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#### Abstract

A combination of five characters supports the arrangement of three species in the Anthocharis sara complex (Lepidoptera: Pieridae: Pierinae: Anthocharidini) consisting of Anthocharis sara Lucas, 1852 (Sara orangetip), Anthocharis thoosa Scudder, 1878 (southwestern orangetip), and Anthocharis julia W.H. Edwards, 1872 (Julia orangetip). These five characters include adult phenotypes, fifth instar larval coloration, pupal cone curvature and color, number of overwintering cycles, and interspecific contact zone behavior. This taxonomic treatment is generated from extensive life history studies from 12 western U.S. states through most of the sara complex distribution.


Key words. Sara orangetip, Anthocharis thoosa, Anthocharis julia, caterpillar, pupae.

## Introduction

Over the last half century, there have been several interpretations regarding the number of species in the Anthocharis sara complex ranging from one to four. These interpretations have primarily depended on adult wing characters. This paper will review five separate characters of adult phenotypes, fifth instar larval coloration, pupal cone curvature and color, number of overwintering cycles, and interspecific contact zone behavior to support the arrangement of three species-level taxa- Anthocharis sara Lucas, 1852, Anthocharis thoosa Scudder, 1878, and Anthocharis julia W. H. Edwards, 1872.

Historical review. The initial impetus for the reexamination of the sara complex was provided by Geiger and Shapiro (1986) wherein the taxa Anthocharis sara and Anthocharis stella W. H. Edwards, 1879 (Stella orangetip), were shown to represent distinct species and it was suggested that A. julia was also a distinct species. Subsequently, Opler (1999) recognized four species within the sara complex ( $A$. stella, A. sara, A. thoosa, and A. julia). Opler's treatment is an expansion on Geiger and Shapiro (1986).

The Pelham catalogue $(2008,2017)$ currently places all named subspecies of the complex under $A$. sara pending further research which is the main purpose of this paper.

## Materials and Methods

Extensive rearing studies of 96 populations of all subspecies of the sara complex were performed between 1995 and 2016 to photograph fifth instar caterpillars, pupae, and adults. Photographic equipment included a Canon Rebel XTi and Canon EOS 60D with a $100-\mathrm{mm}$ fixed macro lens. Eggs were mostly obtained from field-collected gravid females. Eggs and larvae were also located in the field on mustards (Brassicaceae) including Descurainia pinnata, Walter, 1894, Guillenia lasiophylla Rydberg, 1923, Isatis tinctoria Linnaeus, 1753, Streptantella longirostris Watson, 1906, Cardamine californica Nuttall, 1891, Brassica nigra Linnaeus, 1833, Arabidopsis thaliana Linnaeus, 1842, Boechera hirsuta Linnaeus, 1772, Boechera holboellii Hornem, 1827, Boechera sparsiflora Nuttall, 1838, Boechera perennans Watson, 1887, Boechera retrofracta Graham, 1827, Boechera microphylla Nuttall, 1838, Turritis glabra Linnaeus, 1753, Boechera stricta Graham, 1829, and other unidentified species of Boechera (formerly Arabis).
Rearing methods. Species identification of pierid ova was facilitated in the field by three factors: Oviposition location, color of the freshly laid ova, and numbers of ova laid in close proximity. These
factors were helpful because Pontia sisymbrii Boisduval, 1852, Pontia protodice Boisduval and Le Conte, [1836], Euchloe ausonides Lucas, 1852, Euchloe olympia W. H. Edwards, 1852, Euchloe hyantis W. H. Edwards, 1871, Anthocharis cethura Felder and Felder, 1865, and Anthocharis lanceolata Lucas, 1852, share the same host plants with the sara complex at varying locations.

Females of A. sara, A. thoosa, and A. julia frequently lay eggs singly on the pedicels of rock cresses whereas females of $E$. hyantis, $E$. olympia, and $E$. ausonides usually oviposit on unopened flower buds. Contrastingly, females of $P$. sisymbrii prefer to oviposit one or multiple eggs on the lower leaves and stems. Similar to females of the sara complex, females of P. beckerii W. H. Edwards, 1871, P. protodice, and P. occidentalis Reakirt, 1866, also prefer to oviposit one or several eggs on host pedicels whereas sara complex females usually oviposit a single egg on a pedicel.

Freshly laid fertile ova of North American Pontia spp., Euchloe spp., and Anthocharis spp. change color from a lighter whitish, yellowish, or greenish hue to orange within 24 hours. First instar caterpillars generally hatch within four days in the lab and five days in the field (Guppy and Shepard 2001; James and Nunnallee 2011). Before turning orange, the color of freshly laid ova can also assist in species-level identifications. For example, fresh ova of sara complex are off white, E. hyantis are whitish light blue, E. ausonides and E. olympia are ivory white, P. sisymbrii are greenish yellow, and A. cethura are light yellow. In northern California, ova of A. lanceolata lanceolata are notably larger than those of $A$. sara sempervirens Emmel et al., 2008, or A. sara sara where both species utilize the same host plants.

Because of larval cannibalism, ova obtained from gravid females were hatched separately in small disposable restaurant cups and placed onto unopened inflorescence of either cuttings or potted host plant-mostly Isatis tinctoria and Boechera spp. Larvae feed rapidly and generally pupate within 15 days of hatching (James and Nunnallee 2011).

Labels with data were placed on host plants, pupal overwintering tubs, emergence containers, glassine envelopes with papered adults, and with pinned adults. Data from figures containing adult or early stages are found in Appendix 1. All rearing data has been recorded onto spreadsheets.

Pupae of the sara complex (specifically) and other genera of Papilionoidea (generally) do not require several months of natural summer warmth prior to overwintering. Most lab pupal overwintering occurred during natural winters either in a refrigerator or in a protected outdoor enclosure (Stout 2009). To encourage the breaking of diapause during a four-month overwintering cycle in the lab, pupae were placed in overwintering tubs (with screen lid) and misted with distilled water at least once a week for the last two months of the cycle, simulating a wet winter; and creating ideal conditions for eclosure even though some pupae extended diapause for multiple cycles. To accelerate the breaking of diapause of $A$. thoosa, the species in the complex with the highest proclivity for multiple overwintering cycles, pupae were sometimes overwintered twice during a calendar year between December and March (breaking diapause or not in April) and again between June and September (breaking diapause or not in October).

Attempts at captive breeding (placing multiple males with virgin females in a flight cage to obtain pairings) or hand pairing adults failed to produce any successful copulation during these rearing studies.

Material examined. The specimens examined during this study have been retained in the following collections: The Todd Stout collection, Ken Davenport collection, Jim Brock collection (JBC), Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah (BYU), and the McGuire Center for Lepidoptera and Biodiversity, Gainesville, Florida (MGCL). All adults and early stages shown in figures are retained in the Todd Stout collection, unless indicated otherwise in Appendix 1.

## Species Overview

The distribution of all subspecies of A. sara, A. thoosa, and A. julia is shown in Fig. 1. Intergradation between adjacent subspecies is not indicated for map clarity. Contact zones between species are shown through colored diagonal lines superimposing one species over another and discussed in detail in the interspecific contact zones section.

Anthocharis sara. Anthocharis sara is primarily a California endemic species with its distribution extending from the peninsular ranges of Baja California North including Cedros Island northward throughout cismontane Southern California through the Sierra Nevada northwest into extreme southwest


Figure 1. North American distribution of all subspecies of A. sara, A. thoosa, and A. julia.
Oregon (Emmel and Emmel 1973; Brown et al. 1992). The common name pacific orangetip which previously assigned subspecies A. s. flora W. G. Wright, 1892, and A. s. alaskensis Gunder, 1932, to A. sara is obsolete, as larval and pupal characters assign these subspecies to A. julia (Opler 1999).

Adults of A. sara from Cedros Island, BCN, are well illustrated in the Butterflies of America website and appear to be more phenotypically similar to southern California A. sara sara than A. sara gunderi Ingham, 1933, (Warren et al. 2017). San Diego County cismontane populations of A. sara sara can be found to the east in the western portion of the Colorado Desert through Anza Borrego Desert State Park into extreme western Imperial County, California.

Bivoltine populations of A. sara sara in southern California and A. sara gunderi from Santa Catalina and Santa Cruz Islands (Los Angeles County) have larger second brood adults with more faded ventral hindwing mottling than first brood examples (Emmel and Emmel 1973; Shapiro and Manolis 2007). Note: These second brood wing characters are also consistent with occasional second-generation A. thoosa inghami (Tom Kral pers. comm.) (Gunder, 1932), from Pima County, Arizona, (spring rains permitting) and more generally with other multivoltine pierids such as $P$. protodice, $P$. occidentalis, and $P$. beckerii. In all these species, adults emerging from non-diapausing pupae can be larger and have more faded ventral hind wing markings as compared to their respective early spring forms emerging from overwintered pupae.
A. sara sempervirens is reviewed in detail by Emmel et al. (2008) in the original description based upon the unique habitat of Redwood National Park coupled with some examples similar to the allotype female where the orange apical patch is replaced by yellow.
A. sara pseudothoosa (Austin, 1998), which has higher frequency of white females than nominotypical A. sara, is univoltine and flies in the White and Inyo Mountains of California to the east slope of the Sierra Nevada east towards the Sweetwater Mountains of Douglas County, Nevada, north past Lake Tahoe Region into Washoe County, Nevada (Austin 1998).

Based upon field observations and examined museum records, $A$. sara has produced more strays than A. thoosa or A. julia. Mark Walker and Brian Banker collected a second brood of A. sara sara in the Dead

Mountains of San Bernardino County, CA. (Walker pers. comm.). Paul Opler (pers. comm.) also provides a record of A. sara sara from Benton County, Oregon, in McDonald National Forest, approximately 130 miles to the north of established populations of A. sara sara in Josephine County.
Anthocharis thoosa. Anthocharis thoosa is mainly a denizen of pinyon juniper habitat of the Great Basin of Nevada and Utah (A. thoosa thoosa) as well as lower Sonoran Desert scrub of SE Arizona (A. thoosa inghami) transitioning to Oak Woodland habitat of central Arizona east to montane NW New Mexico (A. thoosa coriande Scott and Fisher, 2008) north through western Colorado (A. thoosa colorado Fisher and Scott 2008). Anthocharis thoosa thoosa also has been taken at higher elevations of mountainous regions of the Mojave Desert of Clark County, Nevada, and in the Kingston, Providence, New York, Clark, and Old Woman Mountains as well as at Mountain Pass, San Bernardino County, California (Emmel and Emmel 1973; Wikle pers. comm. 2008; Davenport pers. comm. 2009).

On occasion, $A$. thoosa can also be found in desert scrub habitat of the Mojave Desert where it poorly competes with P. beckerii, P. protodice, E. hyantis lotta Beutenmuller, 1898, and A. cethura mojaveensis Emmel et al., 1998, on annual mustards such as D. pinnata, G. lasiophylla, and S. longirostris. For example, an ovum of A. thoosa thoosa was found in Washington County, Utah, in typical A. cethura mojaveensis habitat of Navajo sandstone rock formations with Prunus fasciculata (Torr.) (A. Gray), Larrea tridentata (Dc.) Coville, and Yucca baccata Torr. where host plants were taking refuge under the creosote bush, in rocky outcroppings, or in desert washes. Also, an ovum of A. thoosa was found in lower elevation desert scrub habitat west of Christmas Tree Pass in the Newberry Range of Clark County, Nevada, where one would find A. cethura mojaveensis and E. hyantis lotta on wing in early March following sufficient and timely winter precipitation.
Anthocharis julia. The species with the most expansive distribution within the sara complex is $A$. julia as it frequents mountain canyons and forested riparian situations from mid-range elevations of the central Sierra Nevada (A. julia stella) east through the higher elevations of the Great Basin of northern Nevada and western Utah (A. julia sulfuris Pelham, 2008). Prior to the description of A. julia sulfuris, the distribution of A. julia stella was expansive from central California and western Nevada north and east through portions of several states and Canadian provinces discussed below in the current distribution of A. julia sulfuris (Pelham 2008).

Adult phenotypes of Northern Utah populations of A. julia suggest that A. julia browningi Skinner, 1906, is restricted to the Wasatch and Bear River Range (Cache County) and is surrounded in the state by populations of $A$. julia sulfuris both to the west in isolated, higher elevational forested habitat of the Great Basin as well as to the east of the Wasatch Range in the Uinta Mountains and southeast along portions of the Colorado Plateau.

In western Colorado, A. julia prestonorum Stout, 2012, flies on the west side of the continental divide and A. julia julia flies on the east side of the continental divide (Fisher 2012). Anthocharis julia julia can also be found to the north in SE Wyoming where a void is created in Wyoming's Red Desert (Warren pers. comm.). Anthocharis julia sulfuris is prevalent in northern and western Wyoming east to extreme western South Dakota extending northwest into Montana and western Alberta. From western Wyoming, A. julia sulfuris can also be found west throughout much of Idaho into eastern Oregon and eastern Washington east of the Cascade Range. Populations in Oregon and Washington, west of the Cascades north through portions of western British Columbia pertain to A. julia flora Wright, 1892. The extent of intergradation between A. julia sulfuris and A. julia flora in the Cascades is unclear (Hinchliff 1994, 1996; Pyle 2002) as adult wing, larval, and pupal characters are similar confirming these taxa as conspecific.

In British Columbia, the distribution of A. julia flora, A. julia alaskensis Gunder, 1932, and A. julia sulfuris, (as A. sara flora, A. sara alaskensis and A. stella, respectively,) is outlined through dot maps (Guppy and Shepard 2001). The distribution of A. julia flora includes Vancouver Island and southern coastal areas. The distribution of A. julia alaskensis also includes coastal areas of Central British Columbia north into extreme southern Yukon and northern portions of the Alaskan panhandle. In British Columbia, A. julia sulfuris flies more in the interior of the province southeast to southern Alberta (Bird et. al 1995).

