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THE BIOLOGY, LIFE HISTORY, AND TAXONOMY OF *CELASTRINA NEGLECTAMAJOR* (LYCAENIDAE: POLYOMMATINAE).

HARRY PAVULAAN¹

494 Fillmore Street, Herndon, VA., 22070

AND

DAVID M. WRIGHT

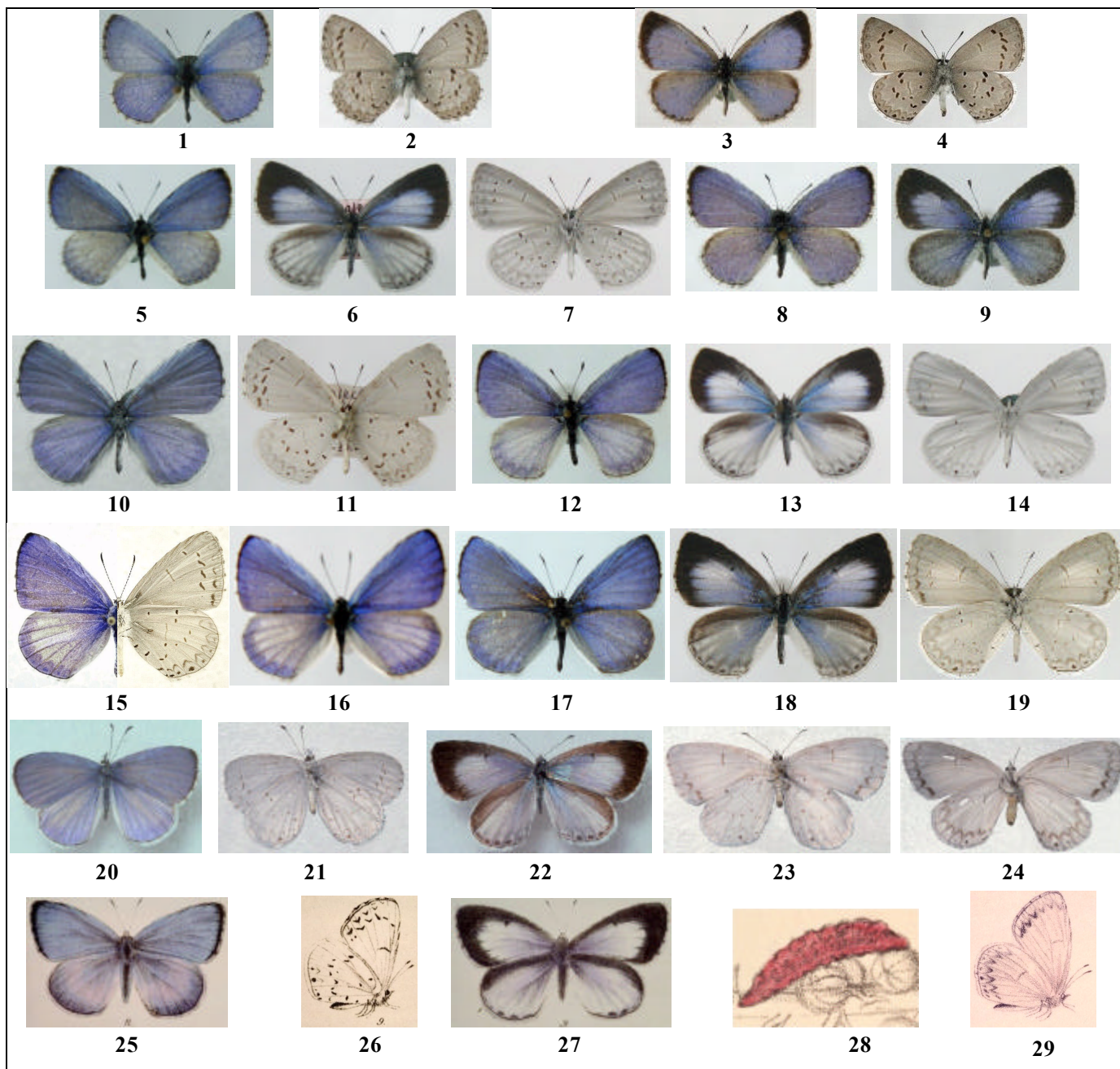
100 Medical Campus Dr., Lansdale, PA., 19446

ABSTRACT. The biology and life history of *Celastrina neglectamajor* is described. This lycaenid butterfly was first described from West Virginia by 19th century lepidopterist, William H. Edwards, as a redescription of *Lycaena pseudargiolus* (Boisduval & Le Conte). Edwards provided evidence of its unique late spring flight, Appalachian affinity, and larval host *Cimicifuga racemosa* (Ranunculaceae). Edwards and subsequent authors, most notably Samuel Scudder of New England, treated it as an infrasubspecific form of the common eastern *Celastrina ladon*. In 1908 Tutt applied the form name *neglectamajor*, describing it from one of Edwards' 1884 figures. For nearly a century, confusion persisted over its precise taxonomic status as evidenced by subsequent works which questioned its rank, listed improper synonymies, or provided incorrect host plant reference. Opler and Krizek elevated *neglectamajor* to species rank in their major 1984 eastern North America work, but debate over its rank nevertheless continued in the literature. A definitive work was needed to resolve this problem. We present the results of our long-term study, begun in 1983, that confirms *neglectamajor* as a valid species. The butterfly is sympatric with several members of a *Celastrina* sibling-species complex in the Appalachian and Ozarkian regions. It shows no field or laboratory evidence of interbreeding. The major differences separating it from its siblings are its adult size, unique host, larval first instars, and allochronic flight period. Lectotypes are designated from the Edwards collection at the Carnegie Museum for *Celastrina argiolus pseudargiolus* f. *neglecta-major* Tutt and *Celastrina neglectamajor* Tutt.

HISTORICAL SYSTEMATIC TREATMENT

The large "Azure" inhabiting the Appalachian Mountain region was first recognized as a valid taxon by William H. Edwards, who intentionally redescribed it (Figs. 25-29) as *Lycaena pseudargiolus* (Boisduval & Le Conte) in his early work on West Virginia butterflies (Edwards, 1866, 1868). Edwards considered *pseudargiolus* to be distinct from his newly described species *Lycaena neglecta* (Edwards, 1862), an insect which he believed to be of more northerly regions: "Massachusetts, New York, Wisconsin, Lake Winnipeg", and *Lycaena violacea* (Edwards, 1866) of the central Appalachian region. Edwards (1869) also stated that a sparse second brood flew in July in West Virginia, which he believed was the offspring of May *pseudargiolus*. He did not adequately explain why he identified this brood with May *pseudargiolus* [sensu Edwards], instead of his more northerly *L. neglecta*. In subsequent works he would identify West Virginia summer broods as *neglecta*. It is apparent to us that *neglecta* was not common in Coalburgh, WV, where he lived at the time, and Edwards' faulty interpretation of his rearing results led him to believe that *pseudargiolus* produced the small numbers of summer adults that he found in nature.

¹ Research staff member, The International Lepidoptera Survey, Goose Creek, SC.



Figures 1-29. *Celastrina* species. **Figs. 1-2.** ♂ *C. ladon* (D/V): Boone Co., WV, Fork Creek PHA, 20 April 1990. **Fig. 3-4.** ♀ *C. ladon* (D/V): Montgomery Co., MD, Seneca, 12 April 1992. **Figs. 5-7.** ♂ *C. neglecta* (D): same site as 1, 12 June 1990. **Figs. 6-7.** ♀ *C. neglecta* (D/V): Loudoun Co., VA, Bluemont, 18 June 1988. **Fig. 8.** ♂ *C. neglectamajor* (D): small form: Clarke Co., VA, Berrys, 22 May 1999. **Fig. 9.** ♀ *C. neglectamajor* (D): small form: same data as 8. **Figs. 10-11.** ♂ *C. neglectamajor* (D/V): same site as 8, 10 May 1999. **Fig. 12.** ♂ *C. neglectamajor* (D): Ozark segregate, Iron Co., MO, Royal Gorge, nr. Glover, 25 May 1988. **Figs. 13-14.** ♀ *C. neglectamajor* (D/V) same data as 12. **Figs. 15-16.** ♂ *C. neglectamajor* (D/V & D): same site as 1 and 5, 15 May 1990 (specimen photographed in different light angles). **Fig. 17.** ♂ *C. neglectamajor* (D): Bucks Co., PA, St. Game Lands # 157, 28 May 1992. **Figs. 18-19.** ♀ *C. neglectamajor* (D/V): Clarke Co., VA, Berrys, 10 May 1999. **Figs. 20-21.** ♂ **lectotype** *C. neglectamajor* Tutt (D/V): Coalburgh, West VA (full data in text). **Figs. 22-23.** ♀ paralectotype *C. neglectamajor* Tutt (D/V): same data as 20. **Fig. 24.** ♀ **lectotype** *C. argiolus pseudargiolus* ab. *obsoleta-lunulata* Tutt (V): Coalburgh, West VA. **Fig. 25.** ♂ *Lycaena pseudargiolus* spring f. *pseudargiolus* (D): from Edwards 1884, Vol. 2, 50:8. **Figs. 26-27.** ♀ *L. p.* spring f. *pseudargiolus* (V/D): from Edwards 1884, Vol. 2, 50:9. **Fig. 28.** *L. pseudargiolus* (= *neglectamajor*): mature larva on *Cimicifuga racemosa*: from Edwards 1884, Vol. 2, 51:2. **Fig. 29.** Ventral of 24 as drawn in Edwards 1884, Vol. 2, 50:22. All figures proportionately enlarged. (Note: Figs. 1, 5, & 15, depict three species from same site and year.) (D = dorsal, v = ventral. Photos: 1-19 by Joe Mueller, 20-24 by David Wright. All Photos computerized/edited by Ron Gatrell.)

By 1875, Edwards changed his mind on the separate specificity of *pseudargiolus* [sensu Edwards], *neglecta* and *violacea* in West Virginia. Edwards (1875) now identified *violacea* with *pseudargiolus*, but the status of *neglecta* was left uncertain. At this time he still believed that the July and September flights in West Virginia were the progeny of May *pseudargiolus* [sensu Edwards], and reported on a rearing experiment involving the offspring of September adults: "...unexpected result shows *violacea* to be the spring form of *pseudargiolus*." Of *neglecta*, he added: "I am prepared to believe that *neglecta* may prove to be one of the summer broods of *pseudargiolus* in this latitude... There are differences between the two forms sufficient to make me regard them as distinct..." At this point, Edwards still did not identify the West Virginia summer broods with his *neglecta* of the north.

