



The Taxonomic Report

OF THE INTERNATIONAL LEPIDOPTERA SURVEY



***CELASTRINA IDELLA* (LYCAENIDAE: POLYOMMATINAE): A NEW BUTTERFLY SPECIES FROM THE ATLANTIC COASTAL PLAIN.**

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ABSTRACT. A new species of Polyommatae, *Celastrina idella*, is described from the sandy Atlantic coastal plain of the eastern US. It is presently known to occur from southern New Jersey through Georgia. *C. idella* larvae have been recorded from four species of *Ilex* (holly). *C. idella* is distinguished from sympatric *C. ladon* and *C. neglecta* by differences in larval host, flight period, pupal diapause, and adult size and wing characters. In the New Jersey pine barrens the butterfly is univoltine and flies in the spring between the flights of its sympatric congeners.

CONCEPTS OF *CELASTRINA* SYSTEMATICS

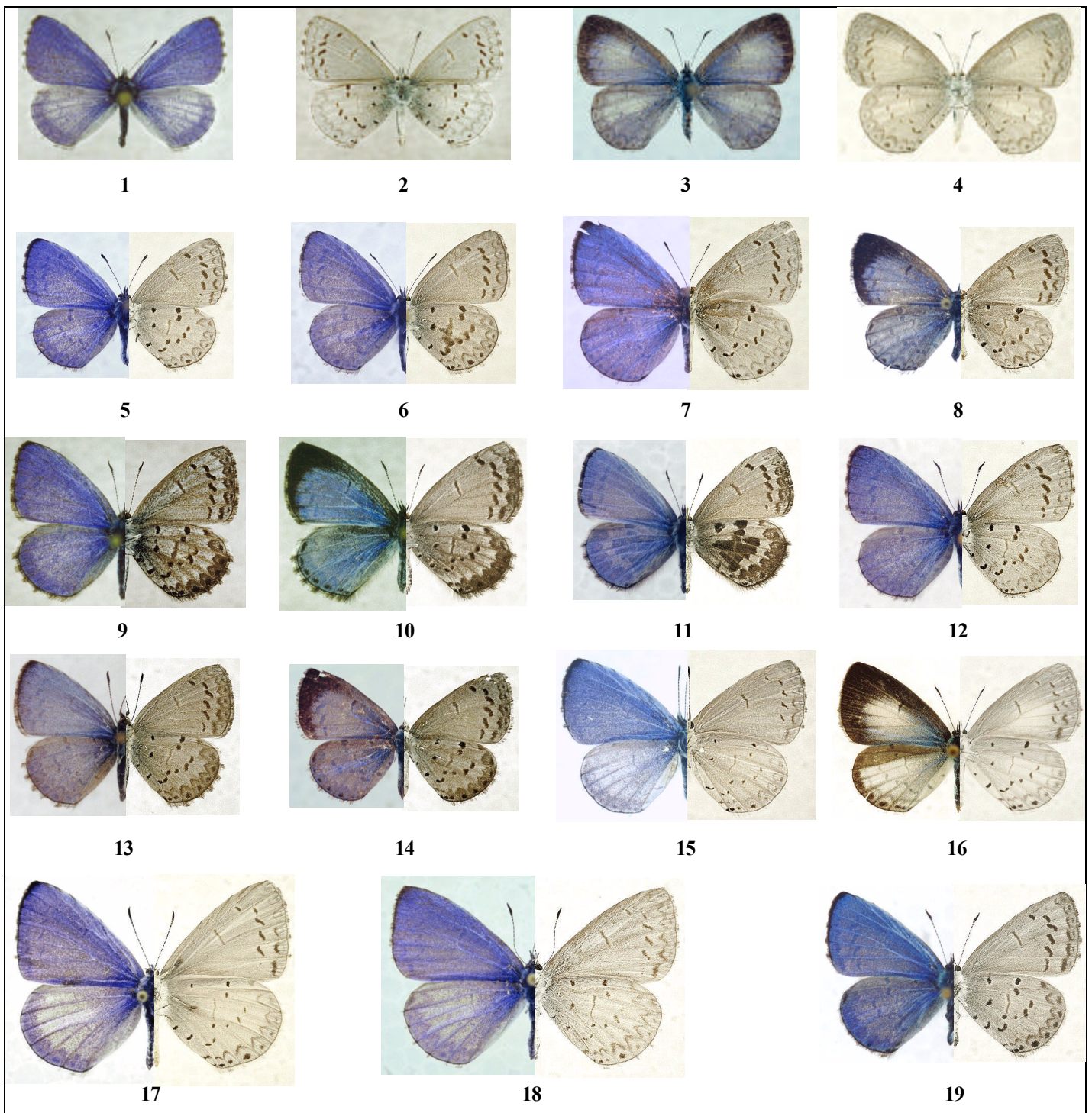
Two hundred years ago John Abbot, the famous Georgian naturalist, found larvae of a species of *Celastrina* Tutt, 1906 on *Ilex* L. (holly). He reared these to adults and in 1792 wrote: "The butterfly is not common, but is more frequent in Hammocks and near swamps... tied itself up 30th April, changed into chrysalis 2 May, bred March 12 following [year]." Abbot's historical description is remarkable on several accounts. We believe it to be the first reference to a heretofore undescribed species of *Celastrina* which we now describe in this paper. It is also one of the earliest insect life histories from the New World.

The above quote was not included with Abbot's plate in Smith (1797). It was uncovered later by Scudder (1872, 1876) who examined the original plates and unpublished manuscript in London. In Smith (1797), Abbot described a different *Celastrina* caterpillar found in June. This taxon fed on a wild legume and gave rise to a second brood without diapausing.

Unfortunately, Abbot's differing life history accounts have been largely overlooked taxonomically. Abbot's two very different life history descriptions indicated that at least two species of *Celastrina* were present in the eastern US. Specifically, an earlier flying univoltine species whose larvae feed on holly, and a later flying multivoltine species whose larvae feed on a different host(s).

Concepts of *Celastrina* systematics have emerged gradually. Prominent 19th century worker, W.H. Edwards of Coalburgh, WV, provided the first systematic study of American taxa. He reared many of them and correctly recognized them as distinct from Old World *C. argiolus* (Linnaeus, 1758). Edwards (1883) discovered that pupae derived from eggs of the spring generation hibernated, and accurately concluded the first generation was single-brooded. He then arbitrarily, and incorrectly, reasoned that all generations were interrelated and lumped them together as "one polymorphic species" – *pseudargiolus*. Again, accurate life history information was taxonomically overlooked. This view prevailed for nearly a century.

