta* larvae will refuse to eat *Cornus florida* (Flowering Dogwood) - the primary *C. ladon* host. In the 2012-2014 study, captive females of sympatric *C. ladon* and spring flight *C. neglecta* (*ex* Leesburg, VA.) were confined in containers with cuttings of *C. florida* flower buds. While *C. ladon* females readily oviposited on *C. florida*, *C. neglecta* females refused to oviposit on the same plant under identical conditions. On the other hand, *neglecta* females confined with cuttings of *Viburnum prunifolium* readily oviposited on that host, while *C. ladon* females did not. In the rearing experiment, individual flower buds containing *C. neglecta* eggs were removed and strategically placed on cuttings of *C. florida* flower buds so that newly-hatched larvae would have the direct choice of feeding on *Cornus florida*. Newly hatched larvae were also transferred from *V. prunifolium* buds to *C. florida*, thus leaving them no choice but to feed on *C. florida*. Most of the first instar *C. neglecta* larvae ignored the *C. florida*, subsequently starving. A few remaining *neglecta* larvae attempted to feed on *C. florida* --- not on the flower buds, but rather boring into the base of the underside of the white bracts or into the basal portion of the flower buds. All *C. neglecta* larvae confined on *C. florida* died. Subsequent attempts in 2016-2018 and in 2020 replicated the earlier results, with all *neglecta* larvae preferring to starve rather than to eat *C. florida*. When returned to *V. prunifolium* buds, *neglecta* larvae immediately resumed feeding. In 2018, young fourth instar larvae of *neglecta* were transferred to *C. florida*. While those larvae did initially feed on *C. florida*, they all died within 3 days of transfer, while remaining in a feeding position. It is concluded that *Cornus florida* is toxic to *C. neglecta*. Curiously, while captive *C. ladon* females would not oviposit on *V. prunifolium* buds in this study, *ladon* larvae were once found on a *V. prunifolium* shrub in nature. These larvae, when offered the same host in the laboratory, accepted it and produced adults.

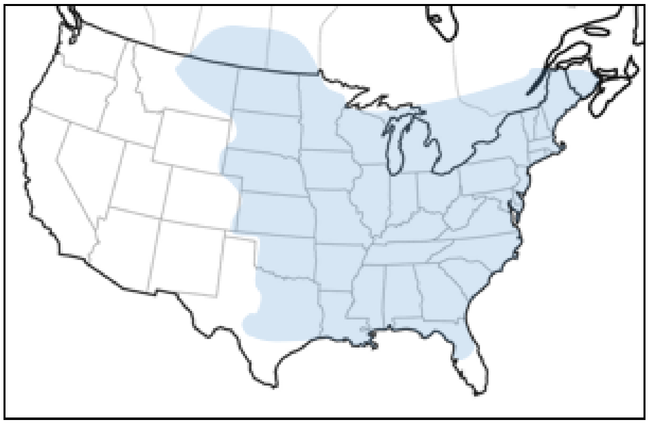
DISTRIBUTION AND RANGE

C. ladon is essentially an Appalachian-Ozarkian endemic, and the range of *C. ladon* (**Map 1**) coincides very precisely with the historic range of *Cornus florida*, considered the primary host. Due to the regional demise of *C. florida* beginning around 1983 and maximizing around 1998, due to *Discula destructiva* (Dogwood Anthracnose) fungal blight, *C. ladon* populations have gone into a dramatic decline in areas where Anthracnose has had greatest impact on *C. florida*. For example, in study areas throughout northern Virginia and central Maryland, the primary "Spring Azure" since around 1990 is *C. neglecta*, which has essentially replaced *C. ladon* in many areas, and has become noticeably very common in late winter and early spring. *C. ladon*, on the other hand, with relatively few surviving (fungal resistant?) *C. florida* trees in the same areas, now hangs on as a relatively rare species. In some areas where *C. ladon* successfully utilizes alternate hosts, the species remains fairly stable, such as in the Appalachian Mountains (on *Prunus serotina*) and the Chesapeake Bay Region (on *Ilex opaca*) in Maryland and Virginia.

The range of *C. neglecta* extends considerably beyond the range of *C. ladon*, completely encompassing the range of the latter. *C. neglecta* ranges from southeastern Canada, south to the Gulf Coast, and west through the Great Plains region into southcentral Canada (**Map 2**). All over its range, *C. neglecta* has been documented on an extensive range of hosts and its populations appear to be stable.



Map 1. Documented range of *C. ladon*. Map courtesy of David M. Wright.



Map 2. Documented range of *C. neglecta*. Map courtesy of David M. Wright.

