

# A NEW CELASTRINA FROM THE EASTERN SLOPE OF COLORADO

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Abstract. Celastrina humulus (new species) is named and compared to related and sympatric Celastrina. It is univoltine, and usually sympatric with the univoltine Celastrina ladon sidara and barely overlaps the end of the sidara flight, as adults emerge from post-diapause pupae later than sidara. It has a different habitat, and a different host (most populations feed on male flowers of hop Humulus lupulus, but one set of populations feeds on Lupinus argenteus flower buds). Adults are whiter than sidara. Adults are electrophoretically most similar to the eastern Prunus serotina gall feeding host race, and are somewhat similar to eastern neglecta. 1st-stage larval setae differ slightly from C. ladon sidara, mature larvae are variable but differ slightly in the frequency of color forms, and pupae differ somewhat in color, and in size of black spots.

## Celastrina humulus Scott and Wright,

# **NEW SPECIES**

(Figs. 1-16)

DIAGNOSIS. Adults are similar to the other whitish Celastrina taxa (neglectamajor, neglecta, argentata, and eastern gall-feeder): males are mostly light blue above (sometimes with a slight amount of whitish on uph), they lack the transparent long dorsal scales of "violacea" type I (defined by Pratt et al. 1994) and Celastrina nigra; females are usually mostly light iridescent blue above with some whitish but in some females the blue is mostly replaced by white (Fig. 7); and the underside is white with reduced markings like that of other whitish *Celastrina* including neglecta. The underside varies from white with very little black pattern, especially in females (Figs. 3-4, 9-10, 15), to whitish with stronger maculations (Figs. 5-6, 14, 16). It differs from all other whitish Celastrina by geographic distribution and by eating the male flower buds of Humulus lupulus (hop) in most populations (except a single known population eats flower buds of Lupinus argenteus), and adults differ electrophoretically. Adults have a whiter underside with often-smaller black spots than sympatric Celastrina ladon sidara (nothing approaching form lucia is observed; the only spot enlargement noted on ventral hindwing was one spot elongated to 2 mm length on several males, Fig. 16), adults greatly differ electrophoretically from it, adults fly several weeks later than sidara on the average and barely overlap its flight, pupae take longer to develop to adults after winter, the hosts differ, adults fly only in gulch bottoms (versus north-facing slopes from ridge to gulch for sidara), several setae on first-stage larvae differ in length, older larvae have fewer reddish forms, and pupal color and black spot size differ slightly. C. humulus is a distinct biological species that rarely if ever interbreeds with C. ladon sidara.

This taxon is named as a species here because its closest relative in eastern U.S., namely "violacea" II (of Pratt et al. 1994) whose larvae eats *Prunus serotina* galls, is being named as a species. Future work will determine whether it is a subspecies of that taxon or of *Celastrina neglecta*.

**TYPES:** Holotype male and allotype female (both deposited in British Museum Natural History) Red Rocks, Jefferson County, Colorado, 1973 (holotype June 14, allotype June 24). Numerous paratypes will be distributed later, from the foothills of the Front Range at S & SE of Deermont, S of Wilds Peak, Phillipsburg, and Tinytown (these localities are of the lupine host-race discussed below, while the following localities are for the hop host race), gulch S Morrison, W Idledale, Cherry Gulch, Red Rocks, Mother Cabrini Shrine, Apex Gulch, Chimney Gulch, Indian Gulch, Bull Gulch, Coal Creek, all in Jefferson Co., Gregory Can. and Lefthand Can. in Boulder Co., into the mountains along North Clear Creek in Gilpin Co. Colo. and along the South Platte Canyon at Nighthawk in Douglas Co., and barely onto the plains along Clear Creek in Wheatridge, Jefferson Co. (where the host is also *humulus*).

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**RANGE.** So far known only from the Colorado Front Range from Douglas Co. north to Larimer Co. Scott found it in Douglas, Jefferson, Gilpin, and Boulder Cos., and examined several specimens from Arapahoe Co. Colo. that also seem to be C. humulus (Cherry Creek Res. where a small amount of Humulus grows, 1 male July 1, 1991, 1 female June 26, 1993, 1 female July 29, 1993; and an apparent stray worn female not near hop at Greenwood Village, July 29, 1993; all coll. Andrew Warren; the late dates of several of these we cannot explain). C. humulus was collected in Elbert Co. by Andy Warren (2 males near Humulus at Boy Scout Camp, June 8, 1996), and in Larimer Co by Paul Opler. A record of unknown Celastrina from Adams Co. Colo. might be C. humulus. It may occur southward in the Front Range to El Paso Co., and further south to the Wet Mountains, if a few records of whitish adults are this species: six whitish Celastrina have been found in El Paso Co.: a worn female Little Fountain Creek, El Paso Co. Colo, Aug. 9, 1971, J. Scott; Rock Creek, 8000', June 24, 1962, Samuel A. Johnson; Rock Creek, June 12, 1932, F. M.Brown, Allyn Museum; Foster Ranch 5700", T15S, R65W, sec. 22, NE 1/4, July 28, 1976, Allyn Mus. presumably F. M. Brown; one female Colorado Springs, Aug. 1, 1905, USNM); one merely "El Paso Co.", July 28, 1976, Allyn Mus. And one whitish Celastrina has been found in the Wet Mts. in Pueblo Co. Colo.: a male 4 mi. S Beulah, Aug. 4, 1962, J. Scott. However, these records may be some other taxon (a summer form "neglecta" of C. ladon sidara?), because 8000' seems too high altitude for C. humulus, and the records from July 28 to Aug. 9 are later than any definite C. humulus. But they might possibly be C. humulus because Scott has failed to rear any white adults from C. l. sidara. Actual populations will have to be found, and associated with a host, before a definite identification can be made. Two Celastrina specimens from middle elevation in Jefferson Co. (Cheeseman Res., 6800'1 female Aug. 16, 1986, P. Opler, and Wellington Lake, Sept. 2, 1989, A. Warren) might also be a summer form "*neglecta*" of *sidara*. A record of Celastrina from Denver Co. Colo. is Scott's old sight record in this developed city, which cannot be verified as to species. Scott caught one male in a western suburb of Denver (Lakewood in Jefferson Co.) July 16, 1996, but this male might be *Celastrina neglecta* instead; however, Scott has since found one Humulus plant growing around a telephone pole one block away, and the nearest Cornus found is 1.5 km away. Eastward on the plains, a record from Weld Co. is a spring sidara Celastrina neglecta evidently enters eastern Colo. in Logan, Sedgwick, Prowers, & Baca Cos., as this species occurs throughout Kansas and Nebraska and extends westward to Goshen Co. Wyo. C. humulus could possibly occur north to the Laramie Range in S Wyoming, but is not yet known from Wyoming. Similar habitats in the Bighorn Mts. of N Wyo. (Sheridan & Bighorn Cos., based on Scott's records and those of F. M. Brown etc.) contain *C. neglecta* (evidently the *Cornus* sericea=stolonifera race that also occupies W Neb.-Iowa-S Minn.), and three counties in C Montana evidently possess C. neglecta.

