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Recognition of the Spring Flight of *Celastrina* (Tutt) (Lycaenidae: Polyommatainae) in Southern New England as an Introgressed Hybrid Species.

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ABSTRACT. Populations of *Celastrina* (“Azure”) butterflies in southern New England have historically been referred to as either *Celastrina ladon* (Cramer) or *Celastrina lucia* (W. Kirby) by various authors. Following the discovery of elongated dorsal wing scales in males of *C. ladon* (D. Wright & Pavulaan, 1999; Ômura et al., 2015)—structures that replace the androconia that are typically present in most *Celastrina* species—it was believed that this trait was restricted to *C. ladon*, *C. nigra* (W. Forbes), and, more recently, *C. iryna* (Pavulaan, 2025). Microscopic examination of male “Spring Azure” specimens from across southern New England has revealed the presence of these elongated dorsal wing scales. The present author initially interpreted this population as representing a northern subspecies of *C. ladon*. However, comprehensive life history characteristics indicate that this population belongs within the *lucia* guild of *Celastrina*. It is therefore proposed that the elongated wing scale trait introgressed into northeastern populations of *C. lucia*, replacing androconia and making *C. isadora* (new species) the fourth species within the *Celastrina* complex known to possess this distinctive scale morphology.

Additional key words: Introgression, androconia, elongated wing scales.

INTRODUCTION

Celastrina isadora is herein described as a new species of Azure butterfly from southern New England. This taxon represents an additional, recently recognized example of character introgression, likely resulting from ancient hybridization, whereby a distinctive dorsal wing scale morphology—previously characteristic of *C. ladon*, *C. nigra* and more recently *C. iryna*—has introgressed into regional populations of *C. lucia*. Introgression, or introgressive hybridization, is the movement of genes from one species into another through repeated backcrossing of hybrids with a parent species. The process typically unfolds over many generations before noticeable genetic incorporation occurs. Unlike most gene flow, which happens within a species, introgression involves genetic exchange between different, yet closely related species. Hybrid introgression is known to occur extensively in members of the *Heliconius* genus (Mavárez, et al, 2006). The precise evolutionary mechanism underlying this introgression, as well as the selective advantage, if any, associated with the absence of androconia, remains unknown. All examined aspects of the natural history of this population, together with preliminary allozyme analyses (D. Wright, unpublished), support its placement within the *C. lucia* guild, with the sole exception of its shared male wing scale structure with *C. ladon*. Hybrid introgression is now widely recognized by entomologists as a significant mechanism contributing to evolutionary diversification and speciation (Dowling & Secor, 1997; Gross & Rieseberg, 2005; Martinsen, et al, 2001; Mavárez, et al, 2006; Arnold, 2006; Harrison, 2014).

The principal justification for recognizing this taxon at the species level is that, although it is generally allopatric with *C. lucia*, it occurs in full sympatry with *C. lucia* at certain localities where their ranges meet. Harry Zirlin (pers. comm.) documented both *C. lucia* and *C. isadora* occurring sympatrically in Westchester County, New York, and David Wright (pers. comm.) reported a comparable instance of sympatry in northern New Jersey. In Rhode Island, the primary focus of the present study, *C. isadora* represents the dominant Azure species, with a mere two typical *C. lucia* specimens recorded at only two sites.

Two additional species may be confused with *Celastrina isadora*. On 5 May 2018, several individuals representing the distinct early-spring brood of the multivoltine ecotype of *C. neglecta* (**Fig. 6**) were first documented in Rhode Island at Norman Bird Sanctuary, Middletown (Gary Leavens, 2018), and at Trustom Pond National Wildlife Refuge, South Kingstown (Bill Thompson, 2018). These individuals were reported online as “Spring Azure,” but exhibited diagnostic characteristics of the early-spring brood of *C. neglecta* and have since been recorded frequently across the state.

In Massachusetts, this *neglecta* ecotype was documented earlier, first at Oxbow National Wildlife Refuge, Harvard (Laurel J. Ramseyer, 2012), also reported online as “Spring Azure,” and subsequently recorded statewide with increasing frequency. Similarly, in Connecticut, the earliest documentation of the early spring ecotype of *neglecta* occurred at Devil’s Den Nature Preserve, Weston (Mike VanValen, 2014), likewise reported as “Spring Azure,” followed by numerous additional records statewide.