Another major writer at the time, Scudder (1876), basing his concept of *Celastrina* taxonomy on an entirely different set of observations taken in New England, disputed Edwards' outline of North American *Celastrina*. Scudder believed that *pseudargiolus* represented large variant individuals of summer "form" *neglecta* in New England. Writing about the three major "forms" of *C. ladon* found in the vicinity of Boston, Massachusetts, he states of the summer brood: "a form...corresponding to the *neglecta* of W. Virginia; occasionally in midsummer large specimens of this are taken, and these I have considered *Pseudargiolus*." Thus, *neglectamajor* was immediately misunderstood by at least one major writer of that time.

Edwards continued to rear West Virginia *Celastrina* and asserted (Edwards, 1878a): "The eggs laid by *violacea* give larvae from which comes *pseudargiolus* last of May..." Further, "The female *pseudargiolus* lays eggs...to produce perhaps *violacea*, but also perhaps the typical *pseudargiolus* again. But a small percentage...give butterflies at irregular intervals during the year." Edwards observed that these adults were always smaller than the parents, an interesting phenomenon which we have also discovered in rearing *neglectamajor*. These "false" summer brood adults are extremely similar in phenotype to *neglecta*, especially with their consistently smaller size. Thus Edwards felt there were two regular annual broods of *Celastrina* in West Virginia, first *violacea* in April and then *pseudargiolus* in May. Of the summer broods (*neglecta*), he felt their occurrence was too irregular to represent a regular annual brood. Edwards apparently found populations of *neglecta* to be rather unpredictable in areas where he studied them, no doubt a local ecological circumstance of heavily forested Appalachian habitats. "...in June, 1866, at Coalburgh, *neglecta* appeared in large numbers...[i]n following years (1867 - 1868) *neglecta* has again been rare in this district." He did not report such fluctuations with *ladon* or *neglectamajor*.

Edwards was never single-minded on the issue of broods and repeatedly revised his own ideas. In 1881 he reasserted that *violacea* produced *pseudargiolus* [sensu Edwards]. In the ensuing years Edwards (1883) rejected his earlier conclusions: "...the fact that the hibernating chrysalids of the May generation (*pseudargiolus*) produce their own form of butterfly... and also that the larger part of the chrysalids of *violacea* appear to hibernate, and that nearly all the butterflies of the first generation must come in direct descent from their own form of the year before." Edwards had come full circle to believe that *neglectamajor* bred true. However, he was still confused by his observation that: "Eggs laid by *Pseudargiolus* produce the same form the same year in very small numbers, but most of the chrysalids hibernate to produce the same form the next spring. The few butterflies which emerge the same summer are sometimes as large as the parent female, but are usually smaller."

We have also discovered that in rearing larvae and maintaining chrysalides under artificial conditions, a false summer brood can be "forced" out of some *neglectamajor*. Some of the resultant adults are phenotypically similar to the natural form, but most are smaller and resemble *neglecta* to an extent. Edwards confused these false *neglecta*-like summer individuals with true *neglecta*..

Edwards (1883) further stated: "The observations on the chrysalids and those on the appearance of the butterflies in the field therefore agree, and together show that *Pseudargiolus* of May cannot proceed from *violacea* butterflies of that year, but must come from hibernating chrysalids. The later butterflies, *Neglecta*...must come from *violacea* butterflies of the same year. A small percentage of the chrysalids from *violacea* give butterflies at fifty or more days from the eggs laid in April, which brings the emergence into June, and the result is *Neglecta*; while nearly all the chrysalids hibernate...to give *violacea* the next spring." He also added: "*Pseudargiolus* is an interpolated and distinct generation, the first in the year of its series. It has no direct connection with the winter forms [*violacea* in West Virginia], but an indirect one through the few individuals which spring from it late in the season." Thus Edwards felt that his *pseudargiolus* must produce some second brood *neglecta*-like offspring in nature, which then bred with *neglecta* to maintain a connection to species *pseudargiolus*. This erroneous conclusion was no doubt based on the artificial rearing conditions that produced some summer adults from *neglectamajor* larvae raised on *Cimicifuga racemosa*. In continuing, he stated: "The few late females sprung from *Pseudargiolus*, and which

emerge from chrysalis irregularly in August and September, lay eggs, and the chrysalids thereupon hibernate and produce *Violacea* in the following spring.” These findings were based on **wild** larvae he found on a *neglecta* host, *Actinomeris alternifolia*, in October. He never realized that his reared summer adults of *neglectamajor* were not the same as the naturally occurring summer insect, *neglecta*, he found ovipositing on *Actinomeris*.

The next year, Edwards (1884) finalized his personal concept of all the North American races and forms. It was plainly evident that he was still very confused over the status of *pseudargiolus*. Edwards said of *neglectamajor*: “The chrysalids from the May generation, or *Pseudargiolus*, probably produce butterflies in small numbers in July and later, after the June *Neglecta* have passed away, but most of them hibernate, and give *Pseudargiolus* the following May, or earlier.” He ultimately realized that both larvae of *neglecta* and *neglectamajor* utilized the same *Cimicifuga* host plants and are often found feeding together (though differing in age) on the same individual flower clusters. Further, he states: “In the spring, there certainly is no connection between *Violacea* and *Pseudargiolus*... It is only by a connection between *Pseudargiolus* and the other forms in the fall that any inter-relationship can be found; that is, some chrysalids of *Pseudargiolus* give butterflies which unite with butterflies from chrysalids of the June *Neglecta* to produce the fall larvae, from which come *Violacea* in April. Otherwise *Pseudargiolus* would be set in the middle of the series, with no link in either direction. The true second generation of the year, in Virginia, is *Neglecta*, appearing in June. *Pseudargiolus* is an interpolated spring generation, the first in the year of its series. Its second comprises a part of the few butterflies which fly between July and October. If these late butterflies were suppressed, *Pseudargiolus* would stand as a distinct species, with no trace of its relation to the other forms.” In Edwards (1885), he repeated this statement and added: “No doubt that is one way in which species come to exist.”

Because of Edwards’ misinterpretation of the emergence of reared *neglectamajor* summer adults, he felt there was some degree of reproductive/genetic connection to *ladon* and *neglecta* (through these partial summer emergences). He was thus blind to the fact that the larvae of two separate taxa, *neglecta* and his *pseudargiolus* (= *neglectamajor*), were actually feeding on the same plant. Rather, he maintained a belief that they were merely two separate forms. He therefore falsely concluded (Edwards, 1884) of the several distinct species of North American *Celastrina* that: “...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, from the boreal regions to Mexico.” With these words, the mistaken concept of a single species of North American *Celastrina* species was cast. A concept that prevailed for over a century! *Neglectamajor* roamed within this conceptual boundary in unquestioned synonymy, misunderstood by one author after another. The account of its rediscovery has taken on the flavor of folklore.

Scudder (1889) continued to consider *pseudargiolus* [sensu Edwards] as merely “large examples of the summer form.” The summer insect found in New England is *neglecta*. It is only slightly variable in size, but not to the extent that Scudder alluded. Others proceeded to follow Scudder’s concept without explanation or further investigation, reinforcing this incorrect alignment. In Comstock and Comstock (1904), *neglectamajor* was given a brief description as the typical, late spring form (*ladon*) of *Cyaniris ladon*, which the authors felt to be the older name. The Comstocks cited Scudder, but misunderstood his concept: “Scudder does not regard *neglecta* as distinct from *C. ladon ladon*, or *pseudargiolus*...according to this view *neglecta* is one of the spring forms as well as the summer form.”

Tutt (1908) applied the name *neglecta-major* to Edwards’ insect, which he considered to be a distinct size form of *Celastrina argiolus pseudargiolus* (Boisduval & Le Conte). His description was extremely brief and misleading. In making a comparison of Edwards’ (1884) illustrations of form *pseudargiolus* to form *neglecta*, Tutt described form *neglecta-major* as: “Exactly parallel pair only larger. Underside white, with contrasting black spots, many, however, obsolete \neq *pseudargiolus*, Edw., pl. ii., figs. 8-9 \neq *neglecta*, large form, Scudder. (No doubt a summer form, which may be called *neglecta-major*, though Edwards insists that it comes from overwintering pupa).”

This incorrect placement was repeatedly reinforced by subsequent writers. Skinner (1915), no doubt following Scudder, wrote of *Lycaena argiolus*: “*Pseudargiolus* and *neglecta* are the same thing.” Field (1938) stated of Kansas Azures: “The form *neglecta-maor* [sic] (Tutt) represents the common summer form.” Comstock (1940) wrote of *Lycaenopsis argiolus pseudargiolus* in New Jersey: “Form vernalis *neglecta-major* Tutt. This form follows the early spring forms and is intermediate in occurrence between them and the first summer brood.” Klots (1951), under *Lycaenopsis argiolus pseudargiolus*, mentioned: “In some regions occurs a partial second brood (*neglecta-major*)... This is ‘spotty’ in its occurrence, but I know some places where it occurs very constantly.” Clark and Clark (1951), referring to the late spring emergence of *Cyaniris argiolus pseudargiolus* in the Piedmont and Coastal Plain regions of Virginia, stated: “in the mountains...it is largely replaced by a larger form (*neglecta-major*)...”

Forbes (1960), in slightly confusing terms, was the first author in three-quarters of a century to hint that this insect might be a separate species. He wrote of *Plebeius argiolus pseudargiolus*: “late spring form *pseudargiolus* Bdv. (*violacea* Edwards) ...has been suspected to be really a separate single-brooded species (Watson in personal discussion).”

Shapiro (1966) recognized this entity around Philadelphia and stated under *Lycaenopsis argiolus*: “From mid V to mid VI there is an emergence of large, bright individuals (*neglecta-major*) resembling the summer forms...This form is not found at all localities.” He further wrote: “It may be a distinct species, but is more likely a formerly isolated population now in secondary contact with, but temporally disjunct from, the other.” Harris (1972) stated of *Celastrina argiolus pseudargiolus* in Georgia: “f. *neglecta-major*, is a rare form that is larger in size than the others. It may appear between the spring and summer broods, usually in June.” Several years later, Shapiro (1974) wrote of *Lycaenopsis argiolus* in New York: “*Neglecta-major* is a large, richly colored insect... It flies in mid V in its localities, between the spring brood and the first regular summer brood (*pseudargiolus*) and there is widespread speculation that it is a univoltine sibling species.” Shapiro was the first author to map the distribution of the species in New York state (Shapiro, 1974, fig. 82).