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Figs. 1-2 (d/v), ♂ holotype *Celastrina idella*, 11 May 1987, nr. Chatsworth, Burlington Co., NJ. Figs. 3-4 (d/v), ♀ Allotype *Celastrina idella*, 19 May 1990, nr. Chatsworth, Burlington Co., NJ. Fig. 5 (d/v), ♂ paratype *C. idella*, 16 April 1995, Bevan WMA, Cumberland Co., NJ. Fig. 6 (d/v), ♂ *C. idella* f. *lucia*, 6 May 1987, Chatsworth, Burlington Co., NJ. Fig. 7 (d/v), ♂ *C. idella*, 24 March 1989, Green Swamp, Brunswick Co., NC. Fig. 8 (d/v), ♀ *C. idella*, same data as Fig. 7. Fig. 9 (d/v), ♂ *C. ladon lucia*, f. *marginata*, 10 April 1992, Chatsworth, Burlington Co., NJ. Fig. 10 (d/v), ♀ *C. l. lucia*, f. *marginata*, same data as Fig. 9. Fig. 11 (d/v), ♂ *C. l. lucia*, f. *lucia*, same data as Fig. 9. Fig. 12 (d/v), ♂ *Celastrina* undescribed sp., 24 May 1997, Pocono Pines, Monroe Co., PA. Fig. 13. (d/v), ♂ *C. ladon ladon*, 22 April 1988, near Rancocas State Park, Burlington Co., NJ. Fig. 14 (d/v), ♀ *C. l. ladon*, 16 April 1995, Alloway, Salem Co., NJ. Fig. 15 (d/v), ♂ *C. neglecta*, 23 July 1988, Red Lion, Burlington Co., NJ. Fig. 16 (d/v), ♀ *C. neglecta*, 20 June 1992, nr. Chatsworth, Burlington Co., NJ. Fig. 17 (d/v), ♂ *C. neglectamajor*, 15 May 1990, Fork Creek PHA, Boone Co., WV. Fig. 18 (d/v), ♂ *C. neglectamajor*, 4 June 1997, Mt. Joy, Hunterdon Co., NJ. Fig. 19 (d/v), ♂ *C. neglecta*, spring form, 21 April 1999, Sumneytown, Montgomery Co., PA.

All figures are enlarged to 1.5 natural size.

(d) = dorsal, (v) = ventral.

Twentieth century advancements in evolutionary theory have propelled the idea of sympatric speciation and have offered a new context in which to view co-occurring entities. Re-examination of many of Edwards' forms and "generations" have proven them to be isolated breeding populations. Several have been resurrected to species level or redescribed as new species.

Host plant adaptation plays a key role in the evolution of phytophagous insects, especially *Celastrina* (Pratt *et.al.* 1994). Their larvae are adapted to feed almost exclusively on flowering parts of their hosts, a short-lived ephemeral resource. By necessity, adult flights are phenologically coupled to their host's flowering period in order that eggs may be laid on the seasonally limited provision. Because host plants often bloom at different periods, host specialization can result in asynchrony of adult flights and isolated mating periods.

Further, genetic isolation through seasonal isolation is believed to be an important mechanism in the evolution of species in sympatry (Smith 1988; Wood and Keese 1990; Pratt 1994). In eastern North America, *Celastrina* have diversified through host specialization. Local populations in nature often occur asynchronously to one another and gene flow between them appears limited to non-existent. Morphologic markers characterize several of these populations and formal description is needed to delineate them for future studies in molecular systematics, phylogenetics, and possible conservation.

In the late 1970's it became apparent to us that two separate entities flew in the spring in the New Jersey pine barrens. Given the changing status of *Celastrina* systematics and the recognition of new sympatric species in the Appalachians, we suspected a sibling species pair occurred in the springtime in southern New Jersey. The first flight, consisting of larger dark individuals (f. "lucia" and "marginata"), flew in April when its blueberry host was in bud; the second flight, consisting of smaller brighter individuals (f. "violacea"), followed in May.

The host of the latter was unknown until one of us (DW) witnessed "violacea" females ovipositing on unopened buds of inkberry holly *Ilex glabra* (L.) near cedar bogs in mid-late May, 1989. Viable larvae were eventually found on inkberry and other *Ilex* species in the pine barrens. After two decades of field studies we were convinced of the distinctness of the two spring taxa. The major distinguishing features between them are contrasting adult phenotypes, asynchronous flights, different larval hosts with staggered flowering periods, and experimental evidence of segregated pupal eclosion times. (A third species, the summer flying *C. neglecta* (W.H. Edwards, 1862) is extremely rare and absent from much of the pine barrens. When present, it occurs well after the spring siblings.) We felt these differences merited sibling species status and formal description of the *Ilex* feeding taxon.

A NEW *CELASTRINA* SPECIES

The Holarctic genus *Celastrina* consists of small polyommata (blue) butterflies whose larvae feed on the flowering parts of a diverse variety of plants. Adult flights vary from early spring to late summer and fall. Their biology and systematics have been the subject of recent investigation (Pratt *et.al.* 1994; Pavulaan and Wright 1994; Wright 1995; Scott and Wright 1998). To this point in time, the *Celastrina* complex in eastern North America consists of four recognized sympatric species; *C. ladon* (Cramer, 1780), *C. neglecta*, *C. nigra* (Forbes, 1960), and *C. neglectamajor* Opler & Krizek, 1984. Additional distinct biological races have been described, from other areas, for which species level designations have been suggested (Wright 1995; Gochfeld and Burger 1997; Allen 1997; Layberry *et.al.* 1998; Glassberg 1999).

Common species *ladon* and *neglecta* are polyphagous and occur in widespread overlapping ranges. Once thought to be different seasonal forms of the same insect (Edwards 1883), *ladon* is now known to be a univoltine spring species and *neglecta* a multivoltine summer species. Recently discovered spring species *nigra* and *neglectamajor* are uncommon monophagous species that fly in restrictive ranges in the Appalachians and Ozarks. Their ranges match those of their unique hosts.