Because of similar phenotypes, A. julia columbia Scott and Kondla, 2008, is treated as a junior synonym to $A$. julia sulfuris based upon priority (Pelham 2008). Adult topotypes of $A$. julia sulfuris from

Kellogg, Shoshone County, Idaho, have been collected and examined ( $n=23$ ). Kondla provided papered males and one female of A. julia from Waneta Dam and Charbonneau Creek, British Columbia, 32-36 aerial kilometers south of the $A$. julia columbia type locality which is located at Brilliant Creek, BC, in the west Kootenay area near Castlegar on the Columbia River. Although these adults are very similar to topotypical A. julia sulfuris, strict topotypes of A. julia columbia have not been examined.

## Adult Phenotypes

As mentioned, the historical treatment of the sara complex relied heavily on adult morphological characters to infer species level distinctions (Opler 1999; Scott et al. 2008). This is problematic because overlap in adult morphological characters of all three species make it challenging to identify wing traits exclusive to any single species. For example, all three species show variation which includes white to yellow dorsal wing colors, thin to thick dorsal and ventral discal cell bars, dorsal forewing black apical borders that either connect or disconnect with the dorsal discal cell bar, weak to strong dorsal hindwing black marginal spots, greenish to grayish ventral hindwing mottling, etc. These similar phenotypes are distributed randomly throughout the sara complex and are not regionally correlated except for $A$. julia nr . prestonorum and $A$. thoosa colorado, which are phenotypically similar and fly in near sympatry in SW Colorado. Examples of these similar individual variants are shown in Fig. 2.

Regional adult comparisons. Distinguishing species-specific adult wing characters is more reliable on a regional level where two species fly in or near sympatry. For example, Davenport (pers. comm. 2007), discussed the differences between A. julia stella and A. sara sara in central California, where A. sara males were dorsally white and A. julia stella males were off white with yellowish over scaling just above the dorsal hindwing marginal spots. Geiger and Shapiro (1986), also provided observations of both taxa at Donner Pass, Lang Crossing, and Castle Peak in the Sierra Nevada Range of California. Davenport (2007) also reviewed the distribution of A. sara sara, A. sara pseudothoosa, and A. julia stella (as A. stella stella) from Yosemite National Park and neighboring regions of central California and stated the possibility of intergradation between species and the need for further research.

Warren (2005) discussed the relationship among A. julia sulfuris, A. julia flora (as A. sara nr. stella and A. sara flora, respectively) and A. sara sara in Oregon. He observed notable variation in the ventral hindwing mottling of a long series of adults collected from Klamath River Canyon, Klamath County, where he suspected $A$. sara sara flies with $A$. julia sulfuris. This observation of two species flying in sympatry is supported through larval examination and is discussed in the interspecific contact zones section.

Austin (1998) discussed adult differences between A. sara pseudothoosa and A. thoosa thoosa (as A. sara thoosa) where $A$. sara pseudothoosa has a paler orange forewing apical patch, narrower discal cell bars that extend more narrowly to the outer margin that generally disconnect from the black apical border, and a lighter shade of ventral hindwing mottling as compared to $A$. thoosa thoosa.

Fisher (2012) provided an extensive overview of the adult differences in Colorado among A. julia julia, A. julia prestonorum, A. thoosa coriande and A. thoosa colorado.

## Fifth Instar Caterpillar Coloration

There are three basic color patterns among fifth instar larvae. In general, these are: dark green $(A$. sara), medium green (A. thoosa), and light green (A. julia). All described subspecies within these three species are closely consistent throughout their ranges, with a single regional exception of $A$. sara from northern California into extreme southwest Oregon as explained below.

Fifth instar caterpillars of the four described subspecies of $A$. sara are dark green with small black pinacula. Compared to those of $A$. sara, fifth instars of the four described subspecies of $A$. thoosa have a lighter shade of medium green with larger dark green pinacula surrounding the setae or tubercles. A. thoosa fifth instars generally have a thinner white lateral stripe which, in many examples, tends to fade as it extends through the larval head capsule as compared to those of A. sara or A. julia (Fig. 3-4). Fifth instar caterpillars of the seven subspecies of $A$. julia have a broader white lateral stripe than those


Figure 2. Comparison of similar phenotypes from different populations of A. sara, A. thoosa, and A. julia. Photo captions with * denote topotypes. (Third row photo of A. t. inghami male from Tucson, AZ, courtesy Jim Brock.)
of A. thoosa and the ground color is lightest shade of green as compared to those of either A. thoosa or A. sara. At the same time, the transitional color change from the white lateral stripe to the light green color is very subtle (Stout 2010, 2012).

Because fifth instar caterpillars of the sara complex darken during the four days it takes them in the lab to feed to pupation, the most noticeably contrasted differences among the three species occur

| Anthocharis sara | Anthocharis thoosa | Anthocharis julia |
| :---: | :---: | :---: |
| Northern California A. s. sara* | NW Arizona A. t. thoosa* |  <br> Colorado A.j.julia* |
|  | Utah A. t. thoosa |  |
| Catalina Island A. s. gunderi* | SE Arizona A. t. inghami* |  |
| Nevada A. s. pseudothoosa* | Colorado A. t. colorado* | Northern Idaho A. j. sulfuris* |
|  <br> Nevada A. s. pseudothoosa* | Colorado A. t. colorado | Western Nevada $A$. j. stella* |
| California A. s. sempervirens* | New Mexico A. t. coriande* | Washington A. j. flora |
| A. s. sempervirens* (Lighter color form) | New Mexico A. t. coriande | Alaska A. j. alaskensis |

Figure 3. Fifth instar caterpillars of all named subspecies of A. sara, A. thoosa, and A. julia. Photo captions with * denote topotypes.


Figure 4. Close up of fifth instar caterpillar color differences of A. sara, A. thoosa, and A. julia. Species-level differences are most noticeable 48 to 54 hours after having molted from fourth instar. Dark green larval pinacula of $A$. thoosa and $A$. julia begin to darken and grow soon thereafter giving these fifth instars a more overall dark green appearance to the naked eye (superficially similar to $A$. sara) approximately 24 hours prior to pre-pupation.
between 48 to 54 hours after having molted to fifth instar. For the sake of consistency, all fifth instar photos shown in Fig. 3 were photographed within this timeframe. After 54 hours, the larval pinacula of A. thoosa and A. julia start to progressively darken and grow until all fifth instars of all three species appear to be dark green to the naked eye. However, closer examination of A. thoosa and A. julia 72+ hour fifth instars show dark green pinacula contrasted against a light green color whereas A. sara $72+$ hour fifth instars are more uniformly dark green (Fig. 4).
Northern California and Southwestern Oregon A. sara. In addition to the typical dark green fifth instar caterpillars, there are some examples of northern California A. sara sara, A. sara sempervirens and southwest Oregon A. sara sara with a slightly lighter shade of green. Superficially, these fifth instars could be confused with those of $A$. thoosa. However, the larval white lateral stripe is typically wider consistent with others of $A$. sara as it crosses from the caterpillar body through its labium and is not faded as is typical of most A. thoosa (Fig. 3). As these larvae pupate, the pupal cone curvature is bent backwards and is longer than those of $A$. thoosa thoosa, which are shorter and bent slightly forwards or are erect. Also, northern California A. sara sempervirens and SW Oregon A. sara sara are hundreds
of miles from the western distributional limit of $A$. thoosa thoosa.

## Pupal Cone Curvature and Color

Pupal cone curvature is the angle between two lines observing the pupa from the side as shown in Fig. 5. The first line starts from the antenna case along the mid dorsum and extends upward. The second line starts at the point where the pupal cone starts to curve and intersects the terminal point of the cone.

Quantified measurements of the curvature of the pupal cone in the sara complex were not attempted because the orientation of subject and camera was difficult to control. Subjective terms such as "erect," "erect and bent slightly backwards", "erect and bent slightly forwards" or "bent backwards" are provided, supported by corresponding photographs.


Figure 5. Pupal cone curvature differences between Colorado A. julia prestonorum (Garfield County) and A. thoosa colorado (Montezuma County).

For example, in Fig. 5 below, pupae from Colorado are compared where the pupal cone curvature of A. julia prestonorum is "bent backwards" (handwritten angle $\theta$ ) whereas the pupa of $A$. thoosa colorado is "erect and bent slightly backwards" (handwritten angle $\varphi$ ) where the angle of A. julia prestonorum is greater than A. thoosa colorado.

As a stand-alone character, pupal cone curvature is not a consistent species level discriminator for the entire complex as all four subspecies of $A$. sara tend to vary between erect to bent backwards with northern California A. sara sara and A. sara sempervirens having the longest cones for that species. However, pupal cone curvature is more consistent with subspecies of A. thoosa and A. julia. For example, pupae of $A$. thoosa are generally erect or bent slightly forward or slightly backward whereas pupal cones of $A$. julia are mostly bent backward with a greater angle. Noting pupal cone curvature, and sometimes, length, has proven taxonomically helpful with identifying blend zones between adjacent subspecies of one species as well as contact zones between two species.

For example, examination of pupal cone curvature is helpful in determining the distribution and blend zones between $A$. thoosa thoosa and $A$. thoosa inghami in northern Arizona. Since the coloration of last instar larvae of both subspecies are similar, it is noteworthy that the pupal cone curvature of $A$. thoosa thoosa is erect and/or bent slightly forward whereas the pupal cone curvature of $A$. thoosa inghami is erect and/or bent slightly backwards where the cone of inghami $(n=34)$ is slightly longer than examples of A. thoosa thoosa. Intermediate pupae and adults were reared from the vicinity of Sitgreaves Pass,


Figure 6. Pupal cone curvature differences between Juab County, Utah, A. julia browningi and A. thoosa thoosa where the two species fly sympatric and synchronic. The third pupa may represent a hybrid between the two species.

Black Mountains, Mohave County, Arizona, where these two subspecies blend.
Another example of pupal cone curvature is the established contact zone between $A$. thoosa thoosa and A. julia browningi in Juab County, Utah, shown in Fig. 6. Anthocharis julia browningi pupae are consistently curved backwards contrasted with the erect pupal cones of $A$. thoosa thoosa shown in the first and second photos of Fig. 6. The pupa from the third photo was found as an A. thoosa caterpillar. The adult from this pupa has not yet emerged; however, it would be interesting to examine as the pupal cone curvature is intermediate between A. julia browningi and A. thoosa thoosa (Stout 2010).

Pupal color. Pupae throughout the complex have both tannish and greenish color forms where most pupae of A. sara and A. thoosa are tan as opposed to green whereas the opposite applies to A. julia pupae, which are green as opposed to tan. Similar to some other species of Papilionoidea, this may be an environmentally cued phenomenon as documented with green and brownish pupae of Papilio and pierid spp. (Hazel and West 1979; Smith 1980; West and Hazel 1985; Hazel 1995).

Some green and tan pupae of A. julia progressively darken to a charcoal gray color as they overwinter as shown with A. julia prestonorum, A. julia julia, A. julia sulfuris, and A. julia flora in Fig. 7. This subsequent darkening of pupae has not been observed with any pupae of $A$. thoosa or $A$. sara ( $n=330$ ) and is independent of the natural darkening that occurs when the imago is developing within the pupa. Examples of pupal cones of all subspecies of the complex are also provided in Fig. 7.

## Overwintering Cycles

The sample size of sara complex caterpillars reared to adult for this study is 715 . The mean number of overwintering cycles for 19 populations ( $n=123$ ) of $A$. sara is 1.41 . The mean number of overwintering cycles for 33 populations $(n=207)$ of $A$. thoosa is 2.83 . The mean number of overwintering cycles for 44 populations $(n=385)$ of $A$. julia is 1.07 (see Table 1 ).

As stated earlier, an overwintering cycle in the lab is defined by exposing pupae entering diapause to at least one month of warmth followed by four months of cold. Keeping track of overwintering cycles is taxonomically relevant in studying interspecific contact zones where two species fly sympatric or nearly sympatric and synchronic, but still have significant differences in the number of overwintering cycles it takes pupae to break diapause and eclose under similar lab conditions. More regional detail will be provided in the interspecific contact zones section.

In addition to species-level differences among the three stated taxa, another explanation for differences in these numerical averages is likely correlated with the general inverse relationship comparing

| Anthocharis sara | Anthocharis thoosa | Anthocharis julia |
| :---: | :---: | :---: |
| Northern California A. s. sara* | NW Arizona A. t. thoosa* | SE Wyoming A. j. julia |
|  | Utah A. t. thoosa |  |
| Catalina Island A. s. gunderi* |  | Northern Utah A. j. browningi* |
| Nevada A. s. pseudothoosa* | Colorado A. t. colorado* | Idaho $A$. j. sulfuris |
|  | Colorado A. t. colorado | Western Nevada A. j. stella* |
| Northern California A. s. sara | New Mexico A. t. coriande* | Washington A. j. flora |
| Northern California A. s. sara | New Mexico A. t. coriande | Alaska A. j. alaskensis |

Figure 7. Pupae of all subspecies of A. sara, A. thoosa, and A. julia. Photo captions with * denote topotypes.
overwintering cycles vs. typical yearly rainfall in a given habitat which, based upon informal lab observations, has also been noted with rearing other pierids such as A. cethura, E. hyantis, E. olympia, E. ausonides, and P. sisymbrii. (Note: My longest example of pierid extended lab diapause occurred with $A$. cethura pima from the xeric Mojave Desert, Clark County, Nevada, where an egg was collected in March of 1997 and the corresponding 1997 pupa emerged in March of 2008 after 11 overwintering cycles of extended hibernation).