Langston (in Howe, 1975) dropped the name *neglecta-major* and reverted to Edwards’ use of *pseudargiolus*, sinking it back into synonymy under *Celastrina argiolus pseudargiolus*. He also improperly described the female: “The name *pseudargiolus* applies to the second or early summer brood... The uppersides, especially of the females, are characterized by large white areas in the discal region.”

In the Miller and Brown (1981) catalogue/checklist, adopted by the Lepidopterists’ Society as the “official” standard taxonomic treatment of North American butterflies, *neglectamajor* Tutt was catalogued as a form of *C. ladon ladon* (Cramer). They noted: “Loc. of type not known (BM?).” Eliot and Kawazoe (1983), in an authoritative revision of the *Lycaenopsis* group, relegated *neglectamajor* to synonymy, reinforcing what earlier authors had stated. Under *Celastrina argiolus ladon*, they stated: “...*pseudargiolus* has been applied, on the authority of Edwards (1870), to a delayed spring emergence from overwintering pupae giving rise to large individuals with the facies of the summer generation. However, this application of Boisduval’s & Le Conte’s name is, in our opinion, based on unsound arguments.” In adopting Scudder as first reviser, Eliot & Kawazoe considered the name *pseudargiolus* to have priority over *violacea* for the early spring generation. They stated: “This will leave the late spring generation without a familiar name, but if one is required *neglecta-major* Tutt, 1908, is available.”

In a sudden shift of prevailing usage, Opler and Krizek (1984) recognized *Celastrina neglectamajor* as a full species and christened it the “Appalachian Blue”. Opler and Krizek also provided the first map of the entire range of the species known at that time. They gave *Viburnum acerifolium* as its host plant, citing Shapiro (1966). Opler and Krizek ascribed authorship of this taxon to Tutt. However, since 1984 the authorship of this name has been unstable. In some of the subsequent popular literature, *neglectamajor* has been attributed to Tutt (e.g. Gochfeld and Burger, 1997) and in others to Opler and Krizek (e.g. Allen, 1997). After much outside consultation, we tentatively hold Tutt as the author under article 45.6.4.1 of the fourth edition of the International Commission of Zoological Nomenclature (ICZN) Code (effective January 1, 2000). Had Opler and Krizek applied the name *neglectamajor* to this species a year later, the name would be attributable to them (Article 45.6.4.1).²

Following earlier concepts of the late-spring flight of eastern U.S. *Celastrina*, Pavulaan (1985) erroneously described “*C. neglecta-major* Tutt” as occurring in Rhode Island. Subsequent research by the present authors shows that this Rhode Island insect is not Appalachian *neglectamajor*, but a distinctly different undescribed species that feeds on cherry galls (Pavulaan and Wright, in prep.). Gatrell (1985) also described *C. neglectamajor* as occurring in south-central South Carolina: “This newly elevated taxon may be the *Celastrina* flying in April in Barnwell and Aiken Counties.” Specimens that were later obtained from Gatrell show several morphological features that do not agree with Appalachian *neglectamajor*. We do not believe this insect is *neglectamajor*; its taxonomic placement is uncertain at present.

Scott’s (1986) major work on North American butterflies reverted *neglectamajor* to synonymy, describing it as a form under the entry of *Celastrina argiolus ladon*. His description of the female as “mostly white” was incorrect. Scott also very closely followed Edwards’ original brood concept by stating: “Both *neglecta* and *neglectamajor* produce other flights like *neglecta* later in the summer...however, *neglectamajor* probably comes from eggs laid by early-spring *violacea*.” Scott also describes the range as being: “...Ga. to Penn., N.Y., N.S., Ont., and the Black Hills

² See footnote three on page 12.

of S.D., and a smaller version of it is found west of Denver.” The inclusion of Black Hills was based on “large specimens” (Scott, per. comm.). However, an extensive series of specimens that we received from the Black Hills, SD, turned out to be large specimens of a highly variable, polymorphic population of *Celastrina*, associated with the Colorado Front Range taxon *C. ladon sidara*. The Denver, CO, taxon also was not *neglectamajor*. It was eventually described and named *C. humulus* by Scott and Wright (1998). *Humulus* has a univoltine flight in Colorado and flies between *C. ladon sidara* and *C. neglecta*, analogous to Appalachian *neglectamajor*. It feeds primarily on *Humulus lupulus* (Hop Vine) and *Lupinus argenteus* (Lupine). Shull’s Indiana work (1987) entirely misunderstood Opler & Krizek’s treatment of *C. neglectamajor*, placing it under *Celastrina ladon ladon*: “Paul Opler...is calling the summer brood *Celastrina neglectamajor*, a separate species...Differences among the experts may prevail for some time.”

Several works have recently appeared, which follow the Opler & Krizek species concept of *neglectamajor*. Iftner et.al. (1992) provided an extensive description of the biology of *neglectamajor* in Ohio. Opler & Malikul (1992) adopted Appalachian Azure as the common name. The host plant was listed as *Cimicifuga racemosa*, correcting the report of *Viburnum acerifolium* in Opler and Krizek (1984). A year later the North American Butterfly Association’s Standing Committee on English Names (Opler being a member) affirmed Appalachian Azure in *American Butterflies* (NABA 1993), as its common name. Glassberg (1993, 1999) retained use of the name Appalachian Azure and correctly described the natural history of *neglectamajor*. Cech (1993) followed with a brief description for the New York City area. Wright (1995) introduced a new concept of the North American “Azures” and described our knowledge of *neglectamajor* to that time. Allen (1997) detailed the insect in West Virginia. Gochfeld & Burger (1997) listed “Tutt, 1908” as the species author and correctly described *neglectamajor*’s natural history for New Jersey. They acknowledge that some historical records in New Jersey may represent the similar-appearing, but smaller *Celastrina idella* (Wright and Pavulaan, 1999) or the undescribed cherry-gall feeding taxon (Pavulaan & Wright, TTR in prep.). Covell (1999) listed *neglectamajor* as part of the Kentucky fauna and ascribed authorship to Tutt.

We would like to acknowledge here that Harry Clench in an unpublished, undated manuscript (Carnegie Museum files) endeavored to review the status of *neglectamajor* sometime between 1972 and 1980. His work remained incomplete and fell into obscurity with his passing. The manuscript draft was discovered by Wright at the Carnegie Museum of Natural History while inspecting the Edwards collection. Clench’s preliminary work not only confirmed what we had learned, but helped us to resolve a major taxonomic problem. Clench identified and intended to designate a lectotype male and paralectotype female from the Edwards collection, based on plates in Edwards (1884) and the writings of Tutt (1908), in anticipation that *neglectamajor* “may one day be raised to species status”.

REGIONAL OBSERVATIONS

Phenology and reproductive isolation. Edwards (1883, 84) reported flight dates for West Virginia *Celastrina* that would imply flight overlaps. However, he never conceded that their flights overlapped. For over a hundred years, the flight period of *neglectamajor* was traditionally stated to occur between the first (spring) and second (summer) “broods” of a single species. These broods were referred to as forms *violacea* and *neglecta*, respectively of *C. ladon*. Today we recognize these occurrences as flights of three distinct species: a univoltine spring flight of *C. ladon*, a univoltine late spring flight of *neglectamajor*, and multivoltine summer flights of *C. neglecta*.

Over most of its range, the span of the adult flight of *neglectamajor* may overlap that of *ladon*, which starts before it and that of *neglecta* which follows it. However, the biological significance of this overlap appears to be negligible or non-existent. We have not encountered interspecific matings, nor reared any larvae to adulthood with hybrid features. By the time *neglectamajor* begins to fly, the *ladon* flight is on the wane and the dwindling *ladon* numbers consist primarily of previously-mated females. Similarly, when the *neglectamajor* flight is nearing its completion, some *neglecta* populations have begun to fly. Once again, the same isolating mechanisms apply. Most, if not all, of the *neglectamajor* females have been previously mated (with *neglectamajor* males) and the females reject additional matings. We have also noted that woodland *neglecta* populations (esp. in southeastern Pennsylvania) begin flight even later than counterpart *neglecta* populations in open habitats. This reduces further the potential for contact with *neglectamajor*, which flies earlier in shaded woodland. Flight dates in southeastern Pennsylvania indicate overlap of flights as follows: *ladon*: mid-April to mid-May (extremes April 5 – May 24); *neglectamajor*: mid-May to mid-June (extremes May 6 – June 21); *neglecta*: usually emerging in early June (earliest date May 18) with continuous multiple broods until fall.

In northern Virginia, Pavulaan studied *neglectamajor* populations from 1985 to 2000 on the Blue Ridge in Clarke, Loudoun, Madison and Page Counties. In the higher elevations (above 3900'), in most years, a few worn *ladon* stragglers were still generally present as late as mid-May, when the first teneral *neglectamajor* emerged. The bulk of the *neglectamajor* emergence usually occurred closer to May 31, with peak numbers in early June. Adults were only found in the vicinity of stands of the host plant, *Cimicifuga racemosa*. At lower elevations of the Blue Ridge, *neglecta* made its appearance generally by the last week of May, and progressively later at the higher elevations where the flight of *neglectamajor* was already in progress. By mid-June, both *neglecta* and *neglectamajor* flew together in areas atop the ridge summit. However, by the third week of June, the *neglectamajor* flight had markedly tapered, while *neglecta* peaked, flying into early July. *Neglectamajor* was generally found only in areas containing *Cimicifuga racemosa*, but much larger numbers of *neglecta* ranged over the entire ridge. *Neglecta* was found in both woodlands and a variety of open habitats (not frequented by *neglectamajor*) where additional *neglecta* hosts were found. *Ceanothus americanus*, a common ridge top plant, was a favorite *neglecta* ovipositional substrate. Additional *neglecta* flights occurred throughout the summer. This flight sequence is typical most years on the Blue Ridge.

Temporal dissociation may not be the sole factor preventing *neglectamajor* and *neglecta* hybridization. In certain areas other factors are operative. In the southern Appalachians, the *Celastrina* emergence pattern is complicated and reveals surprising flights which point to the stability and distinctness of *neglectamajor*. Pavulaan surveyed Great Smoky Mountains populations in North Carolina (Swain Co.) and Tennessee (Sevier Co.) from May 30 - June 1, 1988. Hundreds of freshly-emerged *neglectamajor* males and a single female were observed along streams and dirt roads in a valley bottom at 3120' elevation on the southern flank of the mountain range. Flying with *neglectamajor* at this location were numerous **worn** *neglecta* individuals. These latter were easily differentiated from *neglectamajor* by their size, color, and markings. Their uniformly faded and aged appearance indicated that *neglecta* had emerged several days (or weeks) **before** the appearance of *neglectamajor*. Also, on a previous trip to the same general area, at a slightly earlier period of spring (May 18, 1985), numerous faded and aged *neglecta* were observed feeding on the blossoms of Blackberry (*Rubus* sp.) when *neglectamajor* had not yet emerged and its host *Cimicifuga racemosa* showed no signs of floral bud production.