We divide the common eastern spring species, *C. ladon*, into two broad subspecies. Northern ssp. *C. ladon lucia* (Kirby, 1837) occurs from the Canadian subarctic southward through New England to the pine barrens of coastal southern New Jersey (Figs. 9-11), where its larvae feed on highbush blueberry *Vaccinium corymbosum* L. A high percentage of heavily melanized adults (forms “lucia” and “marginata”) appear in *lucia* populations. Males have androconia and lack long transparent scales. Southern ssp. *C. ladon ladon* occurs from eastern Texas to northern Florida, northward through the central Appalachian Mts. to the Piedmont of Pennsylvania and north central New Jersey (Figs. 13-14). Throughout its range, flowering dogwood *Cornus florida* L. is the principal host. Subspecies *ladon* adults normally are lightly marked on the venter and lack excessive melanization (form “violacea”). Males lack androconia and have long transparent scales overlaying the blue scales of the forewing (Pratt et.al. 1994; Wright 1995; Wright 1998). Interestingly, ssp. *ladon* is often completely absent or rare on the outer coastal plain, presumably due to competitive exclusion by a different spring *Celastrina* species.

We describe here *Celastrina idella* n. sp., a distinctive spring univoltine *Ilex*-feeding species from the middle Atlantic seaboard (Figs. 1-8). It is distinguished from other *Celastrina* by its smaller size, wing color, flight period, pupal diapause, and larval host. At the northern extent of its range, in the pine barrens of southern New Jersey, it is sympatric with *C. ladon lucia*. There, it comprises the second of two easily recognizable allochronic spring flights. From Delaware southward to Savannah, Georgia, it is virtually parapatric to inland *C. ladon ladon*, and serves as the sole spring flight near the coast. *C. idella* flights are completed before the flights of the ubiquitous sympatric summer species, *C. neglecta* (Figs. 15-16).

***Celastrina idella* Wright and Pavulaan, new species**

Description. *Male* (Figs. 1-2, 5-7). Forewing length 10-15 mm (n=167). Southern NJ males average smaller (12.2 mm, n=68) than those from coastal North Carolina (13.2 mm, n=54). Dorsal color uniform light blue; some individuals with distinct purplish-blue tint (especially NJ pine barrens). White insuffusion between veins on DHW common. Androconia present. Wing fringes white; black checkering minimal to absent. Ventral color uniform light gray to white. Black maculations greatly reduced. All are lightly marked, similar to form “violacea”, except in southern NJ where a few (3-6%) have partially fused maculations on the VHW disc (near form “lucia”). *Female* (Figs. 3-4, 8). Forewing length 11-14.5 mm (n=36). NJ females average smaller (12.2 mm, n=19) than those from North Carolina (13.5 mm, n=11). Dorsal color lustrous metallic light blue; many NJ individuals (pine barrens) with purplish tint. Black on DFW costa and outer margin. DHW with series of submarginal black dots. White insuffusion on DHW common; occasionally also on DFW. Wing fringes white; black checkering minimal to absent. Ventral color and pattern as in male.

Types. *Holotype* ♂ (Figs. 1-2): 2.2 km. s. of Chatsworth, Burlington Co., NJ, 11 May 1987, cedar bog in Risley Branch of Wading River, leg. D.M. Wright. *Allotype* ♀ (Figs. 3-4): 8 km. e. of Chatsworth, Burlington Co., NJ, 19 May 1990, cedar bog in Pope Branch of Wading River, ovipositing on *I. laevigata* (Pursh) Gray, leg. D.M. Wright. Holotype and allotype deposited in The Academy of Natural Sciences of Philadelphia (ANSP), Philadelphia, PA. *Paratypes*: 101 ♂♂ and 35 ♀♀: GROUP I (in pine barrens from 26 April - 28 May, 1987-1995): 50 ♂♂ and 20 ♀♀ from Chatsworth, NJ, and vicinity; GROUP II (from outside the pine barrens 15 March - 20 May, 1979 - 1997): 45 ♂♂ and 13 ♀♀ from Bevan WMA and Bear Swamp East, Cumberland Co., NJ; 1 ♂, 2 ♀♀ from N. Dennis and Eldora, Cape May Co., NJ; 5 ♂♂ nr. Pleasant Mills and Egg Harbor Twp., Atlantic Co., NJ. Paratypes deposited in ANSP, United States National Museum (Washington, D.C.), American Museum of Natural History (New York, NY), and collections of authors and contributors (DS, DI, JP).

Etymology. *Idella* is a feminine name derived from several possible Latin roots (id, ida, idea). We interpret it as a corrupted form of Latin idealis, meaning “model embodying perfection.” Its common name should be **Holly Azure**.

Synonymy. *Papilio argiolus* L. in Abbot (1792), “Caterpillar feeds on...Holly &c. [F]requent in Hammocks and near swamps.” [GEORGIA]; *Cyaniris pseudargiolus* (Bsd. & Le C.) in Scudder (1876, 1889), “...*Ilex*, on which Abbot found it.” [GEORGIA]; *Lycaena ladon* (Cramer), form “violacea” Edw. in Smith (1910), “occurs in April and May... foodplants...are *Ilex*.” [NEW JERSEY]; *Lycaenopsis argiolus pseudargiolus*, form vern. *pseudargiolus* in Comstock (1940), “...spring forms [*lucia* and *marginata*] occur with *pseudargiolus*...Lakewood [pine barrens]...May 18” [NEW JERSEY]; *L. a. pseudargiolus*, form vern. *neglecta-major* (Tutt) in Comstock (1940), “This form follows the early spring forms and is intermediate in occurrence between them and the first summer brood...Jamesburg [pine barrens] May 30.” [NEW JERSEY]; *Lycaenopsis argiolus*, form *violacea*, in Shapiro (1966), “...majority of spring specimens are form *marginata*...[*V*]iolacea increases in frequency as the spring emergence progresses.” [NEW JERSEY, in part]; *Celastrina ladon* (Cramer), form “violacea” in Gatrell (1986), “from all south coastal counties...form *violacea* emerges at end of February and flies throughout March.” [SOUTH CAROLINA]; *Celastrina ladon*, “*violacea*” in Glassberg (1993) “In our area there may be at least three species -[including] a ‘*violacea*’ type Azure appearing in the pine barrens in early May.” [NEW