**NOMINA NUDA**. The ICZN rules are complex, and most lepidopterists have not read them, so unfortunately butterflies are sometimes named inadvertently (for example *Celastrina neglectamajor* Opler & Krizek). The name *Celastrina humulus* has been in print several times before: twice in the Season Summary of the Lepidopterists' News, and again in a North American Butterfly Association checklist. These printings represent nomina nuda, because they failed to describe how the butterfly was distinguished, and ICZN Article 13(a)(i) states that "every new scientific name published after 1930...must be...accompanied by a description or definition that states in words characters that are purported to differentiate the taxon" (and we note also that Art. 12(c) states that "The mention of any of the following does not in itself constitute a description, definition, or indication: a vernacular name, locality, geological horizon, host, label, or specimen.").

**GENETIC RELATIONSHIP**. Electrophoresis of adults from Red Rocks by Wright and Gordon F. Pratt proved that *C. humulus* is most closely related to whitish eastern U.S. taxa, not to *sidara*. It is most similar to the *Prunus serotina* gall feeder "*violacea*" type II (defined by Pratt et al. 1994), and has the same electrophoretic alleles, but allelic frequencies differ significantly. Electrophoretically, it is slightly less similar to *C. neglecta*.

*C. humulus* is not related to *C. neglectamajor* Opler & Krizek of eastern U.S., even though it was called *neglectamajor* by Scott (1986) and was mapped as *neglectamajor* by Stanford & Opler (1993). *C. humulus* is whitish like *C. neglectamajor*, and both fly several weeks after *ladon* form "*violacea*". But *neglectamajor* is often larger than *C. humulus*, their hostplants differ (exclusively *Cimicifuga racemosa* for *neglectamajor*), they differ electrophoretically, and Wright has found that *neglectamajor* 1st-stage larval setae differ somewhat from Colorado *C. humulus* and *C. ladon sidara*.

**PUPAL DEVELOPMENT AND FLIGHT PERIOD**. Larvae from Red Rocks and Coal Creek, Jefferson Co. Colo, were collected and reared on *Humulus lupulus* male flowers by Scott, and sent to Wright. Four weeks after the last larva in a population had pupated, pupae were placed on moist sphagnum moss and kept in the dark at  $4^{\circ}$ C for four months, then were removed and placed at about 20°C, still in the dark until they eclosed. The number of days to eclosion after removal from  $4^{\circ}$ C were recorded for each pupa. *C. humulus* pupae took an average of 20.9 days to emerge (SE 1.4, range 9-30, n=9). By comparison, larvae of *C. ladon sidara* from Tinytown, Jefferson Co. Colo., collected and reared on *Jamesia americana*, took an average of only 8.6 days to emerge (SE 0.7, range 4-15, n=36) under the same lab conditions, a significantly shorter time (p<.01). And the lab difference of 12 days no doubt is greatly lengthened (more than doubled) in the cooler spring temperatures in nature.

Of course this longer post-diapause pupal development correlates with and is the physiological mechanism causing the later flight period of *C. humulus* in nature. The start of the *C. humulus* hop-race flight overlaps the end of the *C. ladon sidara* flight EVERY year (they fly together at EVERY *C. humulus* hop-race site in Jefferson Co. except Mother Cabrini Shrine & Wheatridge); worn female *C. ladon sidara* are likely to be already mated and unreceptive, but a few male *sidara* often fly with emerging female *C. humulus*. *C. humulus* hop-race flies during June, and can be common anytime during June depending on the year (the peak flight is most often mid-June, but may be early June in early years, late June or the end of June in late years such as 1995); there are a few May records (1 male May 25, 2 females May 30) and more July records (as late as July 11 for a male, July 10 for a female, and in the year with the latest flight [1995], as late as July 24 for both sexes and July 27 for three females). In contrast, Colo. *C. ladon sidara* flies from mid April to rarely as late as mid June, and typically peaks in mid or late May.

**HOSTPLANT**. There are two host races. Most known colonies feed on hop *Humulus lupulus americanus* (*=neomexicanus*)(family Moraceae or the splitter family Cannabaceae), and we call them the *C. humulus* hop-race (the *Lupinus argenteus* host-race is treated separately below). 13 ovipositions were found on hop at 9:20, 9:21, 10:15, 10:20, 10:25, 10:30, 11:24, 11:24, 12:07, 12:12, 12:54, 13:25, 13:40 (all 24-hour standard time), and approximately 264 eggs, 25 young larvae, and 105 older larvae were found on hop, at W of Idledale, Red Rocks, Cherry Gulch, Mother Cabrini Shrine, Apex Gulch, Chimney Gulch, Indian Gulch, Wheatridge, Coal Creek Can., all in Jefferson Co. Colo., and at Nighthawk, Douglas Co. Colo. (the detailed host records are in Scott 1992 except for recent records). Nearly all eggs and larvae were found on **male** flower buds, while only a few eggs were found on female flower buds (male and female flowers grow on separate hop plants; the female flowers grow into the pine-cone-like catkins that are harvested to flavor beer).