Table 1. Mean overwintering cycles of 715 adults of all subspecies of A. sara, A. thoosa, and A. julia.

| Taxon | Sample Size | Populations Sampled | Mean Overwintering Cycles |
| :---: | :---: | :---: | :---: |
| A. sara sara | 79 | 14 | 1.30 |
| A. sara gunderi | 15 | 2 | 1.20 |
| A. sara pseudothoosa | 11 | 2 | 2.27 |
| A. sara sempervirens | 18 | 1 | 1.56 |
| Total: A. sara | 123 | 19 | 1.41 |
| A. thoosa thoosa | 98 | 18 | 2.77 |
| A. thoosa inghami | 34 | 7 | 3.09 |
| A. thoosa colorado | 33 | 3 | 3.48 |
| A. thoosa coriande | 42 | 4 | 2.26 |
| Total: A. thoosa | 207 | 33 | 2.83 |
| A. julia julia | 39 | 4 | 1.00 |
| A. julia prestonorum | 79 | 8 | 1.00 |
| A. julia browningi | 37 | 8 | 1.12 |
| A. julia sulfuris | 141 | 17 | 1.11 |
| A. julia stella | 23 | 1 | 1.00 |
| A. julia flora | 50 | 5 | 1.14 |
| A. julia alaskensis | 16 | 1 | 1.00 |
| Total: A. julia | 385 | 44 | 1.07 |
| Total: | 715 | 96 |  |

## Interspecific Contact Zones

This section will review details of sympatry or near sympatry between either A. sara or A. thoosa with A. julia. Attempts to locate intergradation between established populations of A. sara sara and A. thoosa inghami in the Colorado Desert of Imperial County, California, A. sara sara and A. thoosa $\times$ thoosa blend zone in the Mojave Desert of San Bernardino County, California, and A. sara pseudothoosa and $A$. thoosa thoosa in western Nevada have not been successful.

Populations of $A$. sara sara have been located in extreme western Imperial County, California, east of Anza Borrego Desert State Park whereas populations of A. thoosa inghami have been taken to the east in Yuma County, Arizona. Mark Walker has made specific attempts to locate Imperial County populations of the sara complex in the Chocolate, Chuckwalla, and Cargo Muchacho Mountains of the Colorado Desert without success (Walker pers. comm. 2015). Absence of either A. sara or A. thoosa in the desert mountain ranges of Imperial County is interesting considering A. sara sara has established populations in the Colorado Desert of Anza Borrego Desert State Park and A. thoosa inghami thrives in the Lower Sonoran Desert of SE Arizona following wet winters.

Gordon Pratt (pers. comm. 2012) has located populations of A. sara sara in the Mojave Desert in San Bernardino County (Avawatz Mountains) and Inyo County (Argus Range). The Avawatz Mountains record of $A$. sara sara moves this species within 47 aerial miles of an $A$. thoosa record provided by Ken Davenport (pers. comm. 2011) at Mountain Pass, San Bernardino County.

My attempts to find any sara complex adults or early stages in the early spring along the I-15 corridor at Halloran Springs Road, San Bernardino County, have not yet been successful even though John Emmel (pers. comm. 2015) reported seeing sara complex patrolling males at Squaw Mountain following a wet winter.

Mark Walker and Brian Banker (pers. comm. 2012) collected a stray A. sara sara second brood tattered female on 1 May 2004, east of Mount Manchester in the Dead Mountains of San Bernardino County, 15 aerial miles to the south of established populations of $A$. thoosa that fly in pinyon-juniper habitat of the Newberry Mountains of Clark County, Nevada (Fig. 8). This A. sara sara record likely represents a stray as no other sara complex adults have been documented from the Dead Mts. It is interesting to note that John Emmel and I both have proven that A. sara caterpillars will successfully feed through to adult on the invasive sahara mustard (Brassica tournefortii Gouan) which grows in the area and has rapidly spread across the Mojave Desert through Southern Nevada, and, more recently, to Washington County, Utah.

Based upon examination of pinned adults from the McGuire Center, Austin's (1998) reported intermediates between A. thoosa thoosa (as A. sara thoosa) and A. sara pseudothoosa, have not been confirmed from Washoe, Humboldt, Pershing, Churchill, Nye, Mineral, and Esmeralda Counties, Nevada. The closest documented proximity between A. sara pseudothoosa and A. thoosa thoosa is in Pershing County, Nevada, where A. thoosa thoosa was collected from the Humboldt Range by Austin and A. sara pseudothoosa was collected in the Selenite Range by Bauer, 59 aerial miles apart. More field work and immature studies is needed to research possible contact zones between A. sara and A. thoosa in the Colorado Desert, Mojave Desert and western Nevada.

There have been six areas of contact or near contact zones of A. sara or A. thoosa with A. julia which is reviewed below and summarized in Fig. 9 where the upper horizontal red line represents the northern limit of populations of both $A$. sara and $A$. thoosa and the lower horizontal red line represents the southern limit of populations of A. julia.
\#1—California A. sara sara and A. julia stella. There are several reports of contact or near contact zones of A. sara sara and A. julia stella in the Sierra Nevada of California. On 28 May 2002, Davenport

Anthocharis sara sara


Figure 8. Top row: (Left) Second brood A. sara sara stray female collected from the Dead Mountains, San Bernardino County, CA, by Mark Walker and Brian Banker. (Right) Female A. thoosa reared from Christmas Tree Pass, Newberry Mts, Clark County, Nevada, 15 aerial miles to the north of where the Dead Mts. A. sara female was collected. Bottom row: (Left) Second brood female A. sara sara collected from Brand Park, Verdugo Mts., Glendale, Los Angeles County, CA, shown for comparison purposes. (Right) Female A. thoosa reared from Christmas Tree Pass, Newberry Mts, Clark County, Nevada.


Figure 9. Contact or near contact zones between either A. sara or A. thoosa with A. julia in the Western U.S. The top red line represents the approximate northern limit of populations of $A$. sara or $A$. thoosa whereas the bottom red line represents the approximate southern limit of populations of $A$. julia.
reports (pers. comm. 2005) A. sara sara on wing near Bass Lake, Madera County, as well as A. julia stella one mile north of Bass Lake along Beasore Road. Davenport also reported that, on 6 Jun 2002, Jim Brock found A. sara sara flying along the lower levels of Fresno Dome Road (Scenic Road 10) and A. julia stella was present higher up near Fresno Dome Campground in Mariposa County. Davenport also confirmed large numbers of A. julia stella near Fresno Dome Campground on 29-30 May 2007 (Davenport pers. comm. 2005).

On 29-30 May 2007, Davenport collected three males of second brood A. sara sara as well as six males and one female of $A$. julia stella flying sympatric and synchronic at Big Sandy Campground, Madera County, California, along a small stream and adjacent meadow running into Bear Creek upstream towards the end of the campground. No phenotypic intermediates were reported even though one large second brood A. sara male had slightly yellowish tinge on the dorsal hindwing-normally an A. julia stella trait for this area. (Note: I have reared two A. sara sara males from Los Angeles County, California, and Klamath County, Oregon, with slightly yellowish tints on the dorsal hindwing).

Geiger and Shapiro (1986) report A. julia stella is resident where a few males of A. sara sara were taken at Donner Pass, Nevada County, California. They also report strays of both species on the west slope of Yuba Pass at 5000 feet in elevation. On Shapiro's website, he also lists both species at Lang's Crossing and Castle Peak, Nevada County, California (Shapiro 1986).
\#2-Klamath County, Oregon A. sara sara and A.julia sulfuris. Warren (2005, pers. comm. 2005) noted considerable variation in the ventral hindwing mottling from a long series collected in a potential contact zone between A. sara sara and A. julia sulfuris (as A. sara nr. stella) and recommended that I visit and study the early stages from this unique population.

On 6 May 2006, I visited the area to sample adults from this population. Four live females were collected and laid dozens of eggs. All fifth instars caterpillars resulting from these four females were A. julia sulfuris and have been reared to adult. A few eggs were also located on the flower pedicels of a local Boechera spp. where one fifth instar clearly was A. sara sara (reared adult is shown in Fig. 10) confirming Warren's observations of two species flying in sympatry there.

On some of the reared adults of $A$. julia sulfuris, there was considerable variation of black over scaling on the dorsal and ventral surface as well as pronounced dorsal hindwing marginal spots, thicker discal cell bars and corresponding black apical borders which either is natural for this area (Warren noted "considerable variation in the coloration and extent of hindwing marbling") or may be partly attributed to the actual lab rearing of adults. In my rearing studies, there has been a few examples of reared adults


Figure 10. Reared males of A. sara sara and A. julia sulfuris from Klamath River Canyon, Klamath County, Oregon.
of mainly A. sara and A. thoosa demonstrating increased melanism in terms of black over-scaling on the dorsal surface as well as thicker discal cell bars, black apical borders, and pronounced dorsal hindwing marginal spots as compared to wing caught adults. Otherwise, reared adults show identical markings to wing caught adults.

Reared adults of A. julia sulfuris from Klamath River Canyon have been compared with those from Walt's RV Park, 1.1 miles WSW of Chiloquin, 36.5 miles NNE of Klamath River Canyon, Klamath County. Adults of A. julia sulfuris from Walt's RV Park, which is not a contact zone with A. sara sara, showed much less variation and black dorsal markings where reared males are more similar to the two males of $A$. julia sulfuris from of Klamath River Canyon shown in the middle column of Fig. 10 and not similar to the two males shown in the right-hand column.

There is no evidence that population variation of $A$. julia sulfuris from Klamath River Canyon is related to its flying in sympatry with $A$. sara sara as adults of both species can be phenotypically quite similar in this area.

Because of adult similarities of A. sara sara and A. julia sulfuris from Klamath River Canyon coupled with a small sample size of $A$. sara sara obtained there, it is difficult to hypothesize the existence or absence of gene exchange based upon the examination of adults. It was incredibly astute that Warren (2005) suspected that both species were flying in sympatry at this location. This would be another study area for nuclear DNA to help understand the existence or absence of gene exchange between these two taxa.
\#3-California-Nevada A. sara pseudothoosa and A.julia stella. Pinned adults from the McGuire Center were examined where Bauer collected both A. sara pseudothoosa and A. julia stella at Voight Canyon, Alpine County, California, flying sympatric and synchronic at 6,000 feet. Austin also collected adults of both taxa flying at Kingsbury Grade, Douglas County, Nevada, at an elevation of 6,900 feet. Phenotypically, specimens examined by Warren and myself suggest no clear evidence of gene exchange between these two species at these locations.

Davenport (2007) reports that Bret and Bruce Boyd found A. julia stella and A. sara pseudothoosa occurring together in Mono County, California, north of Mono Lake on the Sierra Nevada east slope from Green Canyon north to the Walker area from June to mid-July.

On his UC Davis website, Shapiro (1986) reports A. julia stella and A. thoosa together along his Loyalton Road, Sierra Valley transect in Sierra County, California. Subsequent communication with Shapiro suggests that A. julia stella flies with A. sara, not A. thoosa along this transect. Whether the subspecies of $A$. sara is nominotypical or $A$. sara pseudothoosa remains to be confirmed as an adult of $A$. sara pseudothoosa has been taken 40 aerial miles to the ESE in Storey County, Nevada by Paul Opler. Shapiro's reported contact zone of A. j. stella and A. sara sara strays at Yuba Pass, Sierra County, is only ca. eight miles east of his Sierra Valley transect.
\#4—Utah-Nevada A. thoosa thoosa and A. julia sulfuris. The strategy for locating contact zones between $A$. julia sulfuris and $A$. thoosa thoosa in Nevada and Utah between latitudes represented by the two red horizontal lines shown in Fig. 9 is to locate transition zones between lower elevation pinyon juniper habitat of $A$. thoosa thoosa with higher elevation boreal forested habitat of $A$. julia sulfuris. This necessitates finding mountain ranges high enough to support $A$. julia forested habitat at elevations


Figure 11. Clear Creek Road transect with GPS coordinates showing where adults of A. thoosa thoosa and A. julia sulfuris were sampled from the Raft River Range, Box Elder County, Utah.


Figure 12. Collected males of both A. thoosa thoosa (left column) and A. julia sulfuris (right column; except for fifth row female) flying sympatric and synchronic from Clear Creek Road; Raft River Range, Box Elder County, Utah.
above pinyon juniper. The relationship and habitat preference between $A$. julia sulfuris and $A$. thoosa thoosa in the Great Basin and portions of the Colorado Plateau somewhat parallels that of E. ausonides ausonides and E. hyantis lotta where E. ausonides prefer mountain canyons and higher elevation forested habitat (similar to A. julia) and E. hyantis lotta prefers pinyon juniper (similar to A. thoosa). However, both Euchloe spp. have been found at valley floors in Salt Lake County, Utah, where neither Anthocharis spp. can be found.

To date, I have not been able to find both $A$. julia sulfuris and $A$. thoosa thoosa flying in sympatry in central and northern Nevada because of insufficient sampling from the region. I was, however, able to confirm museum records of Elko County A. julia sulfuris in the vicinity of Angel Lake, East Humboldt Range, at an elevation of 7300'. I also found pinyon juniper habitat 2.6 aerial miles NE of this location along Nevada Hwy 231 where ova were collected on Boechera spp. and caterpillars reared to adult turned out to be E. hyantis lotta and E. ausonides ausonides. More field work in the East Humboldt Range may likely find both species flying in sympatry.

Other Nevada mountain ranges that might provide records of $A$. julia sulfuris at higher elevations and possible transition contact zones with A. thoosa thoosa are the Shoshone Mountains, Toiyabe Range, Monitor Range, Hot Creek Range, Eagan Range, and Schell Creek Range.