Our Missouri data indicate that *neglectamajor* and *neglecta* fly nearly concurrently in the Ozarks. Ova of *neglectamajor* were first found on *Cimicifuga racemosa* along the Black River near Williamsville, Wayne Co., on May 13, 1988. However, no *neglectamajor* adults were present. *Neglecta* also was not found, but it was presumed that it had not yet emerged or perhaps was not present at this location. On May 25, a fresh pair of atypical, large Azures, believed to be *neglectamajor*, were taken in an area of the host plant near Royal Gorge, Iron Co. Oddly, only about 1% of the *Cimicifuga racemosa* plants at that location flowered. This was presumed to be a response to localized climatic conditions (cool air and late springtime frosts) in Ozark river valleys. We now believe that the majority of *neglectamajor* in the Ozarks fly comparatively late to coincide with the localized delayed floral bud development of the host. Interestingly, a pair of typical *neglecta* was taken on the same date (May 25), in the same general vicinity, along with ova on *Cornus drummondii*, which is a *neglecta* host. The *neglecta* adults on this date appeared worn and aged, like those in the Great Smoky Mountains field study. Our general impression is that the first *neglecta* brood in the Ozarks emerges with (or somewhat earlier) than *neglectamajor*.

In the northeast during the spring of 1989, there occurred what may only be described as a dramatic "crash" in *neglecta* populations. Flights of *neglecta* were severely delayed, reduced, and in some cases absent. The cause(s) of this population "crash" are unknown, and one can only speculate about the possibilities (climatic, parasitoid density, virus). This natural calamity offered a unique opportunity to observe the uniqueness of *neglectamajor*, which was unaffected.

There was a virtual absence of flights of *neglecta* in much of northern Virginia (including the Blue Ridge), central Maryland, and southeastern Pennsylvania. Abnormally cold spring weather, with late frosts and extended periods of record rainfall, had a significant effect on the progress of the *neglectamajor* flight in the Blue Ridge region. Adults were still quite numerous at the end of June, and oddly, individuals ranged from somewhat aged to freshly-emerged. Females were busily ovipositing on the host plants, which appeared to be several weeks late in the floral development. Only a single very aged *neglecta* female, from near Berryville, VA, was found ovipositing on *Cimicifuga* in late June. (Ova from this female collapsed. We suspect she was either unmated or the eggs were infected with an unknown pathogen.) In southeastern Pennsylvania, *ladon* and *neglectamajor* flew at their expected

times respectively in April and May with normal population sizes. However, *neglecta* was not seen in late May or during the entire month of June. Single individuals finally appeared on July 7, 10, 11, & 22. *Ladon* and *neglectamajor* stood alone, unaffected by the *neglecta* “crash”.

The separation of *neglectamajor* and *neglecta* is certainly maintained by something other than mere temporal isolation. The two insects fly synchronically (to a much greater degree than *ladon* and *neglectamajor*) leading us to speculate that strong undetected behavioral and/or biological barriers exist. Otherwise interbreeding and significant gene flow would reduce them to a single species.

The genus *Celastrina* arose in the Orient (Eliot and Kawazoe, 1983) and dispersed to the New World. This genus reaches its greatest taxonomic diversity in the eastern United States. We hypothesize that *neglectamajor* is an older species than *neglecta*. *Neglectamajor* most likely originated from an ancestral *Celastrina* population in eastern Northern America that came to utilize primarily *Cimicifuga racemosa* as its larval host. Appalachian populations separated from this ancestral *Celastrina* during periods of strong selection for host plant adaptation and allochronic sexual sorting. Host plant specificity and narrow concentration on an ephemeral resource (floral buds) limited the timing of the adult flight and started the divergence toward present-day *neglectamajor*. At some point, polyphagous and multivoltine *neglecta* (we believe a more recent descendant) invaded the sanctuaries of *neglectamajor*. By this time, the two species had diverged to the point where they retained their separate genetic and phenotypic identities.

The idea of *neglectamajor* or *neglecta* arising directly out of the other is a difficult fit. If this were so, they would be very prone to have reunited in areas where they have been back in contact for thousands of years. In other words, while they may look similar there is significant evolutionary distance between the species.

BIOLOGY AND LIFE HISTORY

DESCRIPTION. Edwards was not satisfied with Boisduval & Le Conte’s description of *Lycaena pseudargiolus*, feeling that the description was too general. Edwards (1866) states: “I have re-described *pseudargiolus*, as the description in Boisduval and Le Conte is imperfect, and may well apply equally to this species, or to *neglecta* or to *violacea*” (at this point believing each of the three were distinct species). Edwards (1868) believed that Boisduval & Le Conte’s description of *L. pseudargiolus* was closer to true European *argiolus* than to either the *neglecta* or *violacea* phenotypes, thus stating: “In this rather confused state of things it seems to me proper to fix the name *Pseudargiolus* upon that species which is nearest the true *Argiolus*...” We recognize Edwards’ (1866) detailed description of “*pseudargiolus*” as adequate and correct (except in name) for the taxon we now know as *neglectamajor*. His description is repeated as follows:

Male. Expands 1 4/10 inch. Upper side delicate pale blue, with a pink tinge; costa of primaries silvery; hind margins edged by a black line, which rarely [revised to read “sometimes” (Edwards, 1869)] is expanded on the apical half of primaries into a border; fringes black and white on primaries, white on secondaries.

Under side white, sometimes pure but oftener with a grayish tinge; the spots and markings are pale black or brown, and often nearly or quite wanting; when distinct, primaries have a discal streak, a transverse row of six spots, mostly elongated, the 3rd, 4th and 5th turned obliquely, the 6th frequently wanting; a marginal row of dots, each preceded by a serrated tooth.

Secondaries have three dots in a transverse row near the base; a discal streak; a row of eight minute spots across the disc, the two next costa much in advance of the others, the next four and the 8th nearly parallel to the margin, the 7th back of the line; the margin bordered by a row of black points, each preceded by a serrated tooth as on primaries.

Body above blue, below white; palpi black above, white below, tipped with white; antennae black, ringed with white; club black tipped with ferruginous.

Female. Same size. The apical half of costal margin and the whole of hind margin of primaries and costal of secondaries broadly, and basal half of primaries narrowly, edged with blackish; the rest of primaries metallic violet-blue, (sometimes lilac or green), except a large whitish patch on the disc; secondaries a duller blue, not metallic, the hind margin edged with a row of small, rounded, blackish spots.

Under side purer white than the average of males. [Revised to add “Fringes as in the male.” (Edwards, 1869).]

We here introduce additional comments on the female. HW dorsum: broad costal fuscous (gray) border reaching from the costal margin inward across cells SC+R1 toward the costal edge of the discal cell and less-markedly across cell RS to vein M1. In some specimens, cell RS is primarily pale blue with some gray tending toward the costal side; in some others, the entire cell is uniform dark gray.

We have evaluated adult wing lengths of three major population clusters: (1) southeastern Pennsylvania, (2) northern Virginia, and (3) western North Carolina. The forewing length (base of wing at costal margin to farthest distance at the apex) of 525 individuals was recorded and statistically compared (Table 1). The resulting table reveals a slight north-south cline in adult wing size, with western North Carolina populations averaging 1.5 mm larger than those in south-eastern Pennsylvania.

Opler and Krizek (1984) list the species forewing size as follows: “Male forewing: $X = 1.67$ cm, range 1.57-1.73 cm.; female forewing: $X = 1.67$ cm, range 1.57-1.77 cm.” Two males located in the Carnegie Museum measured 19 mm. These specimens, bearing labels in the handwriting of Edwards, were attributed to Virginia, with no accompanying data.

TABLE 1.

Population Group	Number of specimens	Minimum size (mm.)	Maximum size (mm.)	Mean (mm.) (S.E.)	Median size (mm.)	Mode (mm.)
Southeastern Pennsylvania	60	11.5	17.0	14.7 (± 0.2)	14.7	15.0
Northern Virginia	272	11.0	17.5	14.9 (± 0.2)	15.0	16.0
Western North Carolina	192	13.0	18.5	16.2 (± 0.1)	16.1	17.0

The smallest adults (11-14 mm) from northern Virginia (Figs. 8 & 9) frequently display deeper dorsal violet-blue in both sexes, and have heavier ventral markings, thus approaching the general appearance of *ladon*. One specimen, a male collected on May 13, 2000 near Berrys, VA (Clarke Co.), in addition to having very enlarged ventral hindwing spots, has an enlarged discal streak, giving the appearance of approaching the “*lucia*” form of *C. ladon*.

The Ozarkian sample is insufficient to ascertain consistent morphological differences from Appalachian populations. A pair from eastern Missouri (Figs. 12-14) falls in the average size range of the Virginia and Pennsylvania samples. The male (Fig. 12) measures 14 mm. and the female (Fig. 13) measures 15 mm. The male phenotype falls well within the range of variation found in eastern populations. However, the female differs markedly from Appalachian females in having extensive areas of white on the dorsum, especially on the hindwing. We have not seen this amount of white in eastern females.

Differences in size, color, and intensity of wing markings separate *neglectamajor* (Figs. 8-19) from *ladon* (Figs. 1-4). However, the principal difference is in the presence of an overlay of unique, long clear scales on the dorsal FW of *ladon* (Wright & Pavulaan, 1999), which is lacking in *neglectamajor* and *neglecta*. Although microscopic, these scales appear as a whitish satiny film on the dorsum of *ladon* males when viewed against strong light at different angles. By comparison, *neglectamajor* males do not possess overlay scales, but instead possess neat alternating rows of androconia (visible only microscopically) and “velvety” blue scales. The unique scale character of *ladon* can be detected by use of a portable field magnifying lens (10X) and a steady hand. *Ladon* also lacks androconia.