**ORIGIN OF** CELASTRINA HUMULUS. Humulus lupulus is evidently native to the Colo. mountains, because the leaves of the native H. l. americanus (which ranges from N.B. to Mont., south to W. Va. and New Mex.) are more incised than those of cultivated H. l. var. lupulus (which is introduced from Europe). One could speculate that beer breweries could have planted cultivated hop to flavor their beer, and C. humulus could have discovered the abundant and non-harvested male inflorescences and founded a population on Humulus. The large Coors Brewery in Golden, Jefferson Co. Colo., was started in 1873, and the first Colo. brewery (Rocky Mountain Brewery, later Zang's Brewery) was started in Denver Nov. 1859. But there is no evidence that hop was ever cultivated in the Front Range, and hop is not cultivated in the area now (beer hops are grown in Idaho etc.). All the evidence indicates that H. l. americanus and C. humulus hop-race have been present in Colo. for many thousands of years. The hostplant has been in Colo. for many million years, as *H. l. americanus* fossil leaves have been found in Oligocene shale at Florissant Colo. Because C. humulus is closely related to eastern whitish taxa such as C. neglecta, it probably entered Colorado from the east. The progenitor could have reached Colo. during peak glaciations when the great eastern deciduous forest reached the foothills; in this scenario, the C. humulus progenitor also evolved into the present eastern Prunus serotina gall feeder. Alternatively, the progenitor may have arrived along one of the river corridors such as the South Platte River. At a plains population of C. humulus, hop vines grow on floodplain bushes and small trees as noted below. At the end of the Ice Age, hop was probably present all along plains rivers (even along the South Platte River in Nebraska where it is now absent) and so the progenitor of C. humulus may have spread along the river floodplain then to Colorado.

**HABITAT.** C. humulus hop-race is very local, and only occurs where Humulus grows, generally only at the edge of gulch bottoms, mainly in sunny rocky/steep areas, because the hostplant grows well on rockslides (although one site is a plains riverside floodplain, and one mountain site is a nonrocky brushy area beside a stream). In the mountain foothills, the hop vines grow on large rocks, such as a talus slope next to a gulch bottom, and on shrubs of *Prunus americana*, *P. virginiana*, Crataegus macracantha, and sometimes Acer glabrum, Prunus pensylvanica, Physocarpus monogynus, Ribes inerme, Rhus glabra, Corylus cornuta, Ribes cereum, Salix monticola, Salix exigua, and Cercocarpus montanus, and on lower plants including Carduus nutans, Rhus toxicodendron, Rubus idaeus, Conium maculatum, Bromus inermis, Agropyron repens, Lactuca serriola, Urtica dioica gracilis, Dactylis glomerata, Solidago canadensis, etc.; on the plains, the hop vines grow on top of floodplain plants (mostly shrubs and short trees) including Salix exigua most often, but also on Prunus americana, Acer negundo, Salix ligulifolia, Ulmus sibirica, Alnus tenuifolia, Asparagus officinalis, Sambucus canadensis, Rhamnus cathartica, Cornus sericea, Thalictrum dasycarpum, Glycyrrhiza lepidota, Helianthus nuttalli, Apocynum cannabinum, Agropyron repens, Rhus toxicodendron, Ranunculus macounii, Polygonum coccineum, Rubus idaeus, Bromus inermis, and Parthenocissus quinquefolia. In short, the hop vines will grow over nearly any plant, but are abundant only on talus or rather dense bushes. In contrast, C. ladon sidara occurs on wooded north-facing slopes (from the gulch bottom to the ridgetop).

**REARING STUDIES.** Prior to about 1990, Scott thought that *C. humulus* hop-race was just a variety of *C. argiolus*, because all the wing pattern and hostplant differences between it and *C. ladon sidara* could possibly be environmental: *C. humulus* hop-race resembles the eastern U.S. *C. neglecta*, and several E. U.S. workers (William Henry Edwards and Charles Oliver) have reared form "*neglecta*" from form *C. l. ladon* form "*violacea*". Also, mature-larval color pattern of *C. humulus* hop-race and *C. ladon sidara* are similar in Colo. (Tables 1, 3). Scott once thought that *C. humulus* hop-race and *C. ladon sidara* are similar in Colo.

humulus hop-race develops from eggs laid by early-emerging C. ladon sidara, with most of the pupae of both forms (except for the early "violacea") hibernating. But in 1991 a late spring resulted in both flights overlapping much more than usual, with only a week or two average difference, obviously a time far too short for one to produce the other. Again in 1995, the very late spring pushed the end of the sidara flight into the C. humulus flight. There is almost never enough time in nature for the earliest C. ladon sidara larvae to grow on Jamesia americana flowers and pupate in time for the C. humulus hop-race flight; both have just one yearly generation (considerable time has been spent at C. humulus hop-race sites and nearly all adults have been found during June to July 2, except rare adults occur in late May and early July, and two whitish adults found in early Aug. in El Paso and Pueblo Cos. might be C. humulus). And Scott has now reared both C. humulus hop-race and C. ladon sidara in Colo., and nearly all the pupae of both forms hibernated at least in lab conditions, and all the C. humulus adults that emerged--even after refrigeration--were whitish and not like spring-form C. ladon sidara. Three lab rearings of C. humulus hop-race were done: 1973 pupae were not refrigerated and several adults with unh even whiter than usual emerged from pupae in early Aug. while most pupae stayed in diapause and never emerged; 1987 pupae diapaused and did not produce adults; 1989 pupae were refrigerated and about half produced adults of normal white appearance ~6 weeks after removing them from refrigeration in early Jan. and the remaining pupae did not produce adults. And the two rearings described above in Pupal Development and Flight Period showed that the C. humulus flight period is later because of delayed emergence from the pupa.