These observations underscore the persistent regional confusion among *Celastrina* taxa, which are generally reported collectively as “Spring Azures” (*C. ladon*). The spring form of *C. neglecta* is the palest and least heavily marked ventrally among the spring-flying *Celastrina* species in the region. This ecotype of *C. neglecta* appears to be expanding northward into the range of the primarily bivoltine (July/September) summer ecotype of *C. neglecta* long documented in New England (traditionally referred to as the “Summer Azure”). Where the two ecotypes occur sympatrically, their broods overlap in an alternating pattern, giving *C. neglecta* the appearance of continuous brooding.

A second spring-flying species that may contribute to identification confusion is *Celastrina serotina*, the Cherry Gall Azure (**Fig. 7**). *C. serotina* typically emerges approximately two to three weeks after the initial emergence of *C. isadora*, with adult flight activity occurring primarily in May. Although the flight periods of *isadora* and *serotina* overlap, the two species are readily distinguished by the diagnostic dorsal wing scale structure of male *C. isadora*, as described herein. Upon emergence, *C. serotina* adults are fresh and exhibit a bright white ventral ground color, whereas *C. isadora* individuals, which have normally emerged earlier, generally show signs of age wear and appear darker and more abraded ventrally.

***Celastrina isadora* Pavulaan - new species**

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Description: Male (Fig. 1-right side). Forewing length 10-15 mm, averaging 12.6 mm (n=80). Dorsal color uniform light blue; but variable with some individuals with a slight violet-blue tint. Like *C. lucia* males. Wing fringes, especially on the hindwing display strong black checkering. In *C. ladon* (**Fig. 5**), this checkering along the wing fringes is somewhat subdued, with most individuals having minimal checkering. The primary difference from *C. lucia* males (**Fig. 4**) is the absence of androconia and the presence of elongated wing scales in *C. isadora*. This character gives males a unique matte-like reflectance, unknown in nominotypical *C. lucia*. The ventral markings are denser and darker than in

nominotypical *lucia*. This species differs from *C. ladon* by being bluer, whereas *ladon* (especially the females) tends to be more violet blue [thus the name *violacea* (Edwards)]. Ventral ground color uniform light gray. Black maculations and individual variation like *lucia* but considerably more heavily marked, with the ‘*lucimargina*’ form (Scott, 1981) (**Fig. 1-right side**) being dominant and representing the species’ holotype. Ventrally-patched, margined (form “*lucimargina*”) and margined individuals (form “*marginata*” of authors) (**Fig. 2-upper image**) dominate, approximately 50/50, while ventrally spotted forms are much less common (**Fig. 2-lower image**). The “*lucia*” form (of authors), displaying only the ventral HW patch and spotted margin are exceedingly rare in the study area.

Female (Fig. 1-left side). Forewing length 11-14 mm, averaging 12.6 mm (n=40). Dorsal color metallic blue as in *lucia*, with a broad black outer margin on DFW. Wing fringes gray to white; black checkering present. Ventral color and pattern as in male. Females are extremely difficult to differentiate from nominotypical *lucia*, and are best identified by association with males having the elongated dorsal forewing scale structure. These are readily differentiated from *ladon*, which are darker violet dorsally. Ventrally, *ladon* displays a sharper, more reduced spot pattern than *isadora*, whereas in the ventrally-spotted form of *isadora* the spot pattern is somewhat less sharp.

Hosts: Females were observed in association with and ovipositing on several species of Blueberries in Rhode Island: *Vaccinium angustifolium* (Lowbush Blueberry), *V. pallidum* (Hillside Blueberry) and *V. corymbosum* (Highbush Blueberry). Mature larvae were located on *V. corymbosum*. O’Donnell, et al (2007) list *Viburnum acerifolium* (Maple-leaved Viburnum) and *V. dentatum* (Arrowwood) in Connecticut. Anecdotal reports of *Prunus serotina* (Black Cherry) flower buds and leaf galls in Massachusetts requires confirmation. *P. serotina* is a primary host in northern Virginia for both sympatric *Celastrina lucia* and *C. ladon* (Pavulaan, 2014). Interestingly, *C. isadora*’s host choices are similar to populations of *C. lucia* throughout the northern Appalachian Mountains, being primarily Blueberry feeders.

Flight Period: Single brood. In Rhode Island, verified records span from March 20 to June 4. In Massachusetts, records commence April 1 but due to large scale confusion with other members of the *Celastrina* complex, late dates are undetermined. In Connecticut, records commence March 29, with a late specimen verified on June 12. Peak flight dates vary considerably from season to season, depending heavily on severity of winter and unpredictable spring weather in the region, with greater numbers reported in April.