TAXONOMIC CONSIDERATIONS

Clench & Miller (1980) designated a neotype for *Papilio ladon* Cramer [1780] and differentiated it from Eurasian *C. argiolus*. They selected a specimen with a type locality stated as: "Anne Arundel Co.: Patuxent River, 19.iv.1964", which was later found to possess the unique *ladon* male forewing scale structure. The authors noted association with the name *pseudargiolus* (Boisduval & Le Conte, [1835], and considered the latter name a synonym of *ladon*. Clench & Miller did not recognize the unique elongated scale of the *C. ladon* neotype and thus assumed "specimens from later broods…" were broods of *C. ladon*. Ironically, the authors stated of North American *Celastrina*: "the androconial scales differed between New and most Old World *argiolus*-group butterflies. It is not clear what the authors intended to convey in regard to differences in androconia, as this was not illustrated in their paper. Ômura, *et al.* (2015) studied the androconia of Eurasian and North American *Celastrina* and illustrated differences in the androconia of the studied species (*C. argiolus argiolus, C. a. iynteana, C. a. ladonides, C. filipjevi, C. lavendularis himilcon, C. oreas arisana, C. sugitanii kyushuensis, C. echo cinerea, C. neglecta, C. idella, C. lucia* and *C. neglectamajor),* but most significant in their study was a clear demonstration of the absence of androconia and presence of the long overlay scale in *ladon* which replaces androconia typically found in *Celastrina* (**Fig. 3**). Clench & L. D. Miller also illustrated differences in male genitalia between European *C. argiolus* and *C. ladon*, but it is not known which species, *ladon* or *neglecta*, were examined under their concept of *ladon*. *C. argiolus* also differs phenotypically from both *ladon* and *neglecta* by the deep violet coloration of the dorsal side of the wings. On the ventral side of *C. argiolus*, the ground color is a pearly white and there is an area of greenish blue clouding at the base of the hindwings. Current mtDNA studies (in progress) show significant divergence of all North American *Celastrina* from Eurasian *C. argiolus*.

CONCLUSIONS

(1) The two taxonomic entities *Celastrina ladon* and *C. neglecta* are distinct sympatric species throughout the smaller range of *C. ladon*. The range of *neglecta* (**Map 2**) completely overlaps the range of *ladon* (**Map 1**) and extends considerably beyond the range of *ladon*.

(2) In much of the eastern U.S. Piedmont region, the spring brood of *C. neglecta* is persuasively our common "Spring" Azure. Since the demise of *Cornus florida*, *C. ladon* has become localized and otherwise rare throughout the Piedmont and Atlantic Coastal Plain regions, but is apparently stabilized in deciduous forest habitat containing abundant *Ilex opaca* understory in the Chesapeake Bay region, and in many locations in the Appalachian Mountains where it utilizes *Prunus serotina*.

(3) *Cornus florida*, the primary host of *C. ladon*, is toxic to *C. neglecta* larvae, though the species share other hosts in common.

(4) *Celastrina ladon*, by possessing a male forewing scale structure unique among the blue members of the genus, is separated at the species level from all other *Celastrina*.

(5) It is important to note that reliable identification and differentiation of the two species depends entirely on examination of the dorsal forewing surfaces (especially males). Though it is possible to differentiate a percentage of the two species from ventral views (generally considered unreliable), there is considerable overlap in variation and requires considerable training and experience to accurately distinguish most specimens by their venters.

(6) The following species arrangement is hereby confirmed for eastern United States *Celastrina* and Eurasian *C. argiolus* (historically treated as representing the North American species):

Celastrina argiolus (Linnaeus, 1758) [extralimital (Eurasia)]
Celastrina ladon (Cramer, 1780)
    =***pseudargiolus*** (Boisduval & Le Conte, [1835])
    =***violacea*** (W. H. Edwards, 1866)
Celastrina lucia (W. Kirby, 1837)
Celastrina neglecta (W. H. Edwards, 1862)
Celastrina nigra (W. Forbes, 1960)
Celastrina neglectamajor Opler & Krizek, 1984
Celastrina idella D. Wright & Pavulaan, 1999
Celastrina serotina Pavulaan & D. Wright, 2005

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A sincere thanks goes to David M. Wright (with whom I have studied North American *Celastrina* for 38 years as of this writing) for previewing the initial drafts of the manuscript for errors, corrections or additions, for the maps and wing images. Also, thanks to one anonymous reviewer who provided helpful comments. A special thanks go to the following Maryland naturalists for lively discussions on *Celastrina* and providing imagery for analysis: Annette Allor, Lydia Fravel, Richard Orr, Matt Orsie, Aaron Graham.

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ADDENDUM

North American *Celastrina* butterflies form a complex grouping of very closely related (recently-evolved) species, ecotypes, biotypes and host-associated populations. Over 30 years of attempts at crossbreeding some of the eastern taxa has proven fruitless, as the males and females seem to be able to identify and respond only to their own kind, certainly by the scent of lactone compounds in the male androconia, and in the case of *ladon* – the lack thereof. Evidence of hybridization between different *Celastrina* has not been documented. Our present knowledge depends heavily on morphological comparison of specimens, field observations, and hostplant acceptance experiments. Microscopic evaluation of the genitalia of correctly-identified *neglecta* and *ladon* awaits future study, since any past examination of genitalia of eastern North American *Celastrina* was based on outdated taxonomy and not clearly identified to species by current definitions. Presently, in collaboration with Dr. David Wright and myself, a team of geneticists at the University of Texas Southwestern Medical Center is conducting intensive genomic sequencing of all North American members of the *Celastrina*. Results will be forthcoming but preliminary analysis clearly shows distinctive differences between *neglecta* and *ladon.*

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A rare case of mosaic gynandromorphism in the Zabulon Skipper (*Lon zabulon*) (Boisduval & Le Conte[1837]) (Hesperiidae).

Annette Allor
aallor@aol.com

On August 15, 2021, I found an odd, yet beautiful example of a Zabulon Skipper (**Figs. 1-6**) in Elkridge, Howard Co., MD (off the Morning Choice Trail), not far from the Rockburn Branch stream. The habitat was at the edge of a forest clearing, typical for the butterfly. A few patches of thistles in peak bloom were covered with Zabulon Skippers. It took me a few seconds to figure out that this particular butterfly was, in fact, a Zabulon Skipper. But what a skipper it was! It had both male and female characteristics. I

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