JERSEY]; *Celastrina ladon*, “Pine Azure” in Walter (1993), “Pine Azure...is associated with pine barren habitats.” [NEW JERSEY]; *Celastrina ladon*, “Late Spring Azure” in Pavulaan and Wright (1994), “especially common in New Jersey white cedar swamps...also very common in New Jersey deciduous swamps, Cape May County.” [NEW JERSEY]; *Celastrina ladon* (Cramer), race “*violacea*” III in Pratt et.al. (1994), “type III feeds on male flowers of *Ilex* species...on coastal plain” [NEW JERSEY to GEORGIA]; *Celastrina* sp., “Cherry Gall Azure” and “Eastern Spring Azure” in Wright (1995), “...sizable populations of Cherry Gall Azures can be found in cedar swamps of the New Jersey pine barrens, where...[they] feed on male flowers of Inkberry (*Ilex glabra*),” and “...along outer coastal plain from Cape May, New Jersey to Georgia, there occurs a brightly-colored, holly-feeding, ‘*violacea*’ variety of the Eastern Spring Azure.” [NEW JERSEY to GEORGIA]; *Celastrina* n. sp., “Late Spring Azure” in Iftner and Wright (1996), as “Holly Spring Azure” [Fig. 1] [NEW JERSEY]; *Celastrina* sp., “Pine Barren Azure” in Gochfeld and Burger (1997), “...this distinct entity may be either a small race...or a distinct species. Forested Coastal Plain including the Pine Barrens...[f]eeds on Inkberry...and American Holly.” [NEW JERSEY]; “Coastal Holly Azure” in Williams (1998), “...coastal holly azures have been discovered so recently that they have yet to be assigned scientific name.” [NEW JERSEY]; *Celastrina ladon*, “Pine Barrens Spring Azure” in Glassberg (1999), “...may eventually merit full species status” [EAST]; “*Celastrina* sp.” Holly [Spring] Azure in LeGrand and Howard (1999)...“This species found in a wide variety of wooded or semi-wooded sites, in the vicinity of hollies...Coastal Plain only” [NORTH CAROLINA].

Biology. Flight period: In the north (type locality), a four-week flight from end of April to end of May and following the flight of *C. ladon lucia* (extreme dates: 25 April - 4 June). To the south (inc. Delaware Bay counties of southern New Jersey), flight is correspondingly earlier (extreme dates: 26 February - 20 May). **Adult Nectar Sources:** Open flowers of highbush blueberry *Vaccinium corymbosum* L., sand myrtle *Leiophyllum buxifolium* (Berg.) Ell., chokeberries *Aronia arbutifolia* (L.) L.F. and *A. melanocarpa* (Michx.) Willd., black cherry *Prunus serotina* Ehrh., red maple *Acer rubrum* L., and rock cress (*Arabis* sp.) **Hosts:** Male flowers of dioecious *Ilex* species (Aquifoliaceae). Eggs and larvae recorded on American holly *I. opaca* Ait., inkberry *I. glabra* (L.) Gray, and smooth winterberry *I. laevigata* (Pursh) Gray in southern New Jersey. Recorded from yaupon holly *I. vomitoria* Ait. in the outer banks of North Carolina and *I. opaca* Ait. in coastal southern Virginia. Possibly tall gallberry holly *I. coriacea* (Pursh) Chapm. in North Carolina. [Note: Wild larvae reared from flowers of Virginia Willow *Itea virginica* L. at Virginia Beach, VA, in May, diapaused and produced *idella* adults. This may be an alternative host, especially near the end of the adult flight when unopened *Ilex* buds are dwindling.]

Immature Stages. Egg white, similar to other *Celastrina*: placed on floral buds of *Ilex* hosts. First instar light green: bores into floral buds. Mature larva (4th instar) variable, light green to creamy white; some lightly contrasted with dorsal white chevrons, maroon prothoracic shield, or rarely with faint rosy mid-dorsal stripe. (Lighter and less boldly marked than larvae of *C. ladon lucia*.) Myrmecophilous larvae on *Ilex glabra* (L.) Gray attended by worker ants of *Camponotus ferrugineus* (F.), *C. nearcticus* Emery, and *Lasius alienus* (Foerster). Hymenopterous parasitoids recovered during rearing include *Trichogramma* sp. from eggs and a small wasp *Cotesia cyaniridis* (Riley) from mature larvae. Pupa light brown (7.2-8.2 mm, n=10), obtect. Pupation dates, June 14-July 3 in New Jersey. Pupae diapause.

Habitat. Wet areas (cedar swamps, cypress swamps, pocosins, bottomlands, wet thickets) and upland dry maritime forests of sandy coastal plain and barrier islands, with holly (*Ilex*).

Frequent Associates. *Mitoura hesseli* Rawson & Ziegler, 1950, in Atlantic white cedar bogs and the *Ilex* associated subspecies (Gatrelle, 1999) of *Deciduphagus henrici* (Grote & Robinson, 1867) in coastal holly woodlands.

Range (Fig. 22). Known localities include: **NEW JERSEY:** ATLANTIC CO.: Atlantic City International Airport, Brigantine, Folsom, Forge Pond, Hammonton, Mays Landing, Mizpah, Pleasant Mills, Pomona, Weekstown; BURLINGTON CO.: Batsto, 2.2 km. s. Chatsworth, 8 km. e. Chatsworth, Duke’s Bridge, High Bridge, Jenkins, 6 km. e. Medford, Ong, Oswego Lake, Penn SF, Quaker Bridge, Red Lion, Speedwell, West Plains; CAMDEN CO.: Atco, Gibbsboro, Kirkwood Lake; CAPE MAY CO.: Belleplain SF, Cape May Point, Dennisville, Eldora, Five Mile Beach, Goshen, Hidden Valley, Higbee Beach, Jake’s Landing, North Dennis, Petersburg, Seaville, Woodbine (Great Cedar Swamp); CUMBERLAND CO.: Bevan WMA, Bear Swamp, Center Grove, Dividing Creek, Hansey Creek, Millville, Manumuskin, N. Port Norris; GLOUCESTER CO.: Iona; MONMOUTH CO.: Allaire SP; OCEAN CO.: Lakehurst, Lakewood, Manahawkin, Ridgeway, Waretown, Warren Grove; SALEM CO.: Alloway, Quinton. **DELAWARE:** KENT CO.: w. Milford (Mispillion River); SUSSEX CO.: nr. Bethel, nr. Lincoln, Nanticoke WMA. **MARYLAND:** ANNE ARUNDEL CO.: Annapolis, Riva; CALVERT CO.: Lusby; CAROLINE CO.: nr. Templeville; CHARLES CO.: Cedarville SF; PRINCE CHARLES CO.: Cedarville; WICOMICO CO.: n. Salisbury (white cedar swamp); WORCESTER CO.: Wango (John’s Tract). **VIRGINIA:** CHESAPEAKE: Northwest River Park.; FAIRFAX CO.: Mason Neck SP; JAMES CITY CO.: Lakewood (nr. Jamestown); NEW KENT CO.: New Kent; PRINCE WILLIAM CO.: Triangle (Prince William Forest); SUFFOLK: Dismal Swamp, nr. Corapeake, NC; VIRGINIA BEACH: Seashore SP. **NORTH CAROLINA:** BEAUFORT CO.: Locality not given; BLADEN CO.: Bladen Lakes SF (nr. Elizabethtown), Jones Lake SP (nr. Elizabethtown); BRUNSWICK CO.: Green Swamp; CAMDEN CO.: Great Dismal Swamp; CATERET CO.: Moorhead City; COLUMBUS CO.: Green Swamp; CRAVEN CO.: Croatan NF (nr. Croatan); DARE CO.: Kill Devil Hills (Outer Banks), Nag’s Head (Outer Banks), Whalebone (Outer Banks); DUPLIN CO.: Kenansville; GATES CO.: nr. Sunbury (Great Dismal Swamp); JONES CO.: Croatan NF (nr. Maysville); NEW HANOVER CO.: Locality not given; ONSLOW CO.: Locality not given; PASQUOTANK CO.: Elizabeth City; PENDER CO.: Angola Swamp; PITT CO.: Locality not given; ROBESON CO.: Locality not given; SAMPSON CO.: Turkey; WAYNE CO.: Locality not given. **SOUTH**