EARLY STAGES: EGG pale bluish-green, becoming greenish-white. FIRST-STAGE LARVA slightly-yellowish cream (slightly yellower when fatter), prothoracic shield cream, D2 short, posterior L seta half the length of other L's; head black. Wright found that 1st-stage larvae of Colo. C. ladon sidara and C. humulus hop-race are very similar, except two setae (D2 and the most posterior abdominal L seta) average slightly longer in C. humulus hop-race than in Colo. C. ladon sidara. MATURE LARVAE (see the CD-ROM photo in Scott 1997) have a darker middorsal band and a darker subdorsal oblique band on prothorax that edge a dark-filled paler triangle (some green larvae have prothorax green on top with a middorsal greenish-white patch), a middorsal darker band (consisting of large square spots on T2-3-A1, anteriorly-directed smaller triangles on A2-6 (or rectangles on A2-3), a variably-shaped spot on A7, a band on A8-10), on each segment a paler dash beside the middorsal band, then a darker slightly oblique streak or dash (sometimes faint, so that a large pale spot is formed of the adjacent pale dashes), then a strongly-oblique pale streak, below it a dark streak (varying to black in the darkest larvae), then a weak pale spot or short dash, a darker area, and a lateral pale band along the larva; head brown. But the overall larval color varies between larvae from yellowish-green to blue-green to green with cream marks and brown middorsal band to brown with cream or yellow markings to brownish-red with cream markings (Table 1); the variation is continuous from the paler to browner larvae, and all the variants except the reddest larvae were reared from Red Rocks in 1973, yellow-green to reddish larvae were reared from Apex Gulch and Chimney Gulch in 1989, but only green larvae were reared from Red Rocks and Apex Gulch in 1987 (probably due to small 1987 sample size). Yellowish-green larvae with whitish marks are most common. Mature C. humulus hop-race larvae are similar in color pattern to C. ladon sidara, and show the same continuous variation from mostly-green to mostly-brown larvae, so we are not sure that mature larvae differ in color pattern; the small differences between larval variants shown in the tables may be due to small sample sizes. Mature larvae are variable, but the variation in both Celastrina species occurs mostly along one green-to-brown gradient, so Celastrina larvae are much less variable than Strymon melinus larvae. PUPA (see the CD-ROM photo in Scott 1997) mottled slightly-reddish brown (on head, thorax and wings, and abdomen, though top of abdomen is usually a little paler), a middorsal dark-brown band on thorax and abdomen (thicker on abdomen), a black spot on shoulder of wing, a subdorsal black spot on T3 (small), A1 (large, adjacent to that on T3), A2 (tiny or absent), A3 (small), A4 (larger, twinned), A5 (large, twinned), A6 (largest, twinned)(some pupae have these subdorsal black spots mostly absent except moderate in size on A1, A5-6); as emergence nears, the eyes and proboscis tip turn black before the rest of pupa. C. humulus hop-race pupae apparently show a real difference from C. ladon sidara pupae, because they are more uniformly mottled brown (thorax and abdomen are more similar in color) and the wings are slightly more translucent brown (C. ladon sidara pupae have a darker top of thorax contrasting with paler [ochre] abdomen & wings), even when one accounts for the darkening with age, although the difference is not enough to identify all pupae. In addition, the C. humulus blackish subdorsal spots on rear of abdomen average larger in size and are sometimes touching on adjacent segments, though they vary greatly in size and are small on some pupae. Pupae hibernate.

**MYRMECOPHILY**. Older larvae are tended by ants. Ant workers of *Formica podzolica* at Red Rocks, and *Tapinoma sessile* at Red Rocks, Apex Gulch, & Coal Creek, were found on larvae present on male *Humulus* flower buds.

**ADULT BEHAVIOR.** Males patrol the hostplant in gulches all day to seek females. Males often visit mud, and may wander as far as 50 m to find it, and both sexes visit various flowers including the cream flowers of *Jamesia americana*. A female was noted to feed on the honeydew of leafhoppers on the underside of *Lactuca serriola* leaves. Adults are rather local: males fly more than females, which often rest for long periods near or on the host, and occasionally fly to oviposit.

Male adults have been found up to 100 m from the host during apparent mate-locating behavior. One female was caught by a robberfly.

#### Celastrina humulus, LUPINE-RACE (Figs. 11-16)

**DIAGNOSIS**. In two adjacent drainages in the foothills of the Front Range of Colo. (Turkey Creek and Deer Creek, Jefferson Co.), the hostplant is *Lupinus*, not hop. Adults appear identical to the hop-race (Figs. 11-16), and show similar variation in amount of blue on ups of females and in amount of black maculation on uns (compare Figs. 14 to 15), and electrophoresis done by Wright on adults prove that this host race belongs to the same named taxon as *Celastrina humulus* hop-race. However, its host preference seems to differ genetically. It flies in non-rocky, mostly-wooded valley bottoms, and overlaps the end of the *C. ladon sidara* flight. A few adults during this overlap have been found that are hard to identify as either taxon, but doubtfully are hybrids. Two males were found with slightly enlarged blackish spots in the middle of ventral hindwing (Fig. 16), without forming a real form "*lucia*" patch which is absent in this species.

**FLIGHT PEŘIOD**. Adults of the lupine-race also fly during June (many records June 1-July 2), peaking from early to late June depending on the year, and rare adults fly as early as May 17 and 21, and as late as July 15, 21, 22, 26.

**HOSTPLANT**. The only host is *Lupinus argenteus* white-flowered variety (though the flowers were bluish-white at one site). *Humulus* is absent at all sites. This *Lupinus* variety has white flowers with no banner spot and plane (non-folded) leaves that are glabrous (except for a few hairs ventrally) and are widest 2/3-3/4 from leaf base to tip (the variety is not *ingratus*, which is described as having white flowers but with a banner spot and folded glabrous leaves); this var. is not widespread, but seems to occur on deep valley-bottom soil. The usual widespread *L. argenteus* variety has light blue flowers and leaves V-shaped in cross section (folded) that are widest in the middle, and the leaf uppersides are glabrous or sometimes somewhat hairy; that usual variety prevails on ridges and S-facing slopes at Tinytown and elsewhere, implying that flower color could possibly be influenced by soil (the deep valley bottom soil producing white flowers, the thinner rockier slope soil producing blue flowers); but the current taxonomic nomenclature of *L. argenteus* is too preliminary to be sure.

24 ovipositions were found, at 10:03, 10:04, 10:51, 11:10, 11:20, 11:22, 11:35, 11:39, 11:53, 11:55, 11:57, 11:58, 12:17, 12:18, 12:20, 12:22, 13:20, 13:42, 14:03, 14:10, 14:11, 14:43, 14:50, and 15:06 (24 hour standard time)(most at Tinytown, but two were seen S and SE of Deermont which is S of Phillipsburg), and 201 eggs, 15 older larvae, and one prepupa (silked to underside of leaf near inflorescence) were found, all on *Lupinus argenteus* white-flowered-variety (except the plants SE of Deermont had bluish-white flowers).