Five contact or near contact zones between A. julia sulfuris and A. thoosa thoosa have been noted in Utah both west and east of the Wasatch Range which is dominated with populations of A. julia browningi.

On 17 and 24 May 2014, Tony Jones and I found A. thoosa thoosa flying sympatric and synchronic with A. julia sulfuris along Clear Creek Road, Raft River Range, Box Elder County, Utah, between 6300' and $6900^{\prime}$ at the extreme NW corner of Utah (Fig. 11). A total of eight males of A. thoosa thoosa, 13 males of A. julia sulfuris, eight females of A. julia sulfuris, with two males having possible intermediate characters were vouchered. Two of the collected A. julia sulfuris females were retained for egg-laying where offspring were all parental $A$. julia sulfuris.

Adults from the contact zone are shown in Fig. 12 with a possible male hybrid is shown in Fig. 13.
The second near contact zone between these two taxa in Utah is in the Stansbury Range of Tooele County where A. thoosa thoosa is ubiquitous in typical pinyon juniper habitat of South Willow Canyon, North Willow Canyon, Davenport Canyon, and Johnson Pass in April and May. While curating sara complex specimens at BYU's Monte L. Bean Life Science Museum, I noticed a pair of A. julia sulfuris (as A. sara) adults from South Willow Canyon collected by Oscar Dorfman in 1981 and 1982 (Fig. 14). My attempts to locate A. julia sulfuris at higher elevations of South Willow Canyon of the Stansbury Range have not been successful.

The third contact zone between A. thoosa thoosa and A. julia sulfuris is found east of the Wasatch Plateau along Huntington Canyon Road (UT Hwy 31) at and near Rilda Canyon, a two-mile mining road traveling west from Huntington Canyon and 10.7 road miles WNW of Huntington City in Emery County, Utah.

It is interesting to note that examined adults west of the Wasatch Plateau along UT Hwy 31 in Fairview Canyon, are A. julia browningi whereas adults blend into A. julia sulfuris on the east side of the plateau into Huntington Canyon, which is part of the Colorado Plateau ecoregion of Utah.

On 30 May 2014, I located three ova of $A$. julia sulfuris and one fourth instar of A. thoosa thoosa at the mouth of Rilda Canyon (Fig. 16). The A. julia sulfuris were reared to adult where one male is shown


Figure 13. Possible hybrid of A. thoosa thoosa $\times$ A. julia sulfuris from Clear Creek Road; Raft River Range, Box Elder County, Utah.


Figure 14. (Left) Anthocharis julia sulfuris (as A. sara) male. (Right) Anthocharis julia sulfuris (as A. sara) female. Both were collected by Oscar Dorfman from South Willow Canyon, Tooele County, Utah.
in Fig. 15, whereas the pupa of A. thoosa thoosa is still in diapause. Another A. thoosa thoosa adult also is pictured in Fig. 15 and was found as a larva in 2010 and emerged in 2014, approximately three road miles SE of Rilda Canyon in typical pinyon juniper habitat.

On 28 Apr and 5 May 2015, I found both taxa flying sympatric and synchronic in Huntington Canyon, 2.4 road miles north of Rilda Canyon at an elevation of $7300^{\prime}$. No collected adults appeared to show intermediate characters. A few ova of A. thoosa thoosa were located on 5 May on Boechera hirsuta and reared to pupae with one male emerging in 2016. Although both larvae and pupae showed parental $A$. $t$. thoosa traits, the male that emerged shows possible $A$. julia sulfuris adult characters (shown in the second row of Fig. 15) based upon the following observations:

First, the dorsal black border is somewhat offset from the dorsal forewing discal cell bar. This variation is not common in A. thoosa thoosa; but is prevalent in A. julia sulfuris. Second, the ground color of the ventral hindwing mottling is slightly more greenish than is typical for $A$. thoosa thoosa, except for adults from Clark County, Nevada, and San Bernardino County, CA, which some authors assign to A. thoosa inghami (Emmel and Emmel 1973). Third, the black border that is adjacent to the orange apical patch and the ventral forewing mottling is intermediate contrasted to a more pronounced black border that is typical with $A$. thoosa thoosa, but is usually absent or reduced in $A$. julia sulfuris. (More on this wing trait will be discussed in differentiating adults of A. thoosa colorado and A. julia nr. presontorum). Fourth, there is a hint of a thin faded yellowish band at the apex of the ventral forewing that extends down the outer wing margin. This trait is more prevalent on A. julia sulfuris, but absent on A. thoosa thoosa (Fig. 15).

Sample size from Huntington Canyon is small as both $A$. thoosa thoosa and $A$. julia sulfuris compete with $P$. protodice, $P$. beckerii, $P$. sisymbrii, $E$. ausonides coloradensis, and $E$. hyantis lotta for the same scattered host plants of D. pinnata, B. perennans, and B. hirsuta.

The fourth near contact zone between these two taxa was observed in neighboring Carbon County, at Nine Mile Canyon Road. On 18 May 2010, a single ovum of A. thoosa thoosa was located along Nine Mile Canyon Road, 1.1 miles SSW of Pine Canyon at an elevation of $6900^{\prime}$. The larva was reared to pupa and a male emerged on 3 Apr 2013. On 12 May 2015, two males of A. julia sulfuris were collected 0.6 aerial miles north of the $A$. thoosa thoosa record, 0.2 miles north of Soldier Canyon Mine at an elevation of $7100^{\prime}$. No intermediate phenotypes were noted with this very small sample size of three.

The fifth near contact zone was located ca. 17 miles SE of Nine Mile Canyon east of Sunnyside, Carbon County, Utah, at Slaughter Canyon along UT Hwy 123. Four A. thoosa thoosa ova were located on 27 Apr 2009; producing two males and two females. On 21 May 2012, I traveled to Water Canyon, 3.4 aerial miles north of the A. thoosa thoosa (Slaughter Canyon) location and collected three worn males and two fresh females of $A$. julia sulfuris. Females laid eggs where a short series of parental $A$. julia sulfuris were obtained. No wing caught or reared adults showed apparent intermediate traits between the two species.

On 24 May 2012, Wayne Whaley and I visited the almost impassible Little Horse Canyon Road, 7.1 miles south of Slaughter Canyon and ca. 10 miles east of UT Hwy 6 on Emery County/Carbon County line at an elevation of 7900'. Several ova of $A$. julia sulfuris, $E$. hyantis lotta, $E$. ausonides coloradensis (H. Edwards, 1881) as well as third and fourth instars of P. sisymbrii were located on this host plant.

Anthocharis thoosa thoosa


Figure 15. (Upper left) Anthocharis thoosa thoosa reared male from 3.1 road miles SE of Rilda Canyon, Huntington Canyon, Emery County, Utah. (Upper Right) Anthocharis julia sulfuris reared male from Rilda Canyon. (Lower) Possible hybrid of A. thoosa thoosa $\times$ A. julia sulfuris male from Rilda Canyon.


Figure 16. Anthocharis thoosa thoosa and A. julia sulfuris contact zone in Huntington Canyon, Emery County, Utah.

Six A. julia sulfuris were successfully reared to adult with one adult possibly having $A$. thoosa thoosa ventral hindwing traits-shown on the right side of Fig. 17.

It is difficult to conclude whether the male on the right of Fig. 17 has A. thoosa thoosa genes. Individual variation in the greenish hue of the ventral hindwing mottling of $A$. julia sulfuris from the Colorado Plateau is usually minimal whereas this male has noticeably darker mottling.
\#5-Utah A. thoosa thoosa and A. julia browningi. The strategy of finding contact zones of $A$. thoosa thoosa and A. julia browningi in the Wasatch Range where A. julia browningi flies commonly from canyon mouths to higher elevations requires two steps. The first step is to find pockets of Great Basin habitat consisting largely of stands of Juniperus osteosperma which replace typical Wasatch Range flora of Quercus gambellii, Acer negundo, Salix exigua, etc. The second step is to search the Wasatch Range in close physical proximity to Great Basin mountains and hills. Both criteria apply to a lesser degree in Utah County, and to a greater degree in Juab County between Nephi and Mona, east of I-15 where $A$. thoosa thoosa has invaded and successfully established breeding populations.


Figure 17. Variation in two out of six reared males of A. julia sulfuris from Little Horse Canyon Road, Emery County, Utah. Both larval coloration and pupal cone shape of both adults were those of A. julia.

It's intriguing to note the elevational extremes of J. osteosperma and its relevance in contrasting contact zones between $A$. julia sulfuris and $A$. thoosa thoosa, discussed previously, with A. julia browningi and A. thoosa thoosa. For example, as discussed previously, the A. julia sulfuris-A. thoosa thoosa contact zone exists near the upper elevational limit of $J$. osteosperma contrasted to the $A$. julia browningi-A. thoosa thoosa contact zone that is found at the lower elevational limit. This suggests that the relationship between A. julia sulfuris-A. thoosa thoosa in the Great Basin and Colorado Plateau may be ancient whereas the relationship of A. julia browningi-A. thoosa thoosa in the Wasatch Range may be more recent.

The 2009 A. julia browningi and A. thoosa thoosa contact zone area east of Nephi is summarized in Table 2 below (Stout 2010). Looking at adult wing characters, these two taxa are the most diverse in comparison with other contact zone taxa where A. sara or A. thoosa flies sympatric or nearly sympatric with A. julia. In the table below, the number of possible hybrids between the two species is documented in the right-hand column and were photographed (Stout 2010: 8-9). However, without knowing the parental species of these possible hybrids, confirming hybridization is subject to interpretation.

Table 2. Summary of wing caught adults of A. julia browningi and A. thoosa thoosa from 2009 research area from Birch Creek, Little Birch Creek and an unnamed creek, NE of Nephi, Juab County, Utah.

| 20-21 Apr 2009 | A. julia browningi | A. thoosa thoosa | Possible Hybrids |
| :--- | :---: | :---: | :---: |
| Birch Creek | 3 | 1 | 1 |
| Little Birch Creek | 4 | 9 | 4 |
| Unnamed Creek | 1 | 1 | 0 |

The 2009 research area and parameters were expanded in 2014 from three to five canyons where both species were found flying sympatric and synchronic at the canyon mouths of all five locations-see Table 3 and Fig. 19. I decided to examine immatures and oviposition preferences of both species and seek out live females of $A$. julia browningi and/or A. thoosa thoosa flying in close proximity to patrolling males of the other species to see if any offspring larvae, pupae, or adults showed any visible evidence of hybridization.

Where they fly together, species differences is not only evident in adult, larval, and pupal characters; but also in male patrolling behavior found in the same ravine where $A$. julia browningi males patrol more slowly and stay in the ravine whereas $A$. thoosa thoosa males patrol more quickly and will exit the ravine to inspect adjacent $J$. osteosperma in search of recently eclosed $A$. thoosa thoosa females that likely fed on Boechera spp. or D. pinnata taking refuge under or near the same junipers (Stout 2010). Within the research area, a higher percentage of Anthocharis ova found on D. pinnata and Boechera spp. growing adjacently to J. osteosperma were A. thoosa thoosa whereas most ova found on Boechera spp. growing along the rocky bottoms of Willow Creek, Mona Creek, and North Creek were A. julia browningi.

A total of four parental A. julia browningi females were collected on 15 Apr 2014 and 19 Apr 2014 at the mouths of North Creek and Mona Creek and were setup to oviposit where the immatures and emerged adults were examined.

F1 offspring from one female from North Creek (six females, zero males) and from two females from Mona Creek (four females, zero males, one unemerged pupa) showed parental A. julia browningi traits with no visible evidence of $A$. thoosa thoosa traits in larvae, pupae, or adults.

Table 3. Summary of wing caught adults of A. julia browningi and A. thoosa thoosa from 2014 research area from Little Birch Creek, Birch Creek, Willow Creek, Mona Creek, and North Creek, east of Mona, Juab County, Utah.

| 12-19 Apr 2014 | A. julia browningi | A. thoosa thoosa | Possible Hybrids |
| :--- | :---: | :---: | :---: |
| Little Birch Creek | 3 | 6 | 0 |
| Birch Creek | 2 | 1 | 2 |
| Willow Creek | 8 | 1 | 1 |
| Mona Creek | 11 | 5 | 3 |
| North Creek | 5 | 1 | 3 |

F1 offspring from another female from North Creek (one female and two males) also showed parental A. julia browningi traits in fifth instar larvae and pupae. However, all three emerged adults have clear A. thoosa thoosa traits and are illustrated in Fig. 18. The remaining three pupae died during the spring of 2017 .

Concluding hybridization between these two diverse taxa while knowing the female parent (A. julia browningi) is not difficult. One reason for this conclusion references phenotypic differences between A. julia sulfuris and $A$. julia browningi. As discussed previously, some male adults of $A$. julia sulfuris (including topotypes from Kellogg, Shoshone County, Idaho) dorsally can have thick dorsal discal cell bars and connecting black borders with a white ground color that can be superficially similar to $A$. thoosa thoosa. However, there is no such variation in the same characters of male A. julia browningi. The black borders are faded and disconnected to a thinner discal cell bar. The ground color of A. julia browningi males is off white (or sometimes yellowish) and not white. The ventral hindwing mottling of $A$. julia browningi is a similar greenish cast that is generally more faded than A. julia sulfuris.

Adults shown in the middle column of Fig. 18 came from a parental A. julia browningi female and clearly show $A$. thoosa thoosa traits.
\#6-Colorado-New Mexico A. thoosa colorado and A. julia nr. prestonorum. The previous subsection discussed contact zones between A. julia browningi and A. thoosa thoosa which have divergent wing characters. Contrastingly, adults of extreme SW Colorado and NW New Mexico A. thoosa colorado and $A$. julia $n r$. prestonorum can be phenotypically very similar.