CAROLINA. AIKEN CO.: Aiken SP; BARNWELL CO.: Barnwell SP; BEAUFORT CO.: Locality not given; BERKELEY CO.: Locality not given; CHARLESTON CO.: Charleston; COLLETON CO.: Locality not given; DORCHESTER CO.: Givhans Ferry SP; GEORGETOWN CO.: Georgetown; HORRY CO.: Nixons Crossroads; JASPER CO.: Locality not given. **GEORGIA:** CHATHAM CO.: Ossabaw Island; LIBERTY CO.: St. Catherines Island; TATTNALL CO.: Ohoopsee Dunes.

Diagnosis: In southern NJ, *C. idella* flies immediately following the flight of sympatric *C. ladon lucia* with minor overlap of flights in certain years. Mean peak flights of *lucia* (April 16) and *idella* (May 13) are nearly a month apart in the pine barrens at Chatsworth, NJ, as calculated from field and museum data (*lucia* n=511, *idella* n=435). South of the NJ pine barrens in the Delaware Bay counties (Cape May Co., Cumberland Co., Salem Co.) mean peak flights of *lucia* and *idella* are fully two weeks earlier. *C. idella* (Figs. 1-2) is distinctly smaller and lighter in color than *lucia*. The wings of both sexes of *lucia* (Figs. 9-10) are larger (FW 13.1 mm, n=42), solid blue in color with no white insuffusion, and strongly outlined in black (often checkered). The *lucia* venter is dark ashen gray and is strikingly contrasted with heavy brown to black maculations and borders (74% form “marginata”; 24% form “lucia”). The sole *lucia* host in southern NJ is highbush blueberry *Vaccinium corymbosum* L. which blooms earlier than *Ilex* species. Larvae of *lucia* are generally bolder in markings; red, green, and brown contrasting morphs are common. *Lucia* pupae (7.5-8.6 mm, n=28) are slightly larger and pupate earlier (May 24-June 8). Under experimental conditions (4 C for four months, then 20 C until eclosion), the mean eclosion time of *lucia* pupae (4.2 days, n=48) is significantly earlier than *idella* (n=13.8 days, n=57, S.E.=0.2) and indicates a genetic basis for the separate *lucia* and *idella* flights in southern NJ. Southward along the coast and westward toward the Piedmont, *idella* is distinguished from nominate *C. ladon ladon* (Figs. 13-14) by bearing androconia and lacking the long overlay scales unique to this subspecies². *C. l. ladon* males often have a satiny matte appearance (not seen in *idella*) because of these scales. A dissecting scope or hand lens is often needed to diagnose this scale pattern. The ultrastructure (SEM) of *C. l. ladon* male scales (Fig. 21) contrasts dramatically with males of other eastern *Celastrina* taxa (e.g. *C. neglecta* in Fig. 20).

Phenotypically, three white-ventered species (*neglecta*, *neglectamajor*, and species undescribed) are most similar to *idella*. However, their larvae do not survive on *Ilex*. The sympatric summer species, *C. neglecta*, nearly always lacks temporal contact with *idella*. *Neglecta* individuals are slightly larger and have more white insuffusion dorsally and ventrally (some near immaculate) (Figs. 15-16). In the NJ pine barrens *neglecta* is virtually absent due to a paucity of suitable summer host plants. In the surrounding Delaware Bay counties of southern NJ *neglecta* is present in early summer (June), but uncommon in late summer. Elsewhere *neglecta* is common throughout the summer (Fig. 25). [A phenomenon of unknown significance is the occasional appearance in early spring (April) of *neglecta*-like individuals in habitats where summer *neglecta* is known to occur. These individuals are never common and we believe they are *neglecta*. We encounter them more frequently inland in wooded and urbanized habitats. On the middle Atlantic coastal plain south of the NJ pine barrens they can be confused with *idella* due to similar appearance. A combination of features help separate these rare spring *neglecta* individuals from *idella*. In general, they are not found in holly habitats, but are closely associated with black cherry *Prunus serotina* and will oviposit on floral buds of this host. The great majority of larvae reared on black cherry do not diapause and eclose to join the bulk of the *neglecta* population which begins flight in late May/June. (Curiously, a few larvae reared on black cherry diapause. We believe this is facultative univoltinism.) When transferred to *Ilex* species, spring *neglecta* larvae die. The venter of the spring *neglecta* individuals (Fig. 19) is slightly grayer than *idella*; ventral maculations are more prominent, but never fused into a “lucia” patch as found in 3-6% of NJ *idella*. Spring *neglecta* males perch near black cherries with wings held vertically over the body. Most *idella* males perch near hollies with wings partially spread at 30-45° to vertical. See Williams (1998) for photo by author (DW) of this phenomenon.] Both *C. neglectamajor* and the undescribed cherry gall species fly between *C. l. ladon* and *neglecta* flights in their respective ranges, neither of which overlaps the range of *idella*. *Neglectamajor* is much larger (Figs. 17-18) and is found only in Appalachian deciduous woodlands (Fig. 27). It feeds solely on black cohosh *Cimicifuga racemosa* (L.) Nutt. The species (Fig. 12) associated with mite-induced leaf galls of cherry trees *Prunus serotina* Ehrh. and *P. virginiana* L. occurs further north from n. NJ to s. Canada. *C. nigra* is separated from all other *Celastrina* species by its black males, Appalachian range (Fig. 26), and unique monophagy. *Nigra*’s foodplant is goat’s beard *Aruncus dioicus* (Walt.) Fern. Despite phenotypic and biological differences, there are no major differences in male genitalia among all the *Celastrina* species in eastern North America. As a group they diverge from the genitalic characteristics of Eurasian *C. argiolus* and are easily separated from that taxon. However, they can not be reliably distinguished from one another. The sclerotized male valva terminates in a narrow apical process with small subsidiary teeth. In most southern NJ *idella* males the upper surface of the apical process, medial to the subsidiary teeth, displays very fine sparse cuticular spinosity (not sensory setae) under high-power magnification (Fig. 28 on CD). This feature is absent in the other eastern *Celastrina* species; it may prove to be most useful in solving the identity of puzzling museum specimens (for instance *idella* versus spring *neglecta*). Lastly, the inner margin of the uncus lobe spine is considerably smoother in *idella* than in the other taxa (Fig. 29).