Ovipositions were seen on two other plant species, but neither seems likely to be anything more than an occasional hostplant. Two ovipositions were seen at Tinytown on *Trifolium repens* young flower heads at 10:30 & 10:47 (she landed on immature *Trifolium* head 3 cm from *L. argenteus* white var. and laid egg, then ignored 2 more *Trifolium* heads, then oviposited on *Trifolium* head about 12 cm from *Lupinus*). About 60 *T. repens* heads searched nearby had no eggs, and no eggs were found on other plants within a few meters including *Astragalus flexuosus* and *Physocarpus monogynus*, so these ovipositions were merely unusual behavior by one female. Also at Tinytown, one female oviposited three eggs on *Verbascum thapsus* (Scrophulariaceae) flower buds (on inflorescences 3, 3, 2 cm long) at 10:25, 10:29, and 10:30, while she ignored *Anemone cylindrica* flower buds (the inflorescence of which somewhat resembles *Lupinus*) and ignored inflorescences of *Solidago* and other nearby plants; and five young eggs were found on flower buds of five nearby (within 8 m) *V. thapsus* plants (the inflorescences 4, 6, 5, 3, 4 cm long); however 88 other *V. thapsus* plants searched at this locality had no eggs, so all these eggs were obviously laid by that one female who had developed a search image for *Verbascum; V. thapsus* may not successfully support larval growth, because three weeks later these inflorescences were carefully examined and no trace of larvae or larval feeding damage was found.

To conclude, females seem to be host-specific to *Lupinus argenteus* white var., and never showed much interest in any other plant, except for the rare ovipositions on *Trifolium repens* and *Verbascum thapsus*, which are obviously just occasional hosts at most. Thus *C. humulus* lupine-race seems to have genetically adapted to this *Lupinus* host despite occurring only about 2 km west of where *C. humulus* hop-race probably occurs. Nearly all eggs were laid on *Lupinus* young flower buds, few on leaf buds near inflorescence, rarely on leaflet uns near base of leaflet; females refuse to oviposit on older *Lupinus* inflorescences 4 cm or longer. Older larvae were found on seedy *Lupinus* inflorescences or on drying pods.

*Lupinus argenteus* is a very common and widespread plant, although the white-flowered variety is local, so this lupine host race should be widespread, but the butterfly has been found so far only in an area 12 km long consisting of two fairly-lush north-south trending canyons in southern Jefferson Co. Colo., while adjacent areas have more-rugged east-west canyons and lack the abundance of this lupine race; exploration of lupine-rich similar habitat southward in Douglas Co. (where most sites had blue-flowered lupines, but one site had whitish flowers) failed to find the butterfly.

EARLY STAGES. EGG pale-bluish-green like all *Celastrina*, becoming greenish-white, sculpturing gives the appearance of conspicuous knobs all over egg in oblique view (each knob resembles an octopus body with ridges radiating outward like arms), but dorsal view shows craters on top (all Colo. Ĉelastrina have the same egg sculpturing). FIRST-STAGE LARVA yellowishcream (yellower when fatter), with a touch of greenish dorsally (bluish-green on T1), D2 short, L3 short but perhaps longer than C. ladon sidara, similar to C. humulus hop-race. HALF-GROWN-LARVA yellowish-cream (heart band darker green, slightly paler edging of heart, 3 oblique palergreen dashes between heart & side, lateral band paler green; or larva cream-green (heart slightly darker), some larvae pale green with cream dashes (beside dark heart & the obliques & lateral band), one larva cream-green with weakly-pink heart-band. MATURE LARVAE (Table 2) more variable than half-grown larvae (like other Celastrina): one larva green with gray heart-band and the usual lines (edging heart, 3 obliques, lateral ridge) are paler green; one larva is also green but differs by having the heart-band brownish-gray (the band's edging and the upper obliques are greenish-cream); four larvae are yellow-green with heart-band reddish-brown, the paler lines yellow-cream (cream edging heart, upper two obliques cream, lower one oblique pale green, lateral ridge cream), and one of the four yellow-green larvae has a dark reddish-brown acute triangle flaring laterally from the top of the front of A1 (one of these five, with green supralateral areas and very creamy obliques beside the heart, appears fairly similar to the most common C. humulus hoprace form); one larva (prepupa) has the red more widespread on top of body. On average, more larvae are creamy (creamy-green) in color than in other Celastrina host races, esp. half-grown larvae most of which were greenish-cream; however if 100 rather than 10 larvae had been reared, various brown forms etc. may have been found, so we cannot say conclusively that the larvae differ in color from other Celastrina. PUPA brown on head & thorax, warm orange-brown on wings & abdomen, a middorsal brown band (blackish on T1, weak T2, formed of dashes on abdomen), subdorsal blackish spots (small on wing base, small on T3, large on front of A1, in pairs [one above & in front of other] on A2-6 [spots rare on A2], largest on A4-6 where the pairs are fused into one large spot), subspiracular blackish dots on A5 and sometimes A6, (these abdomen spots are small on most pupae but were very large on one pupa which in addition had giant blackish subspiracular patches on A5-7 and blackish dashes on A5-6 just lateral to midventral axis), eyes & antenna clubs blackish-brown; attached to substrate by cremaster and a silk girdle at rear of A1. Pupae the same as *C. humulus* hop-race, but some hop-race pupae are orange-brown on front of abdomen and have middorsal brown band usually darker (but only six *C. humulus* lupine-race pupae were reared so these differences may be just individual variation). Thus the thorax and abdomen of the two *C*. *humulus* host-races are more similar in color than *C*. *ladon sidara* pupae, and the blackish subdorsal abdominal spots are often large (they are gigantic on one pupa, rather large on two, small on three). Pupae hibernate.

This second species of Colorado *Celastrina* should be called *ladon* ssp. *sidara* (Clench), type locality Manitou, El Paso Co., Colorado.

**DIAGNOSIS**. Adults fly in a single-spring generation, the male upperside is solid blue to slightly violet-blue by comparison with other whitish *Celastrina* taxa, and the underside is gray to gray-white (generally darker than *C. humulus*, see Figs. 19-24) with small distinct black marks (form "*violacea*"), though the few adults that have larger black unh markings (including form "*lucia*", see below) seem to prove a past link of the taxon to Canadian *C. ladon lucia*. Adults occur basically on north-facing slopes, unlike *C. humulus*, and the usual host is the shrub *Jamesia americana*. Electrophoresis of adults (from Red Rocks, Jefferson Co. Colo.) by Wright and Gordon F. Pratt proved that *sidara* is a rather distinct taxon, rather distant from *C. humulus* and from the eastern whitish taxa, and most similar to boreal N. Amer. *lucia*.