On the dorsum, *ladon* adults are uniformly dark blue to violet. In the central Appalachians the facies are commonly deep violet. Thus, Edwards named them *violacea* in a literal sense. This is contrasted with the lighter violet-blue to blue appearance of *neglectamajor*. *Neglectamajor* adults have a considerable degree of white scaling on the dorsal hindwing, which is lacking in *ladon*. Some *neglectamajor* females have extensive areas of white on the hindwing, completely lacking on *ladon* females. The wing fringes of *ladon*, particularly the hindwings, are often dark gray and checkered to varying degrees. There is no appreciable checkering of the hindwing fringe in *neglectamajor*. In most individuals, the fringe is entirely white.

Ventrally, the *ladon* ground color is generally deep gray, with a heavy black spot pattern. By contrast, *neglectamajor* is very light whitish gray to chalky white. The spot pattern is much reduced compared to *ladon* and varies from very lightly to moderately spotted. In some individuals, the spot pattern is greatly subdued, and in a small percentage of individuals the venter appears immaculate white.

Wing size is a major factor differentiating *neglectamajor* from *ladon*. *Ladon* averages smaller than *neglectamajor*. In southeastern Pennsylvania where we have data for both sympatric species, the forewings of *ladon* average 13.3 mm in length (range 10.0 mm – 15.0 mm) and those of *neglectamajor* average 15.0 mm in length (range 12.6 – 17.0 mm).

Differentiation from *neglecta*. At first glance, adults of *neglecta* (Figs. 5-7) and *neglectamajor* (Figs. 15-19) appear to be similar, almost identical. However, careful examination reveals several consistent minor differences. Some individuals albeit may be difficult to differentiate. Accurate field determination of either species may be virtually impossible based solely on sight identification. Careful note of habitat, presence of hosts, and state of wing wear should be taken.

Dorsally, adults of the two species are extremely similar and most phenotypic differences are found in the statistical averages of several characters. This may be evident only in large comparative series of both species. There is considerable overlap of these characters. For example, *neglecta* averages slightly smaller than *neglectamajor*. The forewings of *neglecta* from southeastern Pennsylvania average 13.9 mm in length (range 11.0 mm – 16.0 mm), while forewings of *neglectamajor*

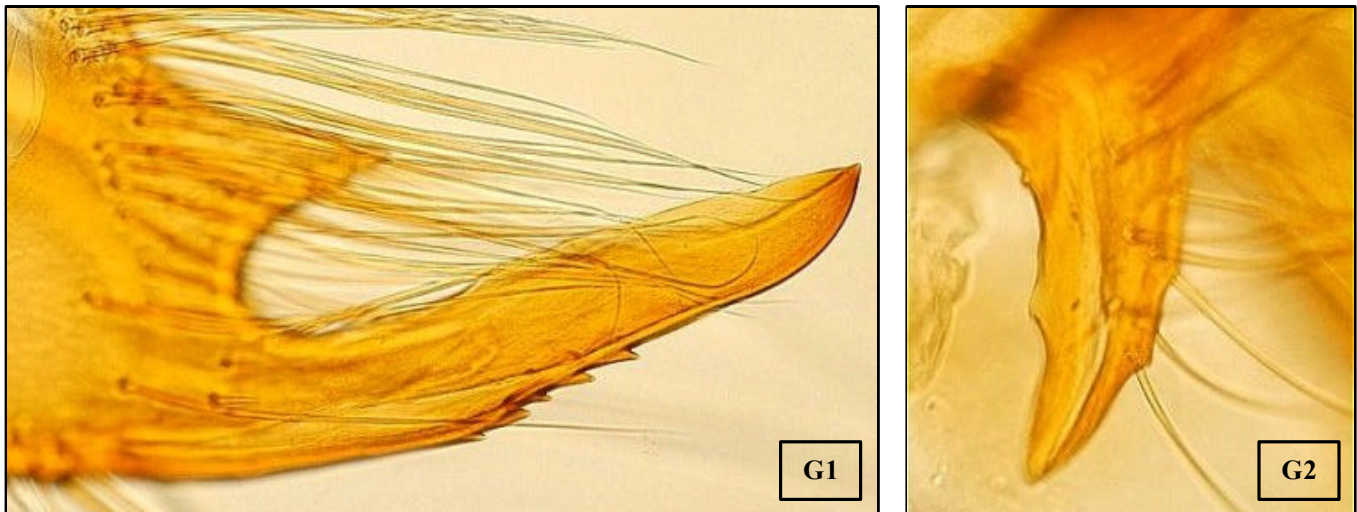
from the same region average 15.0 mm in length (range 12.6 – 17.0 mm). *Neglecta* males are generally slightly more bluish than *neglectamajor* males, which tend toward a slightly more violet appearance. The black marginal edge on the costa of the forewing is slightly wider in *neglecta* males than in *neglectamajor*. Also, the thin black marginal line outlining the hindwing of *neglecta* is bordered by a thin white edge on the interior side. This interior white edge is generally absent in most *neglectamajor* males, where the black marginal line is generally bordered by violet blue.

Ventrally, *neglectamajor* tends toward chalky white ground color, while *neglecta* appears to be slightly more grayish white. This difference is barely detectable. The ventral hindwing marks on *neglectamajor* are more brown in tone, while in *neglecta* they are dark gray. The ventral markings are “sharper” and more distinct in *neglecta* than in *neglectamajor*.

The primary difference between most males of *neglecta* and *neglectamajor* is in the amount and distribution of white scales on the dorsal hindwing. In *neglecta*, the white scaling on the hindwing is concentrated within the wing cells, while blue scaling tends to concentrate along the veins. This produces the effect of white “rays” on the hindwing between the wing veins. This effect may be very strong in some individuals. Some *neglecta* males have very extensive white scaling, giving the hindwing a mostly whitish appearance. In *neglectamajor* males, white scaling is considerably reduced and the hindwing in most individuals appears predominantly uniform violet blue with a faint scattering of white scales. However, some males have varying amounts of white scaling on the hindwing, which is distributed relatively evenly, producing a “clouding” effect rather than the rays of *neglecta*.

Female specimens similarly show differences in the amount and alignment of white scaling on the dorsal hindwing. In *neglecta*, white scales are concentrated in wing cells and the veins are variably outlined with blue or dark grayish-brown scales, forming rays across the entire hindwing. Overall, the hindwings may vary from bluish to almost entirely white, with most females tending toward white. In *neglectamajor* females, hindwing white scaling is not prominently developed into rays as in *neglecta* females, though there is a slightly greater tendency for rays in *neglectamajor* females than in the males. When rays are present in females, white scaling is usually strongest in cell M1 of the hindwing, beginning at the submarginal spot and occasionally reaching the discal streak. Scaling in cell M2 is usually confined to a triangular area pointing inward from the submarginal spot, and in cell M3 it is usually much reduced. About 40% of *neglectamajor* females have entirely blue hindwings. Rarely are the hindwings predominantly white. The Missouri female (Fig. 13) displays considerable white coloration on the hindwing. Reared “false summer” brood females have mostly white hindwings. Another minor character is the dorsal hindwing submarginal band. Many *neglecta* females have a faded scalloped submarginal band, corresponding to the submarginal lunules of the ventral hindwing. This character is generally lacking in *neglectamajor* females. Female genitalia were not compared.

GENITALIA. The genitalia of male *neglectamajor* and *neglecta* diverge slightly. Both species have sclerotized valves that terminate in narrow apical processes. The valve of *neglecta* is thin and bears 4-5 very small, barely perceptible subsidiary teeth. The valve of *neglectamajor* (Fig. G1) is thicker and bears 5-6 prominent teeth. These teeth are nearly as conspicuous as Palearctic *argiolus*, a condition which is not observed in other eastern North America *Celastrina*. The lateral contour of the valves of both *neglectamajor* and *neglecta* (and other eastern *Celastrina*) gently curves in mesial direction, while that of *argiolus* tends to sharply angulate. The upper genital ring bears a small spine on each uncal lobe. This spine is uniformly smooth in *neglecta*, but in *neglectamajor* (Fig. G2) the inferior surface of the spine is thick and irregular.



Figures. G1 & 2. Male genitalia of *Celastrina neglectamajor* Tutt, 1908. Specimen collected at Schwenksville, Montgomery County, Pennsylvania, 15 May 1999. **Fig. G1.** Dorsal view of valve with apical terminal process (100X). **Fig. G2.** Ventral view, close-up of uncal lobe spine (200X).

LARVAE. Four instars. Edwards (1878a, 1884) mistakenly identified five instars. Larval color is quite variable. First and second instar larvae are routinely yellowish or brownish yellow (Fig. C). They may appear whitish green upon emerging from the egg, but quickly develop yellow color. *Neglecta* first and second instar larvae are always whitish green (Fig. D). In third and fourth instar (mature) larvae, the ground color varies from bright green, olive green, dull pea green, yellowish green, cream green, greenish white, cream white, wine red, red brown, violet brown, chocolate brown, grayish brown, blackish brown, to black (Figs. A, B, G & H). The solid red and red-brown morphs (Fig. B) are more common in West Virginia and the southern Appalachians. Edwards depicted this color phase from West Virginia (Fig. 28). The mature larvae are often plainly marked, but some individuals have a brown saddle-like patch on the segments immediately behind the head. Some larvae are ornately marked with contrasting colors, such as olive green, cream white, tan, dark brown or reddish brown. They may be virtually indistinguishable from *neglecta*. A brown form mottled with white has been found. Pure white larvae increase in frequency as the season progresses and *Cimicifuga racemosa* flower buds turn white. As penultimate larvae cease their feeding activity and prepare to pupate, the color always fades to a cream pink. The head is disproportionately small, located at the end of a long extendable neck. The neck is attached to the anterior of the prothorax, which forms a protective shield for the larvae when in the feeding position. The larvae remain motionless on the host plant, with the protective shield pressed well against the plant, concealing the head and neck. Feeding activity, in which the larvae consumes the interior of the host buds, is completely hidden from view. Young larvae rest wholly on the floral bud, curving about it completely. Older larvae seem to rest wherever they can maintain a hold, curving the forward part of their body around the bud, but generally clasping the bud stem with their legs.

PUPAE. Mean pupal size is 9.3 mm., range 8.4-10.1 mm. (Measurements taken from twelve Montgomery Co., PA specimens.) Edwards (1883) reported: "...the chrysalids from eggs of *Pseudargiolus* are nearly twice as large as those of *violacea*...But the little chrysalids of *violacea* will not produce the large butterfly *Pseudargiolus*, and the chrysalis of the latter will not produce the little butterfly *violacea*." We have found, however, that chrysalides of *neglectamajor* can vary, and while generally larger than those of *ladon* and all broods of *neglecta*, a very few are nearly as small as those of *ladon*. However, dwarfed adults from small *neglectamajor* pupae retain their parents' characteristics and generally do not resemble *ladon* in general coloration and detail. Edwards (1883) reported them to average .336 inches in length, and .157 inches in maximum breadth. Later, Edwards (1884) revised this figure to .318 and .159, respectively. Pupae are obtect and brown in color. There are no distinguishing interspecific characters.