Habitat: Common and widespread throughout southern New England. Adults have been found in all forest types except in woodlands dominated by White Pine (*Pinus strobus*). *C. isadora* is primarily associated with Oak (*Quercus* sp.) woodlands with abundant Blueberries, but also in association with Pitch Pine (*Pinus rigida*) and coastal scrub forest where Blueberries are common. Once found in numbers around large *V. corymbosum* shrubs in a cow pasture, with females ovipositing.

Distribution: *Isadora* has been identified in additional counties, based on the male wing scale structure. Listed here are all documented counties in each state within the study area: CONNECTICUT: Fairfield Co., Hartford Co., Litchfield Co., Middlesex Co., New Haven Co., New London Co., Tolland Co., Windham Co. MAINE: York Co. MASSACHUSETTS: Barnstable Co., Berkshire Co., Bristol Co., Dukes Co., Essex Co., Franklin Co., Hampden Co., Hampshire Co., Middlesex Co., Nantucket Co., Norfolk Co., Plymouth Co., Suffolk Co., Worcester Co. NEW HAMPSHIRE: Hillsboro Co., Rockingham Co., Strafford Co. RHODE ISLAND: Kent Co., Newport Co., Providence Co., Washington Co. VERMONT: Rutland Co. Distribution in New York, northern New Jersey, and Pennsylvania needs further study to determine range.



Fig. 1. *Celastrina isadora*: ALLOTYPE female, (left side), April 23, 1984, Great Swamp Management Area, West Kingston, Washington County, R.I., leg. H. Pavulaan. HOLOTYPE male (right side), same data as female.

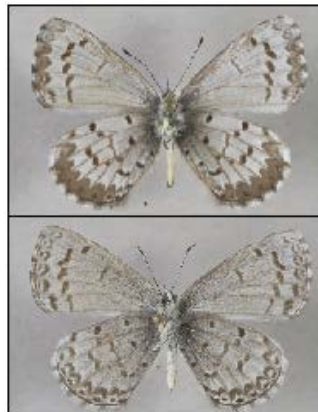


Fig. 2. *C. isadora* margined form (top) (same data as the holotype). Spotted form (bottom) May 6, 1984 (same location data as holotype).

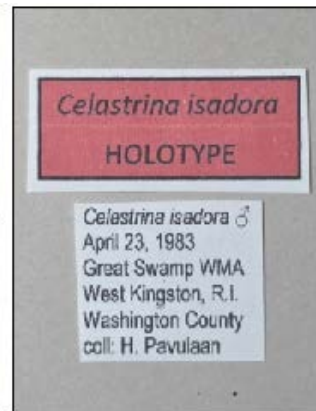


Fig.3. *C. isadora* holotype and data labels.

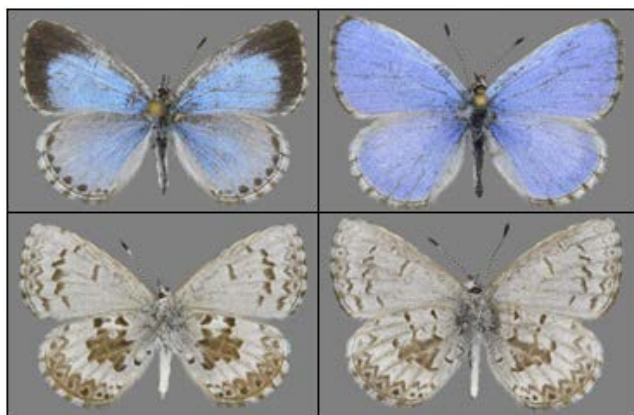


Fig. 4. *Celastrina lucia lucia* from near TL, 5/20/2015, nr. St. Laurent Ferry, South Saskatchewan River, Saskatchewan, Canada. Photos courtesy Norbert Kondla.



Fig. 5. *C. ladon*: female (left side), April 15, 1997, Cedarville, Prince Georges County, MD., leg. H. Pavulaan. Male (right side), March 30, 2002, Clifton, Fairfax County, VA., leg. H. Pavulaan.



Fig. 6. *C. neglecta* spring form: female (left side), April 5, 2013, Veterans Memorial Park, Leesburg, Loudoun County, VA., leg. H. Pavulaan. Male (right side), same data as female.