**FLIGHT PERIOD**. Adults fly in a single generation, mostly during May, peaking in mid May or later in May, extreme records being April 14 to June 27 and rarely even July 7, all records after mid June being from high altitude (9000-10,000 feet).

HOSTPLANT(S) AND HABITAT. Hostplants were proven at W Deckers, Phillipsburg, Tinytown, Mt. Lindo, Falcon County Park, W Idledale, Red Rocks, Apex Gulch, Mt. Zion, Crawford Gulch, Tucker Hill, Van Bibber Creek, Ralston Buttes, all Jefferson Co. Colo.; at Stove Mtn., ~10,000 feet, El Paso Co. Colo.; at Russel Ridge, Douglas Co. Colo.; and at N fork Clear Creek, Gilpin Co. Colo. 14 ovipositions were seen, at 9:47, 10:27, 10:35, 10:36, 10:38, 10:48, 11:16, 11:29, 11:46, 11:54, 12:07, 12:15, 12:28, 12:29, 12:34, (all 24-hr. standard time), and many eggs and larvae were found as noted below (detailed records are in Scott 1992 except for recent records). By far the main host is *Jamesia americana* (a shrub, Saxifragaceae or Hydrangeaceae) flower buds: 10 ovipositions (including two by form "marginata", one by form "lucia") were seen, and 176 eggs, 15 young larvae, and about 40 older larvae were found on J. americana flower buds at many sites and dates. Two ovipositions and 7 eggs were found on Holodiscus dumosus unopened flower buds. One oviposition and 3 eggs were found on Cornus (Swida) sericea (*=stolonifera*) flower buds, and one half-grown larva was found on *C. sericea* growing fruits. Three eggs were found on *Physocarpus monogynus* inflorescence. One oviposition (by form "marginata") and two eggs were found on Prunus (Padus) virginiana melanocarpa inflorescence (and in Nebraska at Sowbelly Can., Sioux Co., May 17-18, 1994, a female of form lucimargina fluttered about P. virginiana upper leaves with many 4 mm by 1 mm galls protruding from leaf tops but did not oviposit, and 2 males were found near P. virginiana; all other records for sidara are from Colo.). One oviposition was seen on Ceanothus fendleri flower buds (two females repeatedly landed on C. fendleri flower buds whereas other females ignored this plant, indicating possible learning of hostplant). One egg was found on *Humulus lupulus americanus* (=neomexicanus) inflorescence (identified as *sidara* because it was weeks earlier than the *C. humulus* flight there). No eggs were found on inflorescences of Rubus (Oreobatus) deliciosus, Aquilegia sp., Crataegus sp., Acer glabrum, a white-flowered Apiaceae sp., Smilacina racemosa var. amplexicaulis, Amelanchier alnifolia, Lonicera involucrata, or Achillea lanulosa. Larvae of some taxa of North American *Celastrina* eat many plant species of numerous families, at least on an occasional basis, and females oviposit only on plants in the proper flower bud stage; so the plants oviposited on change as the season progresses. But in Colorado Jamesia americana is by far the most common host for C. ladon sidara, which has adapted nearly exclusively to it (only one generation occurs in Colo., so there is no adaptation to later-blooming hosts). This adaptation is very obvious, as the butterfly's altitudinal range (foothills to upper Montane Zone) and microdistribution (the butterfly occurs only on wooded north-facing slopes, from gulch bottoms to ridgetops on the N-slopes, except for occasional strays) both match that of J. americana (which also occurs only on N-facing slopes from just above the gulch [and sometimes in a shaded gulch] to just below the ridgetop), and the time of flight of the butterfly perfectly matches the budding time of the plant. Jamesia is an ancient plant, so this host relationship could be quite old: Jamesia caplani is fossilized in volcanic ash near Creede, Colo. The other hosts (Holodiscus dumosus, Cornus sericea, Physocarpus monogynus, Prunus virginiana melanocarpa, Ceanothus fendleri, and Humulus lupulus *americanus*) are chosen only rarely (note that they all have multiple flowers in a tightly-packed cluster as does Jamesia, a requirement for most Celastrina to supply enough flower buds for the larva to grow to maturity). Cornus is a popular Celastrina host in E U.S. and Calif., but the plant is rare in Colo. and is seldom chosen even where it occurs.

**GENETIC FORMS AND REARING STUDIES.** The forms of *C. ladon sidara* (Figs. 19-24) are distributed in an interesting manner in Colo.-N.M.: form "*violacea*" (unh has only small blackish marks, Figs. 19-20) is everywhere, but forms "*lucia*" (unh has a central blackish blotch, Fig. 22), "*marginata*" (unh has blackish marginal band but not central blotch, Figs. 21, 23), and "*lucimargina*" (unh has both central blotch and marginal band, Fig. 24) occur only south to Jefferson Co. on the eastern slope of the continental divide (where they are uncommon; less than two dozen "*lucia*" have been found in Jefferson Co. out of more than a thousand adults seen (Fig. 22); in El Paso Co. the closest adults to "*lucia*" that Scott has found are two with slight enlargement of central dots on only one hindwing); in contrast, these three forms are very common on the wetter