TYPES. Lectotypes are selected from Edwards' series of "form *pseudargiolus*" at the Carnegie Museum. Clench (unpublished manuscript), through a process of elimination based on dates and locations, concluded that two of Edwards' specimens closely match the drawings in Edwards' plates, figures 8 and 9 in *Lycaena* II (Edwards, 1884), and likely served as the original models in the plate. These Edwards specimens (Figs. 20-24) are here designated as the lectotypes of *neglectamajor* Tutt by Pavulaan and Wright. The corresponding drawings in Edwards (1884) are shown (Figs. 25-27, 29). Since Tutt based his description of form *neglecta-major* on Edwards' figures (1884: pl. "*Lycaena* II" figs. 8, 9), the types had to be Edwards' originals from which the figures were created (Art. 74.4, 2000 ICZN Code). The labels read as follows:

Male (lectotype): (1) "*Pseudargiolus* (male) / May. Coalb." [handwriting of W. H. Edwards]; (2) "Collection/W. H. Edwards" [letterpress in rectangular box]; (3) "probably the model / of Edw. pl. "*Lycaena* II" / fig. 8 and un fig. 9 / -therefore lectotype (male) / of *neglecta-major* / Tutt 1908: 407 / H. Clench 1975." [handwriting of H.C. Clench]; (4) "Lectotype. Male. *Celastrina neglectamajor* Tutt 1908. Designated by Pavulaan & Wright." [machine print]

Female (lectotype): (1) "*Pseudargiolus*" (female) / Coalb." [handwriting of W. H. Edwards]; (2) "probable model of / Edw. plate "*Lycaena* II" / fig. 9 (up), and therefore / lectotype (female) of / *neglecta-major* Tutt / 1908: 407 / H. Clench 1975." [handwriting of H. C. Clench]; (3) "Lectotype. Female. *Celastrina neglectamajor* Tutt 1908. Designated by Pavulaan & Wright." [machine print]

The Edwards specimen that was chilled on ice as a pupa and resulted in an aberrant female adult was recently found in the Edwards collection at the Carnegie Museum by Wright. The venter of this individual (Fig. 24) was depicted in Edwards (1884: pl. "*Lycaena* II", fig. 22) (Fig. 29) and subsequently given the form name "*obsoleta-lunulata*" by Tutt (1908: 426). The Carnegie specimen is designated as "Female. Lectotype. *Celastrina argiolus pseudargiolus* spring form *pseudargiolus* ab. *obsoleta-lunulata* Tutt 1908" on a printed label.

ETYMOLOGY. The species name comes from its extreme similarity to *neglecta*, and to its relatively larger size. Opler and Krizek (1984) point out that the Latin name is a combination of "neglectus" (neglected) and "maior" (major or greater). The common name "Appalachian Blue", as first coined by Opler & Krizek (1984), is appropriate for this insect. We recommend that future authors adhere to usage of the name "Appalachian" for this Appalachian (and, to a lesser degree, Ozarkian) endemic. The North American Butterfly Association's Standing Committee on English Names has recommended using the name "Appalachian Azure" instead (American Butterflies, 1993). This is intended for the sake of standardization and is based on the reasoning that all members of the genus *Celastrina* in North America should be referred to as "Azures".

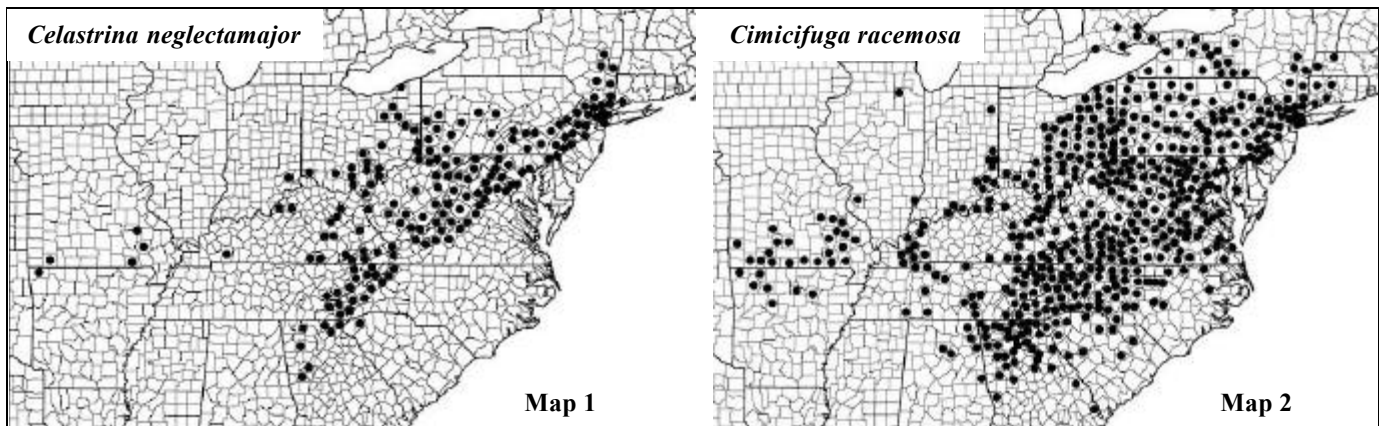
SYSTEMATICS. Tutt's treatment (1908) of *neglectamajor* clearly indicated that the author meant infrasubspecific rank for this taxon. Under the 1985 and 2000 ICZN rules, forms and varieties named before 1961 are not available in cases where the author specifically gave infrasubspecific rank to a taxon. Under this provision, *neglecta-major* Tutt is unavailable. Opler & Krizek (1984) treated the taxon as a species and attributed the name to Tutt. The 2000 ICZN rules (45.6.4.1) state that pre-1961 infrasubspecific names become available from the original author and date if the name is adopted as the name of a species or subspecies before 1985. Thus, under this provision, and if Opler and Krizek met all the rules of availability, the taxon is deemed to be a valid species from Tutt 1908 by action of Opler and Krizek 1984³.

RANGE. The range of *neglectamajor* (Map 1) lies entirely within the range of the host plant *Cimicifuga racemosa* (Map 2). Essentially Appalachian, with separated colonies in the Ozark region. Northernmost records near Albany, N.Y., and easternmost records from Fairfield County, CT; south through the Appalachian highlands to Atlanta, GA. West of the Appalachians it ranges into southern and eastern Ohio, southeastern Indiana and eastern Kentucky. Isolated colonies in Ozark region of southern Missouri and northwestern Arkansas. Outlying colonies have recently been found on isolated ridges and along deep river valleys in the Piedmont region of Virginia and Maryland. Probably occurs in intervening areas in western Kentucky and Tennessee. Not reported from western New York in areas in which the host plant occurs.

RECORDS. The following county records have either been accepted, deemed as valid, or personally examined by us. ARKANSAS: Benton; CONNECTICUT: Fairfield; DELAWARE: New Castle; GEORGIA: Bartow, Coweta, Fulton, Murray, Rabun, Union, White; INDIANA: Ripley; KENTUCKY: Floyd, Graves, Jackson, Jefferson, Harlan, McCreary, Menifee, Owsley, Powell, Rowan, Shelby, Whitley; MARYLAND: Allegany, Baltimore, Cecil, Frederick, Garrett, Howard, Washington; MISSOURI: Barry, Iron, Ripley, Wayne; NEW JERSEY: Bergen, Essex, Hunterdon, Mercer, Morris, Passaic, Somerset, Sussex, Warren; NEW YORK: Albany, Bronx, Columbia, Dutchess, Greene, Kings, New York, Orange, Putnam, Rockland, Ulster, Westchester; NORTH CAROLINA: Ashe, Avery, Buncombe, Graham, Haywood, Jackson, Macon, Swain, Watauga, Yancey; OHIO: Athens, Carroll, Fairfield, Gallia, Hamilton, Highland, Hocking, Jefferson, Lake, Lawrence, Meigs, Muskingum, Pike, Ross, Scioto, Stark, Summit, Vinton, Wayne; PENNSYLVANIA: Allegheny, Beaver, Berks, Bucks, Butler, Centre, Chester, Clearfield, Cumberland, Dauphin, Delaware, Fayette, Franklin, Greene, Huntingdon, Indiana, Lancaster, Lebanon, Lehigh, Montgomery, Northampton, Perry, Philadelphia, Washington, Westmoreland, York; SOUTH CAROLINA: Pickens; TENNESSEE: Blount, Carter, Cocke, Greene, Hawkins, Sevier, Sullivan, Washington; VIRGINIA: Albemarle, Alexandria (City), Alleghany, Amherst, Arlington, Augusta, Bath, Bedford, Botetourt, Clarke, Fairfax, Fauquier, Giles, Greene, Highland, Lee, Loudoun, Madison, Montgomery, Nelson, Page, Prince William, Rappahannock, Roanoke, Rockbridge, Rockingham, Scott, Smyth, Tazewell, Warren, Wise; WEST VIRGINIA: Barbour, Boone, Braxton, Fayette, Grant, Greenbrier, Hampshire, Hardy, Jefferson, Kanawha, Marion, Marshall, Monongalia, Monroe, Ohio, Pendleton, Pocahontas, Preston, Raleigh, Randolph, Summers, Tucker, Wayne, Wetzel.