² The *C. ladon* (Cramer, 1780) neotype designated by Clench and Miller (1980) has this unique scale pattern. The spring taxon *violacea* (W.H. Edwards, 1866), defined in lectotype designated by Brown (1970), also has this scale pattern. Thus, *violacea* (W.H. Edwards) is a junior synonym of *ladon* (Cramer). The taxon described/figured by Boisduval and Le Conte (1833) as *pseudargiolus* has phenotypic features of *ladon* (Cramer) and is properly synonymized under that name.

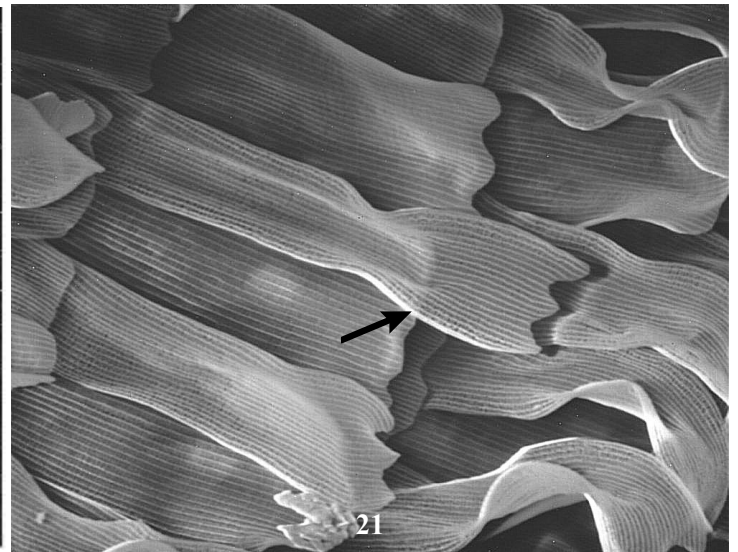
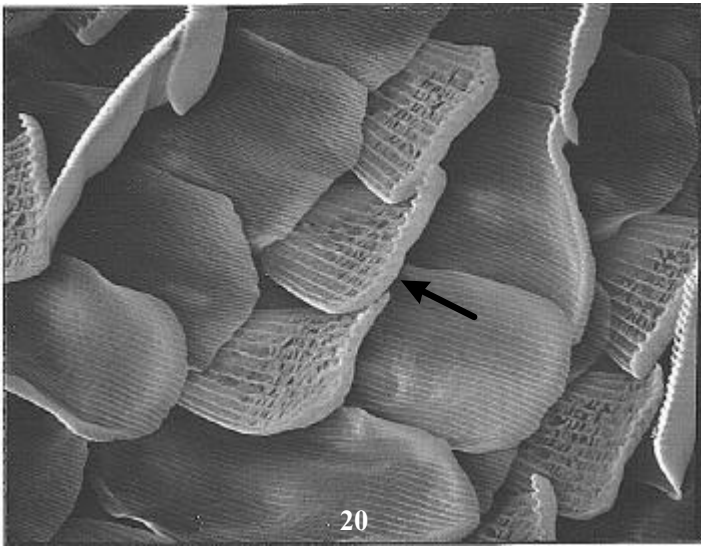
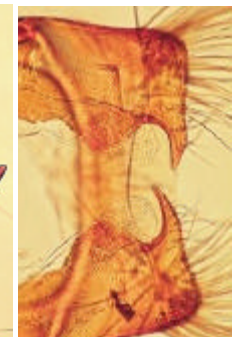
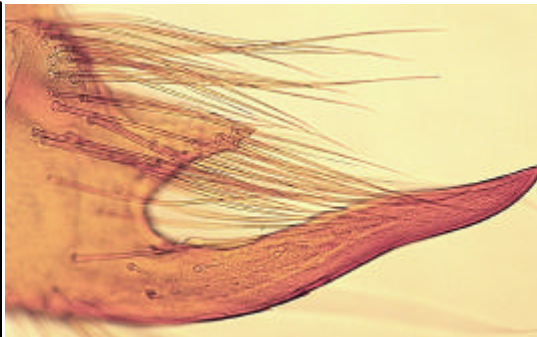
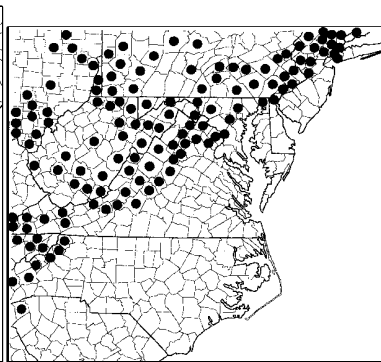
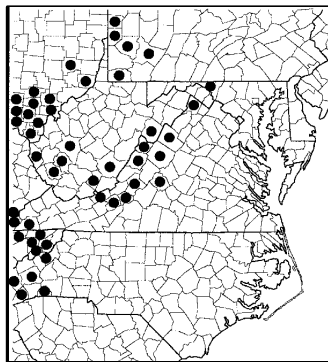
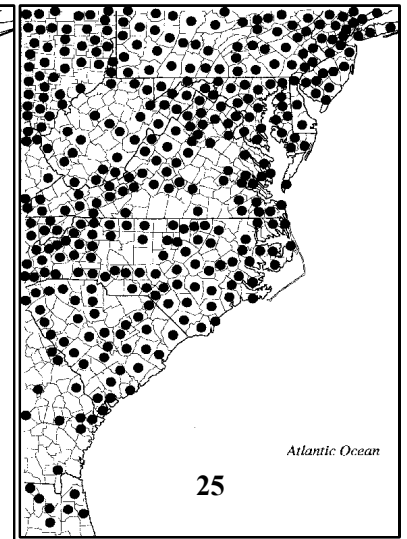
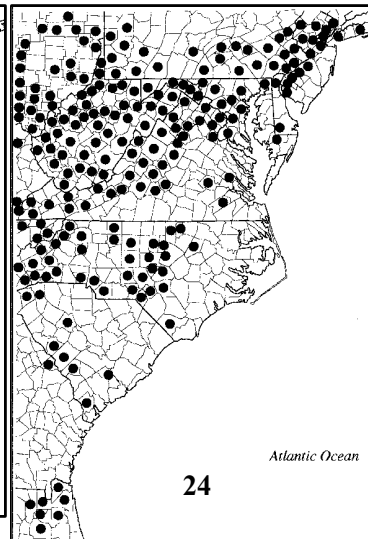
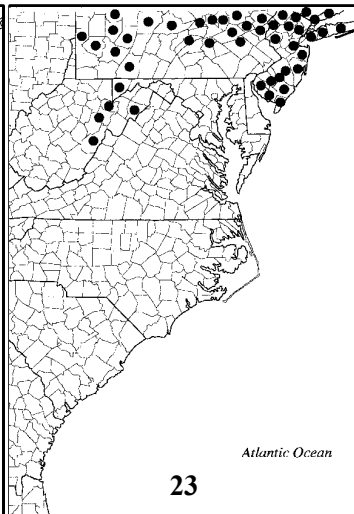
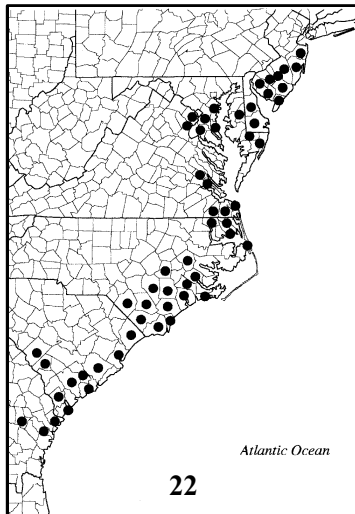