western slope of the continental divide (common south to the San Juan Mts., even into NW New Mex. near Dulce Lake, Rio Arriba Co.), where the black unh blotch of form "lucia" and "lucimargina" is often extremely large (4.5 mm long, the largest Scott has seen anywhere in N. Amer., Fig. 24). In Delta Co. Colo., for instance, nearly half the adults have the "lucia"-patch (the patch often very large), and nearly all have the "marginata"-margin (Fig. 23), thus about half the population is form "marginata", half the population is form "lucinargina" (Fig. 24), and a few adults are form "lucia" (with the central patch but without the dark margin). Evidently the wetter conditions on the western slope cause this difference. Form "lucia" is also common in C. ladon sidara in the Pine Ridge in NW Nebraska (C. neglecta also occurs there). Forms "marginata" and "lucia" are obviously the same species as form "violacea", as they fly together at the same time and in the same habitats, have the same hostplant (ovipositions were seen by "marginata" and "lucia" on Jamesia), and are connected by numerous adults intermediate in wing pattern. Scott once thought that a form "neglecta" (whitish adults that mistakenly emerge in midsummer) occurred--rarely--within populations of Colo. C. ladon sidara, based on two whitish adults (1 female Little Fountain Creek, 7000', El Paso Colo. Aug. 9, 1971; 1 male 4 mi. S Beulah, Wet Mts., Pueblo Co. Colo. Aug. 4, 1962) that he thought were a form of C. ladon sidara instead of C. humulus (which they also resemble); however, Scott has not been able to rear whitish adults from C. l. sidara in the lab, so these two adults may actually be C. humulus. One deformed male resembling form "violacea" (the underside gray with distinct spots) was found very late in the season Aug. 15, 1986, at O'Fallon Park, Jefferson Co., Colo. (only "violacea" occurs at this site), which could suggest that form "violacea" is genetic. Also, several reared 1988 pupae of "violacea" produced deformed adults in the lab in Aug. (most pupae diapause and do not hatch even in the lab) which also resembled "violacea" instead of a whitish summer form or C. humulus (in contrast, lab C. humulus hop-race produced very-whitish C. humulus adults), which also seems to indicate that "violacea" is genetic. It is tempting to claim that the wing pattern differences between the two are genetic, because in Scott's lab rearings "violacea" always produced grayish "violacea" and C. humulus hoprace always produced whitish C. humulus hop-race (and the lack of seasonal forms in Calif.-Ariz.-W Texas Celastrina seems to indicate that the absence of form "violacea" in those whitish populations is genetic). However, Scott's lab rearings merely used the environment of a basement rather than carefully-controlled environmental chambers, and in E U.S. Edwards and Oliver have raised the whitish summer form from one taxon (reported as form "violacea", but the exact taxon is uncertain). But it is possible that only one or two eastern U.S. taxa have the capacity to produce environmental forms, whereas these forms are genetically fixed in the other North American taxa including both Colo. taxa; but this will have to be proven.

EARLY STAGES: EGG pale bluish-green, becoming greenish-white. FIRST-STAGE LARVA yellow-cream (slightly yellower than C. humulus hop-race and C. humulus lupine-race), with a faint darker-yellow middorsal band, after feeding turning greenish inside, prothoracic shield yellowcream, D2 very short or short (apparently averaging shorter than C. humulus), L3 short (apparently averaging slightly shorter than C. humulus); head black. MATURE LARVAE (see the CD-ROM photo in Scott 1997) have a darker middorsal band and a darker oblique band on prothorax, a middorsal darker band (consisting of large square spots on T2-3-A1, anteriorly-directed smaller triangles on A2-6 [or rectangles on A2-3], a variably-shaped spot on A7, a band on A8-10), on each segment a paler dash beside the middorsal band, then a darker slightly oblique streak or dash (sometimes faint, in which case a large pale spot is formed of the adjacent pale dashes), then a strongly-oblique pale streak, below it a dark streak (varying to black in the darkest larvae), then a weak pale spot or short dash, a darker area, and a lateral pale band along the larva; head brown. But the overall larval color varies between larvae, from yellow-green (only 1 larva seen) to bluishgreen (only 1 larva seen) to pale-green to green to green with tan middorsal band to green with maroon-and-white markings to brown with white markings (only 1 larva seen)(Table 3); the variation is continuous from the paler to browner larvae, and all the variants except the extremes are common. Greenish larvae are most common; the larvae are generally less yellow-green than C. humulus hop-race. PUPA (see the CD-ROM photo in Scott 1997) abdomen & wings ochre (paler than C. humulus hop-race), head and top of thorax mottled dark-brown (in C. humulus hop-race the head, thorax, and abdomen are all mottled slightly-reddish brown with the top of abdomen only slightly paler), a middorsal dark-brown band on thorax and abdomen, a black spot on shoulder of wing, a subdorsal black spot on T3 (small), A1 (big; these two spots are adjacent), A3 (tiny), A4 (small, twinned), A5 & A6 (twinned, large in some pupae, tiny in others); as emergence nears, the eyes and proboscis tip turn black before the rest of pupa. Pupae differ from C. humulus hop-race by having the abdomen (& usually the wings) usually paler (C. humulus hop-race has thorax more similar in color to abdomen & wings), thus the top of thorax looks darker, though the difference is not enough to identify all pupae. In addition, the blackish subdorsal spots on rear of abdomen seem to average smaller in size, because they are usually rather small (though they are also small in some C. humulus). Pupae hibernate.

**MYRMECOPHILY**. Older larvae are tended by ants: workers of *Camponotus modoc*, *Formica podzolica*, *F. neorufibarbis*, and *Tapinoma sessile* were found on larvae on *Jamesia* inflorescences at Tinytown.

**ADULT BEHAVIOR**. Males patrol north-facing slopes (from the gulch bottom to the top of the slope) all day to seek females. Males often feed on mud. Both sexes visit various flowers including *Jamesia americana*, *Arctostaphylos uva-ursi*, etc.

## ACKNOWLEDGEMENTS

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 Table 1. Mature larvae of Colo. Celastrina humulus hop-race.