Adult flight period. Single-brooded. The flight period extends from mid-May to mid-June throughout most of the range, with extreme dates from late-April into early-July. Variation in early and late dates for each state is influenced more by elevation and yearly weather patterns than by latitude. Males generally emerge first and females emerge a few days later. "False" (non-diapause) summer brood individuals have been obtained through artificial rearing conditions. Rearing indicates that ova, first-, second- and even some third-instar larvae can easily be coaxed into producing a false summer emergence when reared with indoor temperatures and artificial lighting. Adults reared from field-collected ova produce summer offspring when the larvae are reared indoors. However, field-collected fourth-instar larvae almost always enter pupal diapause. They seem to be "committed" to diapause irrespective of the ambient temperature when found. Exposure to low temperatures at an early stage of larval development (probably 1st/2nd instar), with considerable day/night fluctuation, appears necessary to induce a commitment to diapause. These pupae will eclose the following spring, if kept in cool conditions and refrigerated over the winter. Small numbers of chrysalides may break diapause early under continuous light, high humidity, and warmth. The mechanisms responsible for breaking diapause is not fully understood. Constant indoor warm temperatures

³ Editor's note. Under peer review, Pavulaan and Wright were advised that Opler and Krizek probably did not meet enough of the conditions set forth under the Code's rules of availability (Articles 11-18) to give Tutt authorship. Here are the reviewer's points. "Because Tutt presented *neglectamajor* as an unambiguous infrasubspecific entity it is not an available name under the Code. The only way it can become an available name, with Tutt's authorship and date, is for the name to have been adopted as a subspecies or species before 1985. This would require a description (Article 13.1.1), which Opler and Krizek may have met; and the designation of a type specimen and its proper deposition (Article 61), which Opler and Krizek did not do. Opler, in personal communication to Wright, stated that he and Krizek did not intend to author a species name in their 1984 book and that they thus purposely did not designate a type. It is this reviewer's opinion that this paper may validate the name *neglectamajor* under Article 10.2 which would give authorship to Pavulaan and Wright, 2000. Under the Code, only Tutt or Pavulaan and Wright can be the authors. If Opler and Krizek met the 45.6.4.1 rules of availability and adoption, the authorship is Tutt's from 1908. If they did not, it is Pavulaan and Wright's, 2000."



appear to be responsible for creating non-overwintering pupae in the lab. So far, there have been no confirmed records of a second (summer) brood of *neglectamajor* occurring in nature. A similar laboratory related phenomenon was observed by Wagner and Mellichamp (1978), who inadvertently produced a summer brood of the spring univoltine, *C. nigra* Forbes [= *ebenina*], when no such second brood occurred in nature.

Known flight dates (or extremes) for each state. ARKANSAS: May 18; CONNECTICUT: May 20-June 17; DELAWARE: June 5; GEORGIA: May 4-July 8; INDIANA: May 24; KENTUCKY: April 1 (in error?), otherwise April 25-July 5; MARYLAND: May 6-June 17; MISSOURI: May 13-25; NEW JERSEY: May 13-June 11; NEW YORK: May 14-June 1; NORTH CAROLINA: May 17-July 9; OHIO: April 28-June 17; PENNSYLVANIA: May 6-June 30; SOUTH CAROLINA: April 29; TENNESSEE: April 30-July 1; VIRGINIA: April 28-July 5; WEST VIRGINIA: April 19-June 19.

HABITAT. In northern Virginia, Maryland and Pennsylvania, *neglectamajor* is found mainly in rich deciduous Transition Zone forests atop Appalachian mountain ridges where the host plants flourish, but it also occurs on lower slopes and in valleys wherever the host plants flourish in large colonies. Recently it was found on outlying “monadnocks” in the Piedmont, such as on Bull Run Mtn. near Manassas, VA, and on Sugarloaf Mtn., near Barnesville, MD. Also found along wooded north-facing slopes in steep river valleys in the Piedmont, such as the Patapsco River valley west of Baltimore, and along the Potomac River at Great Falls, west of Washington D.C., where Transition Zone vegetation finds a home in the relatively cool habitat.

In Ohio, reported (Iftner et al. 1992) in cool, moist ravines, and along roads and streams in mesic deciduous forest, and in ridgetop woodland clearings.

In western North Carolina, found primarily in richly-deciduous wooded valleys which flank higher ridges in the Transition Zone. Webster (personal communication) sighted several in the Canadian Zone. If this is correct, they are altitudinal strays.

In Missouri, found in close proximity to rivers, where the hosts grow on wooded slopes or lowlands. Near Williamsville, Wayne Co., MO, found along wooded north-facing river bluffs. All Missouri locations are considered Upper Austral Zone.

Edwards (1869) found it commonly along the Kanawha River, West Virginia, with males mainly along roadsides or edges of woods, but preferring to fly along forest streams. He also reported that females were generally not seen in places that the males frequented, but rather kept to the woods among the shrubs. Strays have been taken far from the nearest known habitats. During the second week of May, 2000, several strays were observed in a suburban residential habitat in Herndon, VA, confirmed by capture of two adults on May 12-13, 2000. This location is about 30 miles east of the nearest permanent populations and many miles from the nearest “suitable” habitats.

Adult habits. Females, as a rule, are generally found about the vicinity of host stands and tend to stay within the primary woodland habitat. There are exceptions (see above). Males frequent more open habitats. Early in the flight period, freshly-emerged males appear to move downslope in mountainous terrain, following watercourses descending through valleys to lower elevations. On May 30, 1988, hundreds of males were observed over a two-hour period moving downstream along a north-flowing creek near Gatlinburg, TN. The males congregate along wooded watercourses at lower elevations, commonly forming puddle parties on streamside damp sand. On June 1, 1988, over 100 *neglectamajor* were observed at a streamside “puddle party”, along with nearly equal numbers of *neglecta* in Big Cove on the south slope of the Great Smoky Mountains near Cherokee, NC. They can also be commonly found along woodland dirt roads near watercourses. In these habitats, the host plant is not necessarily present, but it is usually nearby. Later in the flight, the males appear less frequently along these watercourses and tend to fly in the primary habitat with the host plant stands.

In some localities, *neglectamajor* may become extremely common. The entire Blue Ridge of northern Virginia has a very large, continuous population. In some years, this population irrupts with *neglectamajor* becoming the most common butterfly in the primary habitat. During May, 2000, the population on top of Mt. Weather (an extension of the Blue Ridge forming the boundary between Clarke and Loudoun Counties) near Bluemont, VA, Pavulaan witnessed the largest irruption in 19 years, with dozens of individuals being seen at any one moment and at virtually any location along the entire length of the ridge from State Route 7 to State Route 50. This irruption may have been responsible for the presence of adults in Herndon, VA, 30 miles to the east across hilly Piedmont terrain. In other years, populations may be scarce. This seems to occur more frequent in outlying colonies such as those on the eastern Piedmont.

These outlying colonies consist of low-density populations and may depend heavily on immigration from the Appalachian mountains for their continued presence. The colony atop Sugarloaf Mountain near Comus, MD, where host *Cimicifuga* flourishes at the summit, fluctuates annually, being common some years and absent others. At this location, adults are generally elusive, though the larvae are common. At Great Falls National Park, along the Potomac River in northern Virginia, temporary colonizations occur in some years. Generally only single individuals are seen at Great Falls; the larvae tend to be found more frequently.

Very little is known of the species' habits and population dynamics in the Ozarks. Colonies there appear to be isolated and of considerably low density. They are generally associated with stands of the host plant, but they can be absent even in some "prime" habitat locations such as St. Francois State Park near Bonne Terre, MO. In these cases in the Ozarks, it is often easier to locate larvae to establish whether the species is present.

ADULT FOOD AND NECTAR SOURCES. Females utilize flowers for nectar, while males prefer damp sand. Adults have been found primarily on white flowers of Cut-leaved Blackberry (*Rubus laciniatus*), Toothwort (*Alliaria officinalis*), Garlic Mustard (*Dentaria laciniata*), Sweet Cicely (*Osmorhiza* sp.), Flowering Dogwood (*Cornus florida*) and Gray Dogwood (*Cornus racemosa*). One was observed on Common Wintercress (*Barbarea vulgaris*), a yellow flower. Puddling behavior occurred at damp spots along streamsides and dirt roads, and reportedly also on urine-moistened soil (Iftner et al., 1992). Adults have also been observed on animal droppings and decaying corpses of small animals (mice and frogs) on dirt roads.

LARVAL HOST PLANT. *Cimicifuga racemosa*⁴ (Figs. E & F). Edwards was the first to ascertain this unique plant as the host in 1865. (See Edwards, 1866). It is also locally known as "Black Cohosh", "Rattleweed", "Black Snakeroot", "Squaw Root" and "Bugbane". The plant grows in moist, rich, mixed deciduous forest, mainly on ridge tops in central Appalachians, but also in ravines or along stream margins. In the southern Appalachians, it is found abundantly in upland hollows or on wooded slopes at higher elevations. On the eastern Piedmont, it is found in isolated locations on wooded slopes near rivers. It is even reported in rich, moist woods at some locations on the Atlantic Coastal Plain. In the Ozark region, found in low-lying, forested, valley bottom habitats near rivers, but also thrives on north-facing slopes.

The perennial plant leafs out in April, with flower stalks developing toward late May in most of its range. Young flower stalks grow rapidly and produce small "corn-cob" shaped bud clusters, upon which females oviposit. Eggs are laid on individual floral buds, or tucked tightly between closely packed young buds. Many ova can often be found clustered on a single flower "cob" (Fig. E). Eggs have been amassed on a single flower spike to as many as 128 (no doubt laid by multiple females). Ova have also occasionally been found on very young leaves and stems. The flower stalks mature toward late June and can attain heights up to eight feet. (The majority of Blue Ridge plants measured just under 6 feet). Immature flower buds are green, but turn white when mature. Lower buds open first and the white flowers progressively open along the stem toward the tip of the spike over a period of several weeks (into July). Flower spikes can be several inches long and have been found to support up to five mature larvae on a single spike.

The larvae feed by burrowing into the flower buds and feeding on the inner contents, leaving an empty shell. Older larvae may feed on plant stems (occasionally dissecting the flower spike). They also have been observed feeding on young leaves or chafing the underside of older leaves. In Howard County, MD, in 1991, larvae completely skeletonized older leaves, after flower spikes had been devoured or severed by the larvae feeding on flower stems. Flower spikes eaten by deer also send larvae to the leaves for sustenance. The leaf-skeletonizing behavior could also be an adaptation to evade predators and parasitic insects which frequent the flowers when in bloom. An important point to emphasize is that larvae of *neglecta*, which are also found on *Cimicifuga racemosa*, cannot complete their development on *Cimicifuga* leaves in the laboratory. The leaves are toxic to *neglecta* larvae.

Young *neglectamajor* larvae, when confined in close quarters, will prey upon each other, burrowing into a victim's body as if it were a host bud. Larvae in the wild often bear "bite" scars, and occasionally collapsed, partially-consumed

⁴ Dr. Gwynn Ramsey has informed us of a nomenclature change (Compton et al., 1998) that realigns the genus *Cimicifuga* under the genus *Actaea*. This reclassification has been accepted by many professional botanists and herbaria. The new combination will be known as *Actaea racemosa*.

individuals will be found. In May, 2000, two captive larvae totally devoured several of their siblings, leaving not a trace. Mature 4th instar larvae rarely display this behavior.