Scott (2008) provided significant detailed data records for the sara complex including SW Colorado and NW New Mexico and discussed the relationship between A. thoosa colorado (as A. sara colorado) and $A$. julia nr. prestonorum (as A. julia julia).


Figure 18. (Left) Topotypical A. thoosa thoosa from the vicinity of Mokiak Pass, Mohave County, Arizona. (Middle) Anthocharis j. browningi $\times$ A. t. thoosa hybrids obtained from a gravid parental A. julia browningi female from North Creek, Juab County, Utah. (Right) Topotypical A. julia browningi from City Creek Canyon, Salt Lake County, Utah.


Figure 19. (Left) 2009 A. julia browningi and A. thoosa thoosa contact zone study area Northeast of Nephi, Juab County, Utah. (Right) 2014 A. julia browningi and A. thoosa thoosa contact zone study area in five canyons north of Nephi and adjacent to Mona, Juab County, Utah.

Scott mentions that both taxa interdigitate ranges in SW Colorado and Northern New Mexico; which prompted my investigating the region to look at both adults and immatures for both species to better understand these two taxa. Taxonomic note: Having reared both topotypical $A$. thoosa colorado from Montezuma County, Colorado, and topotypical A. thoosa coriande from Santa Fe County, New Mexico, material from Montezuma County and La Plata County, Colorado are A. thoosa colorado and not $A$. thoosa coriande, contrary to Fisher (2012).

Adult differences between topotypical A. julia prestonorum and SW Colorado/NW New Mexico A. julia nr . prestonorum were reviewed in the original description of $A$. julia prestonorum where some adults are similar whereas other adults of A. julia nr. prestonorum have a purer white dorsal forewing coloration, darker orange apical patches, darker ventral hindwing mottling, as well as thicker dorsal discal cell bars and surrounding black borders and can appear phenotypically similar to A. thoosa colorado (Fig. 20, 22).

Topotypical A. julia prestonorum is diagnostically described as having all white females whereas some A. julia nr. prestonorum females have a yellowish tint on the dorsal surface and more greenish coloration on the ventral hindwing mottling somewhat similar to A. julia julia or A. julia sulfuris even though the distribution of those two subspecies is hundreds of miles either northwest (A. julia sulfuris) or northeast (A. julia julia). Because of this, these A. julia nr. prestonorum may warrant subspecific recognition when the existence or absence of gene exchange with $A$. thoosa colorado has been factored in.

A consistent diagnostic difference in examining a series of adults of A. thoosa colorado vs. A. julia nr . prestonorum is evident in the ventral forewing black mottled band adjacent to the orange apical patch towards the wing margin which are either faint or obsolete in A. julia nr. prestonorum and are more pronounced in $A$. thoosa colorado even when the discal cell bars and connecting black borders are prevalent and similar on the dorsal surface of both species (Fig. 20, 22). When looking to differentiate adults of both species, it is also important to compare those of the same gender over a long series as the ventral forewing black mottled apical band tends to be lighter in females as compared to males. Also, adults of $A$. thoosa colorado tend to subtly differ from $A$. julia nr. prestonorum with slightly darker ventral hindwing mottling.

The first near contact zone between $A$. thoosa colorado and $A$. julia nr. prestonorum occurs in Montezuma County and neighboring extreme western La Plata County, Colorado. In forested habitat and elevation (7400') that appeared to be suitable for A. julia nr. prestonorum, I collected a female A. thoosa colorado north of Summit Reservoir, Montezuma County, on 8 May 2010.

The next spring, I collected a patrolling male of $A$. julia nr. prestonorum 9.1 miles ESE of Summit


Figure 20. From top to bottom, all columns show three females followed by one male. (Left) Anthocharis thoosa colorado from the vicinity of Summit Reservoir, Montezuma County, Colorado. (Middle) Anthocharis julia nr. prestonorum from Target Tree Recreation Area, La Plata County, Colorado. (Right) Topotypical A. julia prestonorum from Grizzly Creek, Garfield County, Colorado are shown for comparison purposes with A. julia nr. prestonorum.

Reservoir at Echo Basin along County Road L. However, I was too early to find ova or live females at this specific location. I did, however, rear six adult A. julia nr. prestonorum from nearby Target Tree Recreation Area (7700') north of CO Hwy 160 and 12.3 aerial miles ESE of Summit Reservoir-see Fig. 21.

The identification of both Summit Reservoir A. thoosa colorado and Target Tree Recreation Area $A$. julia nr. prestonorum was further verified through examining fifth instars, pupal cone curvature, and the average number of overwintering cycles it took both taxa to emerge under the same lab conditions. Summit Reservoir $A$. thoosa colorado required 3.73 overwintering cycles $(n=14)$ and Target Tree Recreation Area $A$. julia nr. prestonorum required 1 overwintering cycle $(n=6)$.


Figure 21. Near contact zone of A. thoosa colorado and A. julia nr. prestonorum (within 9.1 miles) near Mancos, Montezuma County, Colorado.

Anthocharis thoosa colorado
Anthocharis julia nr. prestonorum


Figure 22. (Left) Anthocharis thoosa colorado female (first row) and male (second row) from Carbon Junction Canyon, La Plata County, Colorado. (Right) Anthocharis julia nr. prestonorum female (first row) and male (second row) from east side Lower Wildcat Canyon, La Plata County, Colorado.

Although this contrast in overwintering cycles is similar to other populations of A. thoosa and A. julia, it is also locally surprising considering the proximity, similar habitat, and $300^{\prime}$ elevational difference between these two taxa at these locations. This suggests that A. thoosa colorado may have more recently invaded forested A. julia nr. prestonorum habitat from lower, more xeric pinyon juniper situations similar to the type locality of A. thoosa colorado at McElmo Creek, Montezuma County, at an elevation of 5700'.

The second A. thoosa colorado and A. julia nr. prestonorum near contact zone (within 3.6 miles) occurs in the vicinity of Durango, La Plata County, Colorado. On 29 Apr 2009 and again on 13 May 2009, I visited Lower Wildcat Canyon and found a population of A. julia nr. prestonorum in a forested area, 1.0 miles east of Durango at an elevation of $6800^{\prime}$ where several wing caught adults were obtained as well as reared adults from ova collected on Boechera sparsiflora and Thlaspi montanum Linnaeus, 1753. No A. thoosa colorado were collected at this location.

On 4 May 1973, Mike Fisher collected a single male A. thoosa colorado (reported with possible julia characters) from Carbon Junction Canyon, two miles SSE of Durango and 3.6 aerial miles from the $A$. julia nr. prestonorum Wildcat Canyon location (Scott and Fisher 2008). On 28 and 29 Apr 2009, I visited Carbon Junction Canyon and found three A. thoosa colorado ova on D. pinnata; two of which were successfully reared to adult (Fig. 22-23).

The identification of both Carbon Junction Canyon A. thoosa colorado (6400') and Lower Wildcat Canyon A. julia nr. prestonorum (6800') were also verified through examining fifth instar larvae, pupal cone curvature, and the average number of overwintering cycles, which, for A. thoosa colorado was 2; ( $n=3$.) Lower Wildcat Canyon A. julia nr. prestonorum required 1 overwintering cycle ( $n=14$ ).

On 4 May 2011, to obtain a larger sample size, I revisited Carbon Junction Canyon as well as other nearby pinyon juniper habitat and ravines both north and south of Durango, along US Hwy 160 and US Hwy 550 and found no evidence of $A$. thoosa colorado either on wing or as immatures.

On 5 May 2011, I visited Lower Piedra Campground, Archuleta County, CO, where I found several males and two females of A. julia nr. prestonorum on wing. Several ova were obtained from these two females as well as located on the pedicels of Boechera spp. producing a total of 12 reared adults (three males and nine females).

Since this area was reported as a possible contact zone by Roever (pers. comm. 2011), all larvae and pupae were examined and verified as A. julia nr. prestonorum. All pupae were photographed, catalogued, and illustrated adjacent to the reared adults in Fig. 24. Adults from all 12 pupae emerged after 1 overwintering cycle consistent with other populations of A. julia nr. prestonorum.

The phenotype of the third female of A. julia nr. prestonorum shown in the right-hand column in Fig. 24 that was collected as an ovum is particularly interesting. Looking at adult characters alone, one might hypothesize $A$. thoosa colorado traits both in the ventral hindwing mottling and in the ventral


Figure 23. Near contact zone (within 3.6 aerial miles) of Anthocharis julia nr. prestonorum and A. thoosa colorado from Durango, La Plata County, Colorado.
forewing mottling adjacent to the orange apical patch. The pupal cone is clearly A. julia nr. prestonorum, which is not conclusive because North Creek, Juab County, Utah, hybrid A. julia browningi $\times$ A. thoosa thoosa discussed previously came from a parental $A$. julia browningi female where both larvae and pupae also showed dominating female parental $A$. julia browningi traits; but, the resulting reared adults are hybrids.

At the same time, no parental A. thoosa colorado adults or early stages were found at Lower Piedra Campground. Clearly, more sampling would be helpful in Archuleta County.

On 5 May 2011, I also traveled southeast and found two males of A. julia nr. prestonorum flying along Blanco River Road (FR 656) near Blanco River Campground. Attempts to locate live females or


Figure 24. (Left) Anthocharis julia nr. prestonorum collected and reared males with pupae (where applicable). (Right) Anthocharis julia nr. prestonorum reared females and corresponding pupae from Lower Piedra Campground, Archuleta County, Colorado.


Figure 25. (Left) Anthocharis julia nr. prestonorum reared males with pupae. (Right) Anthocharis julia nr. prestonorum reared females with pupae-all from 0.5 miles NW of Dulce Lake, Rio Arriba County, New Mexico.
host plants with immatures failed at this location.
Later that day, I visited Dulce Lake, Rio Arriba County, New Mexico, where both Jim Scott and Ray Stanford had sampled sara complex adults that were identified by Scott and Fisher (2008) as either as A. thoosa colorado (as A. sara coriande) or A. julia.

I collected a live female which laid many eggs and pupae were obtained. The lighter coloration of fifth instar caterpillars coupled with charcoal gray coloration of some of the pupae with long curved pupal cones suggested that I had collected A. julia nr. prestonorum and not A. thoosa colorado, even though reared males from this population superficially look similar to $A$. thoosa colorado. However, upon closer examination, these reared adults had faded or obsolete black mottled bands adjacent to the orange apical patch which, as discussed previously, is more typical of A. julia nr. prestonorum and not A. thoosa colorado which demonstrate much heavier mottled bands adjacent to the orange apical patch (Fig. 25).

All pupae ( $n=14$ ) emerged after 1 overwintering cycle consistent with other populations of $A$. julia nr. prestonorum. More adults and immatures should be sampled from both Archuleta County, Colorado, and Rio Arriba County, New Mexico.

Based upon examination of a series of A. julia nr. prestonorum from La Plata County, Colorado, Archuleta County, Colorado, and Rio Arriba County, New Mexico, I question Fisher's designation of $A$. thoosa coriande paratypes from West Sandoval Mesa, Archuleta County, Colorado, figured on page 18 of Butterflies of Colorado Part 5 (Fisher 2012). Based upon adult characters alone, I find it more likely that these adults are actually A. julia nr. prestonorum; especially comparing these paratypes to topotypes of $A$. thoosa coriande 120 miles to the SSE in Santa Fe County, New Mexico. More information on $A$. thoosa coriande will be provided in a future paper that discusses all subspecies of the complex.