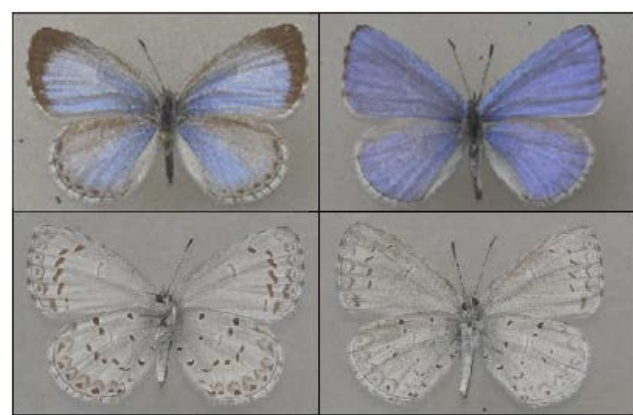


Fig. 7. *C. serotina*: female (left side), May 14, 1990, Great Swamp Management Area, West Kingston, Washington County, R.I., leg. H. Pavulaan. Male (right side), same data as female.

Holotype, allotype, paratypes: Holotype (male) (**Fig. 1–right side**): Rhode Island, West Kingston, Great Swamp Management Area, 23 April, 1983. Collected by Harry Pavulaan. Label images in **Fig. 3**. Allotype (female) (**Fig. 1–left side**): same data as holotype male. Collected by Harry Pavulaan. Both holotype and allotype to be deposited in the McGuire Center for Lepidoptera and Biodiversity, Gainesville Florida. Paratypes: The following specimens are labelled “paratype” with a green label. Number of paratypes in each location are in parentheses. Paratypes in the collection of the author are indicated as “HP” (final disposition to be determined) and in the collection of the Smithsonian National Museum of Natural History (indicated as “NMNH”); “MM” are specimens in Mark Mello collection: **MASSACHUSETTS**: Barnstable Co.: Provincetown (2-MM), Wellfleet (4-MM); Dukes Co.: Chilmark (1-HP), Oak Bluffs (1-HP), Tisbury (1-HP); Hampshire Co.: Granby (1-NMNH); Middlesex Co.: Medford (4-NMNH), Stoneham (1-NMNH); Norfolk Co.: Milton (3-NMNH), Randolph (1-HP, 1-NMNH). **NEW HAMPSHIRE**: Hillsboro Co.: Bedford (1-HP), Brookline (1-HP), Nashua (1-HP); Merrimack Co.: Bow (1-HP), Concord (1-HP); Rockingham Co.: Windham (1-HP); Strafford Co.: Durham (1-HP). **RHODE ISLAND**: Kent Co.: Coventry (20-HP, 3-NMNH), West Warwick (1-HP). Providence Co.: Cranston (1-HP), East Providence (1-NMNH), Providence (2-NMNH). Washington Co.: Charlestown (1-HP), Exeter (25-NMNH), South Kingstown (26-HP, 16-NMNH).

Etymology. “Isadora” is a female name of Greek origin, derived from St. Isidore, as the “gift of the goddess Isis”, the ancient Egyptian goddess of fertility, magic and nature. St. Isidore of Seville is considered the last scholar of the ancient world, as classical culture disintegrated in his time. His most important work was his *Etymologiae*, also known to classicists as the *Origines*, a 20-volume compilation of classical works.

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ADDENDUM

Following is the current, tentative list of North American *Celastrina* taxa:

- 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)
 ssp. *Celastrina lucia lucia* (W. Kirby, 1837)
 = *marginata* (W. H. Edwards, 1883)
 = *quesnellii* (Cockle, 1910)
 ssp. *Celastrina lucia sidara* (Clench, 1944)
 ssp. *Celastrina lucia lumarco* J. Scott, 2006
 ssp. *Celastrina lucia valeriia* Pavulaan, 2025
- Celastrina neglecta*** (W. H. Edwards, 1862)
 = *argentata* (Fletcher, 1903)
- Celastrina echo*** (W. H. Edwards, 1864)
 ssp. *Celastrina echo echo* (W. H. Edwards, 1864)
 ssp. *Celastrina echo cinerea* (W. H. Edwards, 1883)
 = *arizonensis* (W. H. Edwards, 1885)
 ssp. *Celastrina echo bakeri* (Clench, 1944)
- Celastrina gozora*** (Boisduval, 1870)
- Celastrina nigra*** (W. Forbes, 1960)
- Celastrina neglectamajor*** Opler & Krizek, 1984
- Celastrina humulus*** J. Scott & D. Wright, 1998
- Celastrina idella*** D. Wright & Pavulaan, 1999
- Celastrina serotina*** Pavulaan & D. Wright, 2005
- Celastrina asheri*** LaBar, Pelham & Kondla, 2022
- Celastrina iryna*** Pavulaan, 2025
- Celastrina isadora*** Pavulaan, 2026

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