Shapiro (1966) listed the host plant as being *Viburnum acerifolium*. Following up Shapiro's report, Wright investigated the original location where these observations were made (southeastern Pennsylvania) and found *Celastrina* larvae on *Viburnum*, in proximity to flying adults of *neglectamajor*. When raised to adulthood, these larvae yielded *C. ladon* form "marginata". *Ladon* is known to utilize *Viburnum* in many parts of its northeastern range. Opler and Krizek (1984), referring to Shapiro's work, also listed the host plant of *neglectamajor* as *Viburnum acerifolium*. Scott (1986) perpetuated this error and also listed *Humulus lupulus* (Hop Vine) as an additional host plant. The latter was based on observations of feeding behavior of a univoltine *Celastrina* found near Denver, CO, which Scott considered to be *neglectamajor* at the time of his writing. This entity was later named *C. humulus* (Scott and Wright, 1998).

Pratt and Ballmer (1991) reported that *neglectamajor* larvae can be successfully reared on *Lotus scoparius* in the lab. This legume plant is a nearly universal alternative host for a wide variety of lycaenid butterflies. Our rearing experiments also proved that *neglectamajor* larvae can be raised on *Eriophyes* mite galls occurring on *Prunus serotina* leaves, though the resultant adults are dwarfed. In 1990, we switched two separate groups of 2nd-instar *neglectamajor* larvae (ex ova on *Cimicifuga racemosa* in captivity) from Bucks Co., PA and Frederick Co., MD, onto a *neglecta* host (*Cornus amomum*). Both groups of larvae fed on the new host for about five days, then died. We concluded this host was unsuitable.

Larva-ant association. As with *ladon* and *neglecta* larvae, mature *neglectamajor* larvae develop a close relationship with ants. This behavior has been observed in fourth instar and, less frequently, in third instar larvae (Fig. H). The ants will generally be found on or near the larvae, being attracted to them by a secretion from the orifice of a midline dorsal gland of the abdomen (A7). The gland secretes a sweet fluid droplet which the ants consume. This is known as "milking". A pair of eversible tubules located on the eighth abdominal segment (A8) does not seem to attract ants. Edwards (1878b) believed the expansion and contraction of eversible tubules were used to signal the ants to expect fluid from the honey-gland orifice on the A7 segment. These organs are apparently not sufficiently developed in the younger larvae, as ants are indifferent to them.

Ants tending the larvae may be involved either in "milking" behavior or positioned in a protective stance over the larvae. Often several ants can be observed tending to a single larva. Those feeding on larval secretions can generally be seen with their heads near the secretory organ, drinking when fluid is offered. At other times, they run up and down the back of the larvae, frantically drumming and caressing the larvae with their antennae. Ants guarding the larvae can sit motionless for minutes, watching for predators. Occasionally, protective ants will perch on the flower spike just behind the larvae, defending against predators approaching from below. The ants are extremely vigilant and aggressive. They will quickly attack a human finger, biting or stinging with a fury. When flower spikes with larvae are removed and placed into a jar, the ants will remain with the larvae for several days in captivity.

The following attendant ant species (Formicidae) have been identified (det. D. R. Smith). Locations and ants: Mt. Weather, Route 601 nr. Bluemont, Loudoun and Clarke Counties, VA, 6/18/88: *Lasius alienus* (Foerster); *Formica subsericea* (Say); *Camponotus ferrugineus* (Fitch), *Camponotus pennsylvanicus* (DeGeer). Patapsco Valley, nr. Daniels, Howard Co., MD, 5/17/90: *Prenolepis imparis* (Say); *Lasius alienus* (Foerster); *Formica subsericea* (Say). Bucks Co., PA, 6/14/87: *Lasius alienus* (Foerster). Bucks Co., PA, 6/23/87: *Formica neogagates* (Emery), *Camponotus ferrugineus* (Fitch). Also recorded: *Camponotus subbarbatus* (Emery). No doubt there are many others yet to be identified.

PREDATORS. Red mites, which thrive on the host plants, have been seen feeding on ova, presumably sucking out the contents of the egg. Flattened dried eggs can usually be found on the host floral buds. *Podisus modestus* (Dallas), a pentatomid (Hemiptera) (det. T. J. Henry), has been observed attacking mature larvae.

PARASITOIDS. The following parasitoids have been reared and identified (det. P. M. Marsh, R. W. Carlson, D. L. Vincent and S. R. Shaw). Tachinidae (Diptera): *Aplomya* (= *Exorista*) *theclarum* (Scudder). These parasitic flies deposit eggs on the back of young second instar larvae. Maggots burrow into the larva, feeding until the host larva reaches the fourth instar. Fly larvae then emerge and form a hard pupal case. Ichneumonidae (Hymenoptera): *Anisobas luzernensis* (Bradley), *Agrypon cushmani* (Dasch), and *Anomalon* sp. Adult ichneumonids attack the larvae only in the last two instars. Grubs feed within the mature larvae and chrysalids. An interesting finding is the presence of *Mesochorus vittator* (Zellerstedt), an ichneumonid hyperparasite that preys on the larvae of the braconid *Cotesia cyaniridis* inside the *Celastrina* larva. Braconidae (Hymenoptera): *Cotesia* (= *Apanteles*) *cyaniridis* (Riley) (incorrectly identified as *A. congregatus* in Edwards, 1884) and *Glyptapanteles* sp. Eggs are deposited in young larvae by adult female braconids. The grubs feed and emerge when the host larvae are about half-grown, forming a yellow silken cocoon. Trichogrammatidae (Hymenoptera): *Trichogramma minutum* (Riley). Minute parasitoid wasps parasitize butterfly ova and consume the germ plasm. Development takes place entirely within host eggs.

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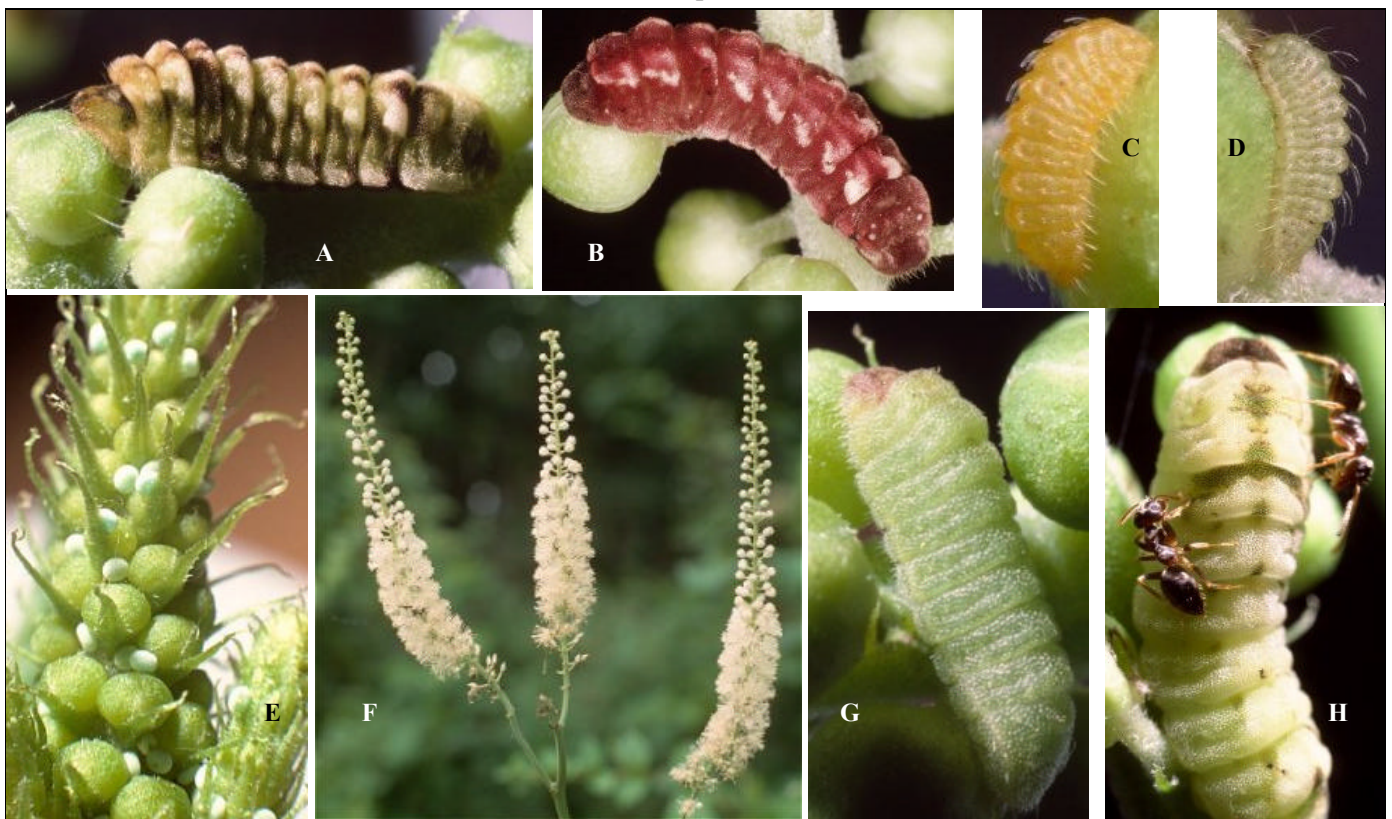
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Figures A, B, G, & H. Mature larvae of *C. neglectamajor* on host. **Fig. A.** Mottled morph, 22 June 1987, St. Game Lands #157 Bucks Co., PA. **Fig. B.** Red morph (most common in cent. & n. Appalachians) mid June, 1992, Elkins, Randolph Co., WV. **Fig. G.** Green morph, June 1987, same site as A. **Fig. H.** Light green morph attended by *Camponotus pennsylvanicus* ants, 23 June 1994, same site as A. **Fig. C.** 1st instar *C. neglectamajor* (yellow with short blunt-end dorsal setae) on *racemosa* bud, 23 June 1987, same site as A. **Fig. D.** 1st instar *C. neglecta* (green with long pointed dorsal setae) on *racemosa* bud, 23 June 1987, same site as A. **Fig. E.** Ova of *C. neglectamajor* on bud spike of *C. racemosa*, 1 June 1990, same site as A. **Fig. F.** Flowering spike of *Cimicifuga racemosa*, Spring Valley Pk., Montgomery Co., PA, 9 July 1994. Photos: B by Tom Allen, all others by Wright.

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