Although using multiple character sets such as analyzing adults, larvae, pupae, and overwintering cycles collectively helps separate identifications of $A$. julia nr. prestonorum from $A$. thoosa colorado in the region, examining this same suite of characters has not helped identify the existence or absence of gene exchange between these two cryptic taxa partly because I was not able to actually find parentals of both species flying in strict sympatry. More regional sampling leveraging tools such as nuclear DNA may be able to answer a question of why these two taxa have similar wing characters from the region.
Anthocharis_julia_aleskensis | 1948A| AK-HainesHwyMi8.5
Anthocharis julia_alaskensis 2005 | 4 AK-Skagway* Anthocharis_julia_alaskensis/2005B|AK-Skagway* Anthocharis_julia_flora| 2010|WA-YakimaCo-BearCyn Anthocharis_julia_floral 2009|WA-YakimaCo-BearCyn* Anthocharis_julia_+lora | 1947A| OR-WashingtonCo Anthocharis_julia_flora| 1940A|OR-PolkCo
Anthocharis julia_floral 1945AlOR-PolkCo Anthocharis_julia_stella|1943A|NV-CarsonCity Anthocharis_julia_stella |2030|CA-NevadaCo-BorealRidge* Anthocharis_julia_stella|2031|CA-NevadaCo-BorealRidge* Anthocharis_julia_sulfuris|1953A|NV-E1koCo Anthocharis_julia_sulfuris 1960A|WY-LincolnCo Anthocharis_julia_browningi|2025|UT-CacheCo-7mEofLogan Anthocharis_julia_browningi WB307|UT-WasatchCo-Sandy
Anthocharis julia_browningi 1956 A UT-SaltLakeCo Anthocharis julia browningi|1954AlUT-DavisCo Anthocharis_julia_sulfuris | 1946A|UT-UintahCo Anthocharis_julia_sulfuris |1958A|UT-DaggettCo Anthocharis_julia_browningi|1950A|UT-UtahCo Anthocharis_julia_browningi|1955A|UT-CarbonCo Anthocharis_julia_nr.prestonorum | 2016| CO-MontezumaCo* Anthocharis_julia_nr.prestonorum|1949A|CO-Durango Anthocharis_julia_nr.prestonorum| 1951A| CO-ArchuletaCo
Anthocharis julia_nr.prestonorum| 1959 | NM-RioArribaCo Anthocharis_julia_prestonorum|1944A|co-GarfieldCo Anthocharis_julia_prestonorum|1957A|CO-GarfieldCo-G Anthocharis_julia_prestonorum|2032|PT|CO-Garfield-Glwd*
Anthocharis_julia_prestonorum|2033|PT|CO-Garfield-Glwd* Anthocharis_julia_julia|2001|WY-AlbanyCo-PoleMt* Anthocharis_julia_julial 2002|WY-AlbanyCo-PoleMt Anthocharis_julia_julia 1952A|CO-BoulderCo Anthocharis_julia_julia|WB306|CO???
Anthocharis_julia_julia 2015 |CO-ParkCo-HallValley* Anthan Anthocharis thoosa_ssp|1962A|ID-OneidaCo Anthocharis_thoosa_ssp|1972A|UT-BoxElderCo Anthocharis_thoosa_thoosa|WB311|UT-TooeleCo-CedarMts Anthocharis_thoosa_thoosa|1968A|UT-JuabCo-BirchCrk Anthocharis_thoosa_thoosa | 1973A|UT-JuabCo-GardnerCrk Anthocharis_thoosa_thoosa | 1987 A |UT-CarbonCo-9miCyn Anthocharis_thoosa_thoosa 1988A|UT-CarbonCo-Slau
Anthocharis_thoosa_thoosa |1964A |UT-WashingtonCo Anthocharis_thoosa_thoosal1990B |AZ-MohaveCo-Mokiak-TL* Anthocharis_thoosa_thoosal 1965A|CA-SanBernardinoCo Anthocharis_thoosa_thoosa|WB297|CA-SBrnrdn-CooksWellSRA Anthocharis_thoosa_thoosal 1989A| AZ-MohaveCo-Sitgreaves
Anthocharis thoosa_troosal 2003|AZ-MohaveCo-BlackMt* Anthocharis_thoosa_thoosal 2003|AZ-MohaveCo-BlackMI* Anthocharis_thoosa_thoosal 2004|AZ-MohaveCo-BlackMt* Anthocharis_thoosa_irghami 19868 AZ-YavapaiCo-Prescott Anthocharis_thoosa_irghami | JN276216|AZ-MaricopaCo Anthocharis_thoosa_irghami | JN276217|AZ-MaricopaCo Anthocharis_thoosa_irghami $\mid$ 1971A|AZ-PimaCo-RttksnkeCyn
Anthocharis thoosa_irghami ${ }^{2011}$ |AZ-PimaCo-Gates-Pass?** Anthocharis_thoosa_irghami|2012|AZ-PimaCo-Gates-Pass! Anthocharis_thoosa_irghami $|2034|$ AZ-PimaCo-Tucson*
Anthocharis thoosa_irghami 2035 AZ-PimaCo-Tucson*
 Anthocharis_thoosa_inghami|WB310|AZ-PimaCo-BoxCyn
Anthocharis thoosa_irghami ${ }^{\text {WB2 }}$. $282 \mid$ AZ-PimaCo-BoxCyn Anthocharis thoosa coloradol 1991 AlCO -MontezumaCo Anthocharis_thoosa_colorado|1961A| CO-MontezumaCo Anthocharis_thoosa_colorado|1967A|CO-MontezumaCo Anthocharis_thoosa_colorado |1992A|C0-Durango Anthocharis_thoosa_coriande |1966A| NM-SandovalCo Anthocharis_thoosa_coriande 2024 |NM-Sandoval-Bandelier* Anthocharis_thoosa_coriande| 2023|NM-Sandoval-Bandelier* Anthocharis_thoosa_coriande 1993A/ NM-SanMiguelCo-Mntzma Anthocharis_thoosa_coriande 1969A|NM-ValenciaCo Anthocharis thoosa_coriandel 2020|NM-Luna-Lttlflori Anthocharis_thoosa_coriande| 2021 |NM-Luna-LttlFloridaM* Anthocharis_thoosa_coriandel1995|NM-DonaAnaCo-Organs* Anthocharis_thoosa_coriande|1996|NM-DonaAnaCo-Organs* Anthocharis_thoosa_coriande 1997|TX E1PasoCo 「ranklins Anthocharis_thoosa_coriande|1998|TX-ElPasoCo-Frank Anthocharis_sara_sempervirens|1976A|CA-HumboldtCo Anthocharis sara_sempervirens/BC-ZSM-Lep-71286|CA Anthocharis_sara_sara|1978A|OR-JosephineCo-Selma Anthocharis_sara_saral 2038|OR-BentonCo-McDonaldForest Anthocharis_sara_saral1979A|CA-SiskiyouCo-LttlCttnwdPk Anthocharis_sara_saral 1941A|OR-KlamathCo
Anthocharis_sara_sara 1980A OR-KlamathCo-KlamathRvCyn Anthocharis_sara_sara| 1975A|CA-PlumasCo-QueenLilyCmpgr Anthocharis_sara_pseudothoosa|2013|NV-StoreyCo-GeigerS*
Anthocharis sara pseudothoosa|2014|NV-StoreyCo-GeigerS* Anthocharis_sara_pseudothoosa|2014|NV-StoreyCo-Gei
Anthocharis_sara_pseudothoosa| $1985 \mathrm{~A} \mid$ NV-DouglasCo Anthocharis sara pseudothoosal CSU-CPG-LEP001812|CA Anthocharis_sara_pseudothoosa|CSU-CPG-LEP001813|CA-Inyo Anthocharis_sara_pseudothoosa|CSU-CPG-LEP001811|CA-Inyo Anthocharis_sara_pseudothoosa|CSU-CPG-LEP001810|CA-Inyo Anthocharis_sara_sara| JN276218|CA-Imperial-3mNOcotillo Anthocharis_sara_saral JN276220|CA-Imperial-3mNOcotillo Anthocharis_sara_saral JN276226| CA-SanDiegoCo4mSEJucumb Anthocharis_sara_gunderi 12026 |CA-SantaCatalinaIsland* Anthocharis_sara_gunderi|2027|CA-SantaCatalinaIsland* Anthocharis_sara_gunderi|WB271|CA-SantaCatalinaIsland Anthocharis_sara_ssp|2017|MX-BCN-SierraSanPedroMartir*


Figure 26. MtDNA COI barcodes of all subspecies of A. sara, A. thoosa, and A. julia. Positions invariant in all specimens were removed. Most frequent nucleotide in each position is on white background, second, third and fourth in frequency nucleotides are shaded red, green and cyan, respectively. This figure is a preview of a more detailed illustration to appear in Opler et al. (in preparation.) Taxa highlighted in yellow represent topotypes.

## Conclusions

The body of evidence presented supports three species level taxa in the sara complex consisting of Anthocharis sara, (Sara orangetip), Anthocharis thoosa, (southwestern orangetip,) and Anthocharis julia (Julia orangetip). This evidence is based upon a combination of five characters including adult phenotypes, fifth instar caterpillar coloration, pupal cone curvature and color, average number of overwintering cycles, and interspecific contact zones, the last of which acknowledges occasional hybridization between A. julia and A. thoosa.

These taxonomic conclusions are further supported by unpublished MtDNA data from Opler et al. (in prep.). One of the coauthors, Dr. Nick Grishin (pers. comm. 2014) acknowledges the arrangement of three distinct species taxa-A. sara, A. thoosa, and A. julia. Portions of the barcodes from that paper showing the sara complex are presented here (Fig. 26), with permission from the authors.

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Review editor Andrei Sourakov.
Appendix 1. Data from figures (adults and early stages)

| 茥 | 3 | Column 1 | Column 2 | Column 3 |
| :---: | :---: | :---: | :---: | :---: |
| 2 | 1 | (Left): Anthocharis sara pseudothoosa male, Ex lrv. 12 Jun 2008, Emerged 7 Feb 2010, Jackass Creek, NFR 067, Sweetwater Mts., 7300', NEVADA: Douglas County. Todd L. Stout leg. (Right): Anthocharis sara pseudothoosa female, Ex ovum 12 Jun 2008, Emerged 4 Feb 2009, North side Desert Creek, 5.6 miles NE Jackass Flatt, Sweetwater Mts., 7500', NEVADA: Douglas County. Todd L. Stout leg. | (Left): Anthocharis thoosa thoosa male, Coll. 16 Apr 1994, Spring Creek, Oquirrh Mts. 6000', UTAH: Utah County. Todd L. Stout leg. (Right): Anthocharis thoosa thoosa female, Coll. 16 Apr 1994, Spring Creek, Oquirrh Mts. 6000' UTAH: Utah County. Todd L. Stout leg. | (Left): Anthocharis julia prestonorum male, Ex females 30 Apr 2012, Emerged 5 Apr 2013, Grizzly Creek, 4.1 miles ENE Glenwood Springs, 6100', COLORADO: Garfield County. Todd L. Stout leg. <br> (Right): Anthocharis julia prestonorum female, Ex females 30 Apr 2012, Emerged 5 Apr 2013, Grizzly Creek, 4.1 miles ENE Glenwood Springs, 6100', COLORADO: Garfield County. Todd L. Stout leg. |
| 2 | 2 | (Left): Anthocharis sara sara male, Ex lrv 1 May 2009, Emerged 1 Feb 2010, Glendora Ridge Road, Mt. Baldy Road, San Gabriel Mts., 1800', CALIFORNIA: Los Angeles County. Brian Banker leg. (Right): Anthocharis sara sara female Ex female 8 Mar 2009, Emerged 29 Jan 2010, Cajon Pass, Cleghorn Road, 3000', CALIFORNIA: San Bernardino County. Brian Banker leg. | (Left): Anthocharis thoosa inghami male, Ex female 19 Mar 2007, Emerged 4 Jan 2008, Hassayampa River, 4600', ARIZONA: Yavapai County. Stan Gorodenski leg. (Right): Anthocharis thoosa inghami female, Ex female 19 Mar 2007, Emerged 29 Jan 2011, Hassayampa River, 4600', ARIZONA: Yavapai County. Stan Gorodenski leg. | (Left): Anthocharis julia julia male, 22 Apr 2006, Gregory Canyon, West side Front Range, 5900', COLORADO: Boulder County. Todd L. Stout leg. <br> (Right): Anthocharis julia julia female, Ex ovum 24 Apr 2012, Emerged 23 Apr 2013, SW side CO Hwy 36, Lyons, 6300', COLORADO: Boulder County. Lynn Monroe leg. |
| 2 | 3 | (Left): Anthocharis sara sempervirens male, Ex female 15 Jun 2010, Emerged 1 Mar 2011, Bald Hill Road, 19 - 21 road miles SE US Hwy 101, 3000', CALIFORNIA: Humboldt County. Ken Hansen leg. (Right): Anthocharis sara sempervirens female, Ex female 15 Jun 2010, Emerged 9 Mar 2011, Bald Hill Road, 19 - 21 road miles SE US Hwy 101, 3000', CALIFORNIA: Humboldt County. Ken Hansen leg. | (Left): Anthocharis thoosa inghami male, 24 Feb 1979, Tucson Mts, near Gates Pass, ARIZONA: Pima County. Jim Brock leg. Retained in JBC. <br> (Right): Anthocharis thoosa inghami female, Ex lrv. 4 Mar 1995, Emerged 2 Apr 1999, Pima Canyon 2800', ARIZONA: Pima County. Todd L. Stout leg. | (Left): Anthocharis julia stella male, Ex ovum 13 Jun 2008, Emerged 22 Jan 2009, North Canyon Road, 4.4 miles South of Marlette Peak, $7100^{\prime}$, NEVADA: Carson City, Todd L. Stout leg. (Right): Anthocharis julia stella female, Ex females 13 Jun 2008, Emerged 25 Jan 2009, North Canyon Road, 4.4 miles South of Marlette Pk, 7100' NEVADA: Carson City, Todd L. Stout leg. |
| 2 | 4 | (Left): Anthocharis sara pseudothoosa male, 10 May 1981, Kingsbury Grade, 4 miles West of NV Hwy 206, Carson Range, 7500', NEVADA: Douglas County. George T. Austin leg. (Right): Anthocharis sara pseudothoosa female, Ex ovum 12 Jun 2008, Emerged 1 Feb 2009, North side Desert Creek, 5.6 miles NE Jackass Flatt, Sweetwater Mts, 7500', NEVADA: Douglas County. Todd L. Stout leg. | (Left): Anthocharis thoosa colorado male, Ex female 8 May 2010, Emerged 7 Apr 2013, North side Summit Reservoir, 7400', COLORADO: Montezuma County. Todd L. Stout leg. <br> (Right): Anthocharis thoosa colorado female, Ex female 8 May 2010, Emerged 20 Feb 2015, North side Summit Reservoir, 7400', COLORADO: Montezuma County. Todd L. Stout leg. | (Left): Anthocharis julia prestonorum male Ex ovum 24 May 2008, Emerged 4 Jan 2009, South Branch Edgerton Creek, 2.8 miles west of Carbondale, 6900', COLORADO: Garfield County. Todd L. Stout leg. <br> (Right): Anthocharis julia prestonorum female Ex females 30 Apr 2012, Emerged 24 Apr 2013, Grizzly Creek, 4.1 miles ENE Glenwood Springs, 6100 ', COLORADO: Garfield County. Todd L. Stout leg. |