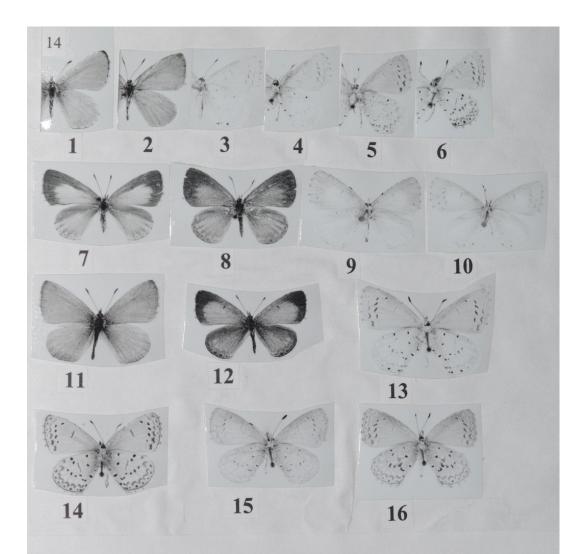
Overall Color	Ground Color	Mid- dorsal Band	Subdorsal & Obliques	Lateral Band	Edge of Laterals
brownish- red & tan (prepupa)	light reddish- brown	dull red	reddish-tan & dark red-brown	reddish-tan	brownish red
red-brown & cream	light brown	red- brown	cream & dark red-brown	tan	light brown
brown & yellow	grainy- brown	maroon- brown	yellow & brown (black below)	yellow	brown
brown & cream	brown- ish- green	brown	greenish-cream & brown (black below)	greenish- cream	green- ish- brown
olive- green, yellow, red-brown	olive green	red- brown	light-yellow & brownish- green	light dull yellow	greenish brown
green, cream, brown	green	maroon- brown	cream and green (dark- green below)	yellowish- cream (maroon- brown at rear of each segment)	green
light- green & brown	light- olive- green	maroon- brown	light-olive- green & brown	brownish-green	tan
light- yellow, maroon- brown	light- olive- green	maroon- brown	light-yellow & light- green (dark- green below)	light-yellow	light- olive- green
green, cream, brown	pale- green	chestnut -brown	cream & tan (dark-green below)	cream	tan
green & white	green	brown- green	white & green	white	light- green
pale-green	0	dark- green	pale- green	pale- green	green
blue- green	blue- green	dark- green	light-green & blue-green	tan-green	
green & greenish- yellow		green	greenish- yellow (or yellow) & green	greenish- yellow (or yellow)	green
blue- green & yellow (prepupa?)			light-yellow & blue-green		

Tuble 2. Mature fai vae of Colo. C. manatus fapilie face.							
Overall Color	Ground Color	Middorsal Band	Subdorsal & Obliques	Lateral Band	Edge of Laterals		
green, faint lines	green	gray	paler- green & green	paler- green	green		
green, weak lines, gray heart	green	brownish- gray	greenish-cream (lower obliques green) & green	green- ish cream	green		
yellow- green, brown heart	yellow- green	red- brown	yellow-cream & olive-green	yellow- cream	yellow- green		
green, yellow, red band	green	brownish- red	yellow-cream & olive-green	yellow- cream	green		
yellow- green, cream, red	yellow- green	reddish	yellow-cream & yellow- green	yellow- cream	yellow- green		

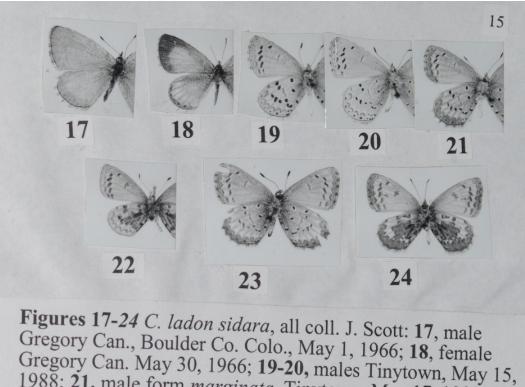
12 **Table 2.** Mature larvae of Colo. *C. humulus* lupine-race.

 Table 3. Mature larvae of Colo. Celastrina ladon sidara.

Overall Color	Ground Color	Middorsal Band	Subdorsal & Obliques	Lateral Band	Edge of Laterals
red- purple	red- purple	dark red- purple	pink	pink	red- purple
red-purple with pink lines	red- purple	purple- red-	pale-pink	pale-pink	red- purple
brown & white	green- ish- white	maroon- brown	white & - slightly maroon (black below)	tan-white (rear of each segment maroon)	pale- maroon brown
green, maroon, white	dark- green	maroon	white & maroon	white (reddish on rear in 1 of 2 larvae)	pale- green
green with maroon & cream	green	maroon- brown	cream & green	cream	pale- maroon
light-green with maroon & cream	pale- olive- green	maroon	greenish-white & pale- olive-green	greenish- white	trans- lucent- pale- maroon
brown, white, green	dark- green	brown	brownish-cream & tan (black below)	brownish- cream	tan
green with brown middorsal	green	brown	greenish-cream & green	greenish- cream	green
green with light-brown middorsal	green	light- brown	light-green & green	light-tan- green	green
mottled bluish- green	pale- blue- green	tan	pale-blue- green & blue-green	slightly- tan-blue- green	pale- blue- green
mottled- pale- green	whitish green	tan	greenish-white & green	greenish- white	green
mottled- green	green	green	pale-green & green	yellow-green	green
green	green	dark-green	lighter-green	lighter-green	green
mottled- yellow-green	yellow- green	dark- green	yellow-green & dark-green	yellow-green	dark- green
mottled- greenish- gray (prepupa?)	green- ish- gray	gray	gray & creamy- gray	creamy-gray	gray



Figures 1-16 Celastrina humulus, all coll. J. Scott. Figs. 1-10, C. humulus hop-race: 1, male HOLOTYPE Red Rocks, Jefferson Co. Colo., June 14, 1973; 2, male Mother Cabrini Shrine, Jefferson Co. Colo., June 24, 1980; 3, male Red Rocks, Aug. 19, 1973; 4, male Mother Cabrini Shrine, June 12, 1980; 5, male SW Morrison, Jefferson Co. Colo., June 11, 1988; 6, heavilymarked male Apex Gulch, Jefferson Co., emgd. Jan. 2, 1990; 7, female Coal Creek, Jefferson Co. Colo., July 1, 1986; 8, female Mother Cabrini Shrine June 24, 1980; 9, female Coal Creek, July 1, 1986; 10, female ALLOTYPE Red Rocks, June 24, 1973.
Figs. 11-16, C. humulus lupine-race, all Tinytown, Jefferson Co. Colo.: 11, male June 24, 1990; 12, female June 24, 1990; 13, male June 2, 1989; 14, heavily-marked male June 4, 1994; 15, female June 24 1990 (oviposited on Lupinus); 16, female (showing the closest to form lucia that exists in C. humulus) June 4, 1994.



1988; **21**, male form *marginata*, Tinytown, May 17, 1988; **22**, male form *lucia* (largest patch known from Front Range), Mt. Falcon, Jefferson Co. Colo., June 5, 1997; **23**, male form *marginata* Surface Creek Delta Co. Colo. May 14, 1984; **24** male form *lucimargina* with largest patch I have seen in Colo., Surface Crk., May 22, 1984.