Fig. 20, Scanning electron micrograph (SEM 640X) of dorsal forewing of ♂ *C. neglecta* showing androconia between blue scales. Specimen taken 17 September 1987, Harleysville, Montgomery Co., PA. **Fig. 21**, (SEM 640X) of dorsal forewing of ♂ *C. l. ladon* showing long overlapping scales and lack of androconia. Specimen taken 23 April 1992, Green Ridge State Forest, Allegany Co., MD.



Figs. 22-27. *Celastrina* distribution in the mid-Atlantic region. **22**, distribution of *C. idella*. **23**, distribution of *C. ladon lucia*. **24**, distribution of *C. l. ladon*. **25**, distribution of *C. neglecta*. **26**, distribution of *C. nigra*. **27**, distribution of *C. neglectamajor*.

Figs. 28-29. Genitalia³ of ♂ *C. idella* from nr. Chatsworth, Burlington Co., NJ, 13 May 1987. **28**, dorsal view of valva with apical terminal process (100X). **29**, ventral view of upper half of ring; uncal lobes with spines (100X).

³ ED. NOTE: Subscribers may "zoom" Fig. 28 on CD to full page size to see detailed features, including cuticular surface of terminal process of valva (400X).

DISCUSSION

Celastrina idella becomes the fifth North American lycaenid described from the New Jersey pine barrens⁴. The region is a natural community with distinctive flora and a rich history of scientific study (Forman 1979). Located on the unglaciated outer coastal plain, the barrens is an “island” of highly acidic, sandy soil which supports large stands of undisturbed pine forests, heathlands, and bogs. Its close proximity to major metropolitan centers and easy access to exploration account for its popularity with naturalists for nearly two centuries. Part of the uniqueness of the pine barrens is its mixed flora. Many plant species of both northern and southern affinity reach their range extremes in the pine barrens where they overlap (McCormick 1970).

In similar fashion, the sibling pair of spring *Celastrina* in the pine barrens represent insects of differing affinities whose ranges overlap only in southern New Jersey. The first taxon, *C. ladon lucia*, is most common in northern woodlands and peatlands of Canada and New England where it feeds on many plant families. Its southernmost coastal population occurs in the New Jersey pine barrens (Fig. 23). This coastal *lucia* population is unique in that it utilizes a single host, flies very early, and is darker blue than northern populations. It may be a remnant of a much larger *lucia* population that once flourished on expanded heathlands of the exposed continental shelf. Physiological constraints prevent *lucia* from extending further south despite the presence of acceptable hosts.

The second taxon, *C. idella*, is a denizen of southeastern coastal swamps and holly forests. It occurs from Georgia to southern New Jersey with its northernmost population in the New Jersey pine barrens. Similarly, physiologic constraints must prevent *idella* from occurring further north even though holly still remains common along the coast. (For instance, *C. idella* is absent from the American holly forest on the dunes at Sandy Hook, Monmouth Co., NJ, just north of the New Jersey pine barrens, and is also absent from the Long Island pine barrens of eastern Suffolk Co., NY, where inkberry is locally common.) Even though these two siblings are adapted to single hosts, it should be stressed that they are also restricted by habitat preferences. Their ranges are smaller than their respective hosts.

How often sympatric speciation creates new species is still a matter of dispute. Once thought impossible, the concept has gained respect among evolutionary biologists (Gibbons 1996). Charles Darwin’s ideas of the formation of species through ecological specialization have been revived (Morell, 1999). Most organisms require geographic isolation (allopatry) to form new species. However, some plant-feeding insects seem to be particularly adept at finding empty niches, exploiting opportunities, and diverging from others sympatrically. Divergence is spurred by strong selection and rapid adaptation.