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| 2 | 5 | (Left): Anthocharis sara sara male, Ex female 13 May 2008, Emerged 8 Jun 2008, Azusa Canyon, Angeles National Forest, 1800', CALIFORNIA: Los Angeles County. Brian Banker leg. (Right): Anthocharis sara sara female Ex female 13 May 2008, Emerged 10 Jun 2008, Azusa Canyon, Angeles National Forest, 1800', CALIFORNIA: Los Angeles County. Brian Banker leg. | (Left): Anthocharis thoosa inghami male, Ex female 19 Mar 2007, Emerged 4 Jan 2008, Hassayampa River, 4600', ARIZONA: Yavapai County. Stan Gorodenski leg. (Right): Anthocharis thoosa inghami female, Ex female 19 Mar 2007, Emerged 29 Jan 2011, Hassayampa River, 4600', ARIZONA: Yavapai County. Stan Gorodenski leg. | (Left): Anthocharis julia nr. prestonorum male Ex female 5 May 2011, Emerged 27 Feb 2012, 0.5 miles NW Dulce Lake, West side NM Hwy 24, 7200', NEW MEXICO: Rio Arriba County. Todd L. Stout leg. <br> (Right): Anthocharis julia nr. prestonorum female Ex female5 May 2011, Emerged 28 Feb 2012, 0.5 miles NW Dulce Lake, West side NM Hwy 24, 7200', NEW MEXICO: Rio Arriba County. Todd L. Stout leg. |
| 2 | 6 | Anthocharis sara sara male, 4 Apr 2008, CA Hwy 78, Vic. Of Scissors Crossing, 1100', CALIFORNIA: San Diego County. Mark Walker leg. | Anthocharis thoosa Hansel Mts. seg. male, Ex female 10 May 2008, Emerged 7 Feb 2010, North Hansel Mts., 4900', IDAHO: Oneida County. Todd L. Stout leg. | Anthocharis julia browningi male, Ex female 26 Apr 2013, Emerged 2 Apr 2014, City Creek Canyon, 2.9 miles NE Salt Lake City, 4800', UTAH: Salt Lake County, Todd L. Stout leg. |
| 2 | 7 | Anthocharis sara sara male, Ex lrv. 17 Apr 2008, Emerged 24 Oct 2008, Queen Lily Campground, North Fork Feather River, 2400' CALIFORNIA: Plumas County. Todd L. Stout leg. | Anthocharis thoosa thoosa male, Ex ovum 4 Apr 2008, Emerged 11 Feb 2010, Quail Hill/ Mokiak Pass, 2.5 miles WNW Seegmiller Mountain, $5100^{\prime}$, ARIZONA: Mohave County. Todd L. Stout leg. | Anthocharis julia flora male, Ex females 12 Apr 2008, Emerged 2 Nov 2008, North side Millcreek Road, 7.2 miles NNE Black Rock, 800', OREGON: Polk County, Dave McNeese leg. |
| 2 | 8 | Anthocharis sara pseudothoosa male, 5 Apr 1981, Kingsbury Grade, 1.4 miles West of NV Hwy 206, Carson Range, 7500 ', NEVADA: Douglas County. George T. Austin leg. | Anthocharis thoosa thoosa male, Ex ovum 4 Apr 2008, Emerged 11 Feb 2010, Quail Hill/ Mokiak Pass, 5100', ARIZONA: Mohave County. Todd L. Stout leg. | Anthocharis julia nr. prestonorum male Ex female 5 May 2011, Emerged 27 Feb 2012, 0.5 miles NW Dulce Lake, West side NM Hwy 24, 7200', NEW MEXICO: Rio Arriba County. Todd L. Stout leg. |
| 2 | 9 | Anthocharis sara pseudothoosa female, Ex ovum 12 Jun 2008, Emerged 1 Feb 2009, North side Desert Creek, 5.6 miles NE Jackass Flatt, Sweetwater Mts, 7500', NEVADA: Douglas County. Todd L. Stout leg. | Anthocharis thoosa inghami female, Ex lrv. 4 Mar 1995, Emerged 14 Jan 1997, Soldier Canyon, Molino Basin, 3000', ARIZONA: Pima County. Todd L. Stout leg. | Anthocharis julia sulfuris male, 7 May 2014, 0.4 miles North of Kellogg High School, 1.3 miles NNW Kellogg, 2400' IDAHO: Shoshone County, Todd L. Stout leg. |
| 2 | 10 | Anthocharis sara sara male, Ex lrv 1 May 2009, Emerged 10 Feb 2010, Glendora Ridge Road, Mt. Baldy Road, 1800', CALIFORNIA: Los Angeles County. Brian Banker leg. | Anthocharis thoosa inghami male, Ex female 22 Feb 2009, Emerged 11 Feb 2010, Sweetwater Trail, Tucson Mts., 2800', ARIZONA: Pima County. Doug Mullens leg. | Anthocharis julia sulfuris male, Ex females 3 Apr 2008, Emerged 29 Oct 2008, Millcreek Road, 7 miles WSW The Dalles, $900^{\prime}$ OREGON: Wasco County, Terry Stoddard leg. |
| 2 | 11 | Anthocharis sara pseudothoosa female, Ex ovum 12 Jun 2008, Emerged 11 Feb 2010, North side Desert Creek, 5.6 miles NE Jackass Flat, Sweetwater Mts, 7500', NEVADA: Douglas County. Todd L. Stout leg. | Anthocharis thoosa Hansel Mts. seg. female, Ex female 10 May 2008, Emerged 10 Feb 2010, North Hansel Mts., 4900', IDAHO: Oneida County. Todd L. Stout leg. | Anthocharis julia prestonorum female Ex ovum 24 May 2008, Emerged 9 Jan 2009, South Branch Edgerton Creek, 2.8 miles west of Carbondale, 6900', COLORADO: Garfield County. Todd L. Stout leg. |


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| 3 | 1 | Anthocharis sara sara fifth instar caterpillar, Ex. lrv. 17 Apr 2008, Queen Lily Campground, North Fork Feather River, $2400^{\prime}$ CALIFORNIA: Plumas County. Todd L. Stout leg. | Anthocharis thoosa thoosa fifth instar caterpillar, Ex ovum 4 Apr 2008, Quail Hill/ Mokiak Pass, 5100', ARIZONA: Mohave County. Todd L. Stout leg. | Anthocharis julia julia fifth instar caterpillar, Ex ovum 15 Jun 2012, Beaver Creek; North of Fairplay; CR 655, 10900', COLORADO: Park County. Todd L. Stout leg. |
| 3 | 2 | Anthocharis sara sara fifth instar caterpillar, Ex female13 May 2008, Azusa Canyon, Angeles National Forest, 1800', CALIFORNIA: Los Angeles County. Brian Banker leg. | Anthocharis thoosa Hansel Mts. seg. fifth instar caterpillar, Ex ovum 4 May 2007, 3.8 miles SE Snowville, Hansel Mts., 5200', UTAH: Box Elder County. Todd L. Stout leg. | Anthocharis julia prestonorum fifth instar caterpillar, Ex lrv. 24 May 2008, Grizzly Creek, 4.1 miles ENE Glenwood Springs, 6100', COLORADO: Garfield County. Todd L. Stout leg. |
| 3 | 3 | Anthocharis sara gunderi fifth instar caterpillar, Ex female 9 Apr 2010, Hermit Gulch Trail, Catalina Island, 300', CALIFORNIA: Los Angeles County, Jim Brock leg. | Anthocharis thoosa inghami fifth instar caterpillar, Ex lrv. 27 Mar 2007, Rattlesnake Canyon, Santa Catalina Mts, 3100', ARIZONA: Pima County. Jim Brock leg. | Anthocharis julia browningi fifth instar caterpillar, Ex ovum 1 May 2009, City Creek Canyon; 2.0 miles NNE Salt Lake City, 5100', UTAH: Salt Lake County. Todd L. Stout leg. |
| 3 | 4 | Anthocharis sara pseudothoosa fifth instar caterpillar, Ex lrv. 12 Jun 2008, Jackass Creek, NFR 067, Sweetwater Mts., 7300', NEVADA: Douglas County. Todd L. Stout leg. | Anthocharis thoosa colorado fifth instar caterpillar, Ex lrv. 28 Apr 2009, McElmo Creek, County Road G, 11.3 miles West of Cortez, 5800', COLORADO: Montezuma County. Todd L. Stout leg. (Location courtesy Mike Fisher) | Anthocharis julia sulfuris fifth instar caterpillar, Ex ovum 7 May 2014, Elk Creek Road, 2.2 miles east of Kellogg, 2400' IDAHO: Shoshone County, Todd L. Stout leg. |
| 3 | 5 | Anthocharis sara pseudothoosa fifth instar caterpillar, Ex ovum 12 Jun 2008, North side Desert Creek, 5.6 miles NE Jackass Flat, Sweetwater Mts, 7500', NEVADA: Douglas County. Todd L. Stout leg. | Anthocharis thoosa colorado fifth instar caterpillar, Ex lrv. 29 Apr 2009, Carbon Junction Canyon, 2.7 miles SSE Durango, 6600', COLORADO: La Plata County. Todd L. Stout leg. | Anthocharis julia stella fifth instar caterpillar, Ex females 13 Jun 2008, North Canyon Road, 4.4 miles South of Marlette Peak, 7100', NEVADA: Carson City, Todd L. Stout leg. |
| 3 | 6 | Anthocharis sara sempervirens fifth instar caterpillar, Ex female 15 Jun 2010, Bald Hill Road, 19 - 21 road miles SE US Hwy 101, $3000^{\prime}$, CALIFORNIA: Humboldt County. Ken Hansen leg. | Anthocharis thoosa coriande fifth instar caterpillar, Ex lrv. 7 May 2010, 0.5 miles west of La Cueva Canyon, 2.4 miles ESE Glorieta, 7400', NEW MEXICO: Santa Fe County. Todd L. Stout leg. | Anthocharis julia flora fifth instar caterpillar, Ex female 25 Apr 2007, Cowiche Creek, T13 $5 \mathrm{~N}, \mathrm{R} 16 \mathrm{E}, 5.5$ miles West of Cowiche, 2300', WASHINGTON: Yakima County, Gary Pearson leg. |
| 3 | 7 | Anthocharis sara sempervirens fifth instar caterpillar, Ex female 15 Jun 2010, Bald Hill Road, 19 - 21 road miles SE US Hwy 101, $3000^{\prime}$, CALIFORNIA: Humboldt County. Ken Hansen leg. | Anthocharis thoosa coriande fifth instar caterpillar, Ex lrv. 6 May 2010, 1.5 miles SSE La Ventana; 16 miles South of Cuba, US Hwy 550, 6600', NEW MEXICO: Sandoval County. Todd L. Stout leg. | Anthocharis julia alaskensis fifth instar caterpillar, Ex females 4-5 Jun 2007, Mile 8.5; 1.6 miles SW Tukgahgo Mountain, 1000', ALASKA: Kenelm Philip leg. |


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| 7 | 1 | Anthocharis sara sara pupa, Ex. lrv. 17 Apr 2008, Queen Lily Campground, North Fork Feather River, 2400' CALIFORNIA: Plumas County. Todd L. Stout leg. | Anthocharis thoosa thoosa pupa, Ex ovum 25 Mar 2014, Quail Hill/Mokiak Pass, 5100', ARIZONA: Mohave County. Todd L. Stout leg. | Anthocharis julia julia pupa, Ex females 2 Jun 2007, Yellow Pine Campground; 0.9 m South of Pole Mountain; Happy Jack Recreation Area, 8500', WYOMING: Albany County. Todd L. Stout leg. |
| 7 | 2 | Anthocharis sara sara pupa, Ex lrv 1 May 2009, Glendora Ridge Road and Mt. Baldy Road, San Gabriel Mts., 1800', CALIFORNIA: Los Angeles County. Brian Banker leg. | Anthocharis thoosa thoosa pupa, Ex ovum 14 Apr 2007, Gardner Creek, 2.7 miles NNE of Nephi; Wasatch Mts., 5500', UTAH: Juab County. Todd L. Stout leg. | Anthocharis julia prestonorum pupa, Ex lrv. 24 May 2008, Grizzly Creek, 4.1 miles ENE Glenwood Springs, 6100', COLORADO: Garfield County. Todd L. Stout leg. |
| 7 | 3 | Anthocharis sara gunderi pupa, Ex female 12 Mar 2013, Divide Road, 1.8 miles west of Avalon, Catalina Island, 1400', CALIFORNIA: Los Angeles County, Mark Walker leg. | Anthocharis thoosa inghami, Ex female 19 Mar 2007, Hassayampa River, 4600', ARIZONA: Yavapai County. Stan Gorodenski leg. | Anthocharis julia browningi pupa, Ex female 26 Apr 2013, City Creek Canyon; 2.0 miles NNE Salt Lake City, 5100', UTAH: Salt Lake County. Todd L. Stout leg. |
| 7 | 4 | Anthocharis sara pseudothoosa pupa, Ex lrv. 12 Jun 2008, Jackass Creek, NFR 067, Sweetwater Mts., 7300', NEVADA: Douglas County. Todd L. Stout leg. | Anthocharis thoosa colorado pupa, Ex lrv. 6 May 2010, McElmo Creek, County Road G, 11.3 miles West of Cortez, 5800', COLORADO: Montezuma County. Todd L. Stout leg. | Anthocharis julia sulfuris pupa, Ex ovum 4 May 2007, Bogus Basin Hwy, 3.8 miles SW of Little Deer Point, 5200' IDAHO: Boise County, Todd L. Stout leg. |
| 7 | 5 | Anthocharis sara sempervirens pupa, Ex female 15 Jun 2010, Bald Hill Road, 19 - 21 road miles SE US Hwy 101, 3000', CALIFORNIA: Humboldt County. Ken Hansen leg. | Anthocharis thoosa colorado pupa, Ex lrv. 29 Apr 2009, Carbon Junction Canyon, 2.7 miles SSE Durango, 6600', COLORADO: La Plata County. Todd L. Stout leg. | Anthocharis julia stella pupa, Ex females 13 Jun 2008, North Canyon Road, 4.4 miles South of Marlette Peak, $7100^{\prime}$, NEVADA: Carson City, Todd L. Stout leg. |
| 7 | 6 | Anthocharis sara sara pupa, Ex. ova 17 Apr 2008, Ash Creek Road; North side CA Hwy 96; Siskiyou Range, 2100' CALIFORNIA: Siskiyou County. Todd L. Stout leg. | Anthocharis thoosa coriande pupa, Ex lrv. 7 May 2010, 0.5 miles west of La Cueva Canyon, 2.4 miles ESE Glorieta, 7400 ', NEW MEXICO: Santa Fe County. Todd L. Stout leg. | Anthocharis julia flora pupa, Ex female 25 Apr 2007, Cowiche Creek, T13 5N, R16E, 5.5 miles West of Cowiche, 2300', WASHINGTON: Yakima County, Gary Pearson leg. |
| 7 | 7 | Anthocharis sara sara pupa, Ex. ova 17 Apr 2008, Ash Creek Road; North side CA Hwy 96; Siskiyou Range, 2100' CALIFORNIA: Siskiyou County. Todd L. Stout leg. | Anthocharis thoosa coriande pupa, Ex female 26 Mar 2007, 5.8 miles SSW Manzano Peak; Belen; Manzano Range, 6500', NEW MEXICO: Valencia County. Dave Ferguson leg. | Anthocharis julia alaskensis pupa, Ex females 4-5 Jun 2007, Mile 8.5; 1.6 miles SW Tukgahgo Mountain, 1000', ALASKA: Kenelm Philip leg. |
| 8 | 1 | Anthocharis sara sara female, 1 May 2004, 1 mile ESE Mt. Manchester, Dead Mountains, 2000', CALIFORNIA: San Bernardino County. Mark Walker/Brian Banker leg. | Anthocharis thoosa thoosa female, Ex ovum 15 Mar 2008, Emerged 1 Feb 2011, 0.3 miles SE Christmas Tree Pass, Newberry Mts., 4100', NEVADA: Clark County. Todd L. Stout leg. | n/a |