Specialization on host floral buds is the niche of *Celastrina* and each separate host represents a potentially different niche. Wherever *C. l. lucia* and *idella* co-occur, host specialization prevents their contact. Adults of the two species fly at different times coupled to the bud stage of their respective hosts. The degree of interbreeding (if any) between these two taxa is unknown. Population genetics models have shown that it takes very little interbreeding to erase differences. The small percent (3-6%) of New Jersey *idella* individuals with imperfect “lucia” disc on VHW (Fig. 6) could be taken as evidence of interbreeding between *C. l. lucia* and *idella*. However, all other phenotypic and biologic characteristics of the taxa remain distinct with no introgression. The “lucia” disc is most likely genetically controlled, but instead of acquisition through recent interbreeding it can be equally explained as an expression of an ancestral gene induced or unmasked by local cold temperatures (especially soil temperatures where pupae rest).

We are not aware of any evidence of interbreeding between *C. l. lucia* and *C. idella* in New Jersey. Further south within its range, *idella* flies parapatrically to inland *C. l. ladon*. *C. l. ladon* is common in the Piedmont and reaches the inner coastal plain (Fig. 24) where there is evidence of partial hybridization with *idella*. The flights of the two taxa overlap chronologically in Virginia and the Carolinas, and contact is inevitable. The width of the hybridizing suture zone is presently unknown, but is suspected to be small.

⁴ Others are: *Epidemia epixanthe* (Boisduval & Le Conte, 1833), *Deciduphagus polios* (Cook & Watson, 1907), *Mitoura hesseli* Rawson & Ziegler, 1950, and *Deciduphagus irus* (Godart, 1824) by designation of neotype in Gatrell (1999).

On the outer coastal plain and barrier islands *C. idella* is the exclusive spring *Celastrina* taxon and *C. l. ladon* is absent. Should the hybridization zone on the inner coastal plain prove to be substantially large, then the two taxa are not separated at the species level in the south. In that case, southern New Jersey would harbor endemic populations of *C. idella*.

The origins of *C. idella* are unknown. We suspect that it originated in the Pleistocene during glacial stages of low sea level when the Atlantic coastal plain was enormously widened and constituted a significantly larger belt of land. During these intervals the exposed outer coastal plain extended 100-200 km eastward from today's shoreline and was covered with similar vegetation (Emery *et.al.* 1967). Given the abundance of *Ilex* and the relative sparsity of flowering dogwood *Cornus florida* on today's outer coastal plain, *idella* was most likely the only spring *Celastrina* flying in this expanded biome during low sea levels from Delaware Bay southward. It may have evolved quickly by a host shift from a closely related ancestor. The hypothetical ancestor presumably had a light venter phenotype similar to present day *neglecta*, *neglectamajor*, or the undescribed cherry gall species. Curiously, *Ilex* flowers are toxic to the larvae of these three species in the lab – they generally do not survive beyond the first instar stage. Selection would have favored a founder with larval resistance to *Ilex* toxins. Allozyme studies are underway to investigate the closest relative(s) of *idella* and its systematic relationship with other taxa.

ACKNOWLEDGMENTS

We acknowledge our deep gratitude to David Iftner, Gordon Pratt, and Dale Schweitzer who provided many stimulating discussions regarding this new taxon and *Celastrina* biology. These individuals also reviewed the manuscript draft and offered valuable critical comments. We greatly appreciate the unselfish assistance given by F. Martin Brown and John Eliot regarding nomenclatural issues. We also acknowledge and extend our warmest thanks to the following individuals and their respective institutions for providing access to reference collections: The Academy of Natural Sciences of Philadelphia (Don Azuma, Jon Gelhaus, and Jason Weintraub), Allyn Museum of Entomology (Jackie and Lee Miller), American Museum of Natural History (Fred Rindge and Eric Quinter), Carnegie Museum (John Rawlins), Cleveland Museum of Natural History (Sonja Teraguchi), Dayton Museum of Natural History (Reed Watkins), Delaware County Institute of Science (John Hallahan), Eastern College (David Unander), Field Museum (Phil Parillo), Florida State Collection of Arthropods (John Heppner), Illinois Natural History Survey (Kathleen Zieders), Los Angeles County Museum of Natural History (Julian Donahue), Michigan State University (Mo Nielsen), Museum of Comparative Zoology (David Furth and Stephan Cover), New Jersey State Museum (David Parris), Newark Museum (John Michalski), The Ohio State University Museum of Biological Diversity (Eric Metzler), Pennsylvania Department of Agriculture (Karl Valley), Pennsylvania Department of Forestry (John Quimby), Pennsylvania Natural Diversity Inventory (Barbara Barton), Purdue University (Arvin Provonsha), Reading Museum (Michael Feyers), Royal Ontario Museum (Chris Darling), Rutgers University (Timothy Casey), Staten Island Institute of Arts & Sciences (Edward Johnson), United States National Museum (Robert Robbins), University of California Riverside (Greg Ballmer and Gordon Pratt), University of Delaware (Dale Bray and Tom Wood), University of Guelph (Steve Marshall), University of Louisville (Charles V. Covell), University of Michigan Museum of Zoology (Mark O'Brien), University of Pennsylvania (Andrew Binns), Wagner Institute (Eugene Bolt and Susan Glassman), Yale Peabody Museum (Charles Remington). We also sincerely thank the following individuals for allowing us the opportunity to examine their private collections and/or forward specimens to us: Chris Adams, Tom Allen, George Balogh, Andrew Beck, Richard Boscoe, John Bowe, John Calhoun, Tom Carr, Charles V. Covell, Harry N. Darrow, Jim Dowdell, David Eiler, Karl Gardner, Robert Gardner, Ron Gatrell, William Grooms, David Iftner, Phil Kean, Ron King, Marc Minno, Mo Nielsen, David Parshall, John Peacock, Jim Popelka, Joe Riddlebarger, Frank Rutkowski, Dale Schweitzer, John Shuey, Ernest Shull, Don Simonds, Richard Smith, Reed Watkins, William Wright, Joe Zeligs, Ben Ziegler, and Harry Zirlin. A special thanks is extended to Carol Spawn (Chief Librarian of The Academy of Natural Sciences of Philadelphia) and Pamela Gilbert (Entomology Librarian, British Museum of Natural History) for aiding in retrieval of the Abbot references;

also to Phil Ackery and Pamela Gilbert (BMNH) for obtaining color transparencies of the original Cramer and Abbot paintings. We are grateful to Jim Springer (North Jersey Butterfly Club) and Steve Walter (New York City Butterfly Club) who kindly shared their databases. Steve Walter also supplied helpful information regarding the Long Island pine barrens. We sincerely appreciate the expertise and efforts of Paul Marsh and Richard D. Smith, Research Entomologists (USDA), who identified the larval parasitoids and ant attendants.

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