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| 8 | 2 | Anthocharis sara sara female, 4 Apr 1989, Brand Park, 2 miles NW Glendale, Verdugo Mts., 1000', CALIFORNIA: Los Angeles County, Todd L. Stout leg. | Anthocharis thoosa thoosa female, Ex ovum 15 Mar 2008, Emerged 20 Feb 2012, 0.3 miles SE Christmas Tree Pass, Newberry Mts., 4100', NEVADA: Clark County. Todd L. Stout leg. | n/a |
| 10 | 1 | Anthocharis sara sara male, Ex ovum 6 May 2006, Emerged 3 Mar 2007, Klamath River Canyon, 0.2 miles SSE Boyle Power Plant, $3700^{\prime}$ OREGON: Klamath County. Todd L. Stout leg. | Anthocharis julia nr. sulfuris male, Ex females 6 May 2006, Emerged 9 Mar 2007, Klamath River Canyon, 0.2 miles SSE Boyle Power Plant, 3700' OREGON: Klamath County. Todd L. Stout leg. | Anthocharis julia nr. sulfuris male, Ex females 6 May 2006, Emerged 6 Mar 2007, Klamath River Canyon, 0.2 miles SSE Boyle Power Plant, 3700' OREGON: Klamath County. Todd L. Stout leg. |
| 10 | 2 | n/a | Anthocharis julia nr. sulfuris male, Ex females 6 May 2006, Emerged 3 Mar 2007, Klamath River Canyon, 0.2 miles SSE Boyle Power Plant, 3700' OREGON: Klamath County. Todd L. Stout leg. | Anthocharis julia nr. sulfuris male, Ex females 6 May 2006, Emerged 4 Mar 2007, Klamath River Canyon, 0.2 miles SSE Boyle Power Plant, 3700' OREGON: Klamath County. Todd L. Stout leg. |
| 12 | 1 | Anthocharis thoosa thoosa male, 17 May 2014, Clear Creek Road, 9.7 miles North of Park Valley, Raft River Range, 6300' UTAH: Box Elder County. Todd L. Stout leg. | Anthocharis julia sulfuris male, 24 May 2014, Clear Creek Road, 9.3 miles North of Park Valley, Raft River Range, 6900' UTAH: Box Elder County. Todd L. Stout leg. | n/a |
| 12 | 2 | Anthocharis thoosa thoosa male, 17 May 2014, Clear Creek Road, 9.7 miles North of Park Valley, Raft River Range, 6300' UTAH: Box Elder County. Todd L. Stout leg. | Anthocharis julia sulfuris male, 17 May 2014, Clear Creek Road, 9.7 miles North of Park Valley, Raft River Range, 6400' UTAH: Box Elder County. Todd L. Stout leg. | n/a |
| 12 | 3 | Anthocharis thoosa thoosa male, 17 May 2014, Clear Creek Road, 9.7 miles North of Park Valley, Raft River Range, 6300' UTAH: Box Elder County. Todd L. Stout leg. | Anthocharis julia sulfuris male, 17 May 2014, Clear Creek Road, 9.7 miles North of Park Valley, Raft River Range, 6300' UTAH: Box Elder County. Todd L. Stout leg. | n/a |
| 12 | 4 | Anthocharis thoosa thoosa male, 24 May 2014, Clear Creek Road, 9.3 miles North of Park Valley, Raft River Range, 6900' UTAH: Box Elder County. Todd L. Stout leg. | Anthocharis julia sulfuris male, 17 May 2014, Clear Creek Road, 9.7 miles North of Park Valley, Raft River Range, 6300' UTAH: Box Elder County. Todd L. Stout leg. | n/a |
| 12 | 5 | Anthocharis thoosa thoosa male, 24 May 2014, Clear Creek Road, 9.3 miles North of Park Valley, Raft River Range, 6900' UTAH: Box Elder County. Tony Jones leg. | Anthocharis julia sulfuris female, 24 May 2014, Clear Creek Road, 9.3 miles North of Park Valley, Raft River Range, 6900' UTAH: Box Elder County. Todd L. Stout leg. | n/a |


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| 13 |  | A. thoosa thoosa ( x A. julia sulfuris?) male, 17 May 2014, Clear Creek Road, 9.3 miles North of Park Valley, Raft River Range, 6900' UTAH: Box Elder County. Todd L. Stout leg. | n/a | n/a |
| 14 |  | A. julia sulfuris male, 30 Apr 1981, South Willow Canyon, Stansbury Range, UTAH: Tooele County. Oscar Dorfman leg. | A. julia sulfuris female, 25 Jun 1982, South Willow Canyon, Stansbury Range, UTAH: Tooele County. Oscar Dorfman leg. | n/a |
| 15 | 1 | Anthocharis thoosa thoosa male, Ex ovum 18 May 2010, Emerged 5 Apr 2014, Huntington Canyon, 0.5 miles North of PacifiCorp Huntington Plant, North side UT Hwy 31, $6500^{\prime}$ UTAH: Emery County. Todd L. Stout leg. | Anthocharis julia sulfuris male, Ex ovum 30 May 2014, Emerged 10 Mar 2015, Rilda Canyon Road, Vic. Utah Hwy 31, Huntington Canyon, 7000' UTAH: Emery County. Todd L. Stout leg. | n/a |
| 15 | 2 | A. thoosa thoosa $\times$ A. julia sulfuris male, Ex ovum 6 May 2015, Emerged 20 Apr 2016, Rilda Canyon Road, Vic. Utah Hwy 31, Huntington Canyon, 7000' UTAH: Emery County. Todd L. Stout leg. | n/a | n/a |
| 17 |  | Anthocharis julia sulfuris male, Ex ovum 24 May 2012, Emerged 1 Apr 2013, Little Horse Canyon Road, 7.6 miles SE of Carbon, Book Cliffs, 7900' UTAH: Emery County. Todd L. Stout leg. | Anthocharis julia sulfuris male, Ex ovum 24 May 2012, Emerged 27 Mar 2013, Little Horse Canyon Road, 7.6 miles SE of Carbon, Book Cliffs, 7900' UTAH: Emery County. Todd L. Stout leg. | n/a |
| 18 | 1 | Anthocharis thoosa thoosa male, Ex ovum 4 Apr 2008, Emerged 11 Feb 2010, Quail Hill/ Mokiak Pass, 2.5 miles WNW Seegmiller Mountain, 5100', ARIZONA: Mohave County. Todd L. Stout leg. | Anthocharis julia browningi $\times$ Anthocharis thoosa thoosa male, Ex parental female $A$. julia browningi 19 Apr 2014, Emerged 6 Mar 2015, North Creek, 3.8 miles NE of Mona, Wasatch Mts., 6100' UTAH: Juab County. Todd L. Stout leg. | Anthocharis julia browningi male, Ex female 26 Apr 2013, Emerged 2 Apr 2014, City Creek Canyon, 2.9 miles NE of Salt Lake City, 5100 ', UTAH: Salt Lake County. Todd L. Stout leg. |
| 18 | 2 | Anthocharis thoosa thoosa male, Ex ovum 4 Apr 2008, Emerged 31 Jul 2011, Quail Hill/ Mokiak Pass, 2.5 miles WNW Seegmiller Mountain, 5100', ARIZONA: Mohave County. Todd L. Stout leg. | Anthocharis julia browningi $\times$ Anthocharis thoosa thoosa male, Ex parental female $A$. julia browningi 19 Apr 2014, Emerged 9 Mar 2015, North Creek, 3.8 miles NE of Mona, Wasatch Mts., 6100' UTAH: Juab County. Todd L. Stout leg. | Anthocharis julia browningi male, Ex female24 Apr 2014, Emerged 12 Mar 2015, City Creek Canyon, 2.9 miles NE of Salt Lake City, 5100', UTAH: Salt Lake County. Todd L. Stout leg. |


| $\dot{. \dot{x}}$ | 3 | Column 1 | Column 2 | Column 3 |
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| 18 | 3 | Anthocharis thoosa thoosa female, Ex ovum 4 Apr 2008, Emerged 22 Feb 2012, Quail Hill/ Mokiak Pass, 2.5 miles WNW Seegmiller Mountain, 5100', ARIZONA: Mohave County. Todd L. Stout leg. | Anthocharis julia browningi $\times$ Anthocharis thoosa thoosa female, Ex parental female $A$. julia browningi 19 Apr 2014, Emerged 13 Apr 2015, North Creek, 3.8 miles NE of Mona, Wasatch Mts., 6100' UTAH: Juab County. Todd L. Stout leg. | Anthocharis julia browningi female, Ex female26 Apr 2013, Emerged 5 Apr 2014, City Creek Canyon, 2.9 miles NE of Salt Lake City, 5100', UTAH: Salt Lake County. Todd L. Stout leg. |
| 20 | 1 | Anthocharis thoosa colorado female, Ex female 8 May 2010, Emerged 20 Feb 2015, North side Summit Reservoir, 7.7 miles NW of Mancos, 7400', COLORADO: Montezuma County. Todd L. Stout leg. | Anthocharis julia nr. prestonorum female, Ex ovum 6 May 2011, Emerged 5 Mar 2012, Target Tree Recreation Area, 5.7 miles East of Mancos, 7700', COLORADO: La Plata County. Todd L. Stout leg. | Anthocharis julia prestonorum female Ex lrv 24 May 2008, Emerged 5 Jan 2009, Grizzly Creek, 4.1 miles ENE Glenwood Springs, 6100', COLORADO: Garfield County. Todd L. Stout leg. |
| 20 | 2 | Anthocharis thoosa colorado female, Ex female 8 May 2010, Emerged 6 Apr 2014, North side Summit Reservoir, 7.7 miles NW of Mancos, 7400', COLORADO: Montezuma County. Todd L. Stout leg. | Anthocharis julia nr. prestonorum female, Ex lrv. 13 May 2009, Emerged 16 Feb 2010, Target Tree Recreation Area, 5.7 miles East of Mancos, 7700', COLORADO: La Plata County. Todd L. Stout leg. | Anthocharis julia prestonorum female Ex females 30 Apr 2012, Emerged 24 Apr 2013, Grizzly Creek, 4.1 miles ENE Glenwood Springs, 6100', COLORADO: Garfield County. Todd L. Stout leg. |
| 20 | 3 | Anthocharis thoosa colorado female, Ex female 8 May 2010, Emerged 7 Apr 2013, North side Summit Reservoir, 7.7 miles NW of Mancos, 7400', COLORADO: Montezuma County. Todd L. Stout leg. | Anthocharis julia nr. prestonorum female, Ex ovum 6 May 2011, Emerged 1 Mar 2012, Target Tree Recreation Area, 5.7 miles East of Mancos, 7700', COLORADO: La Plata County. Todd L. Stout leg. | Anthocharis julia prestonorum female Ex females 30 Apr 2012, Emerged 5 Apr 2013, Grizzly Creek, 4.1 miles ENE Glenwood Springs, 6100', COLORADO: Garfield County. Todd L. Stout leg. |
| 20 | 4 | Anthocharis thoosa colorado male, Ex female 8 May 2010, Emerged 10 Feb 2012, North side Summit Reservoir, 7.7 miles NW of Mancos, $7400^{\prime}$, COLORADO: Montezuma County. Todd L. Stout leg. | Anthocharis julia nr. prestonorum male, Ex ovum 13 May 2009, Emerged 14 Feb 2010, Target Tree Recreation Area, 5.7 miles East of Mancos, 7700', COLORADO: La Plata County. Todd L. Stout leg. | Anthocharis julia prestonorum male Ex females 30 Apr 2012, Emerged 29 Mar 2013, Grizzly Creek, 4.1 miles ENE Glenwood Springs, 6100', COLORADO: Garfield County. Todd L. Stout leg. |
| 22 | 1 | Anthocharis thoosa colorado female, Ex ovum 29 Apr 2009, Emerged 13 Feb 2010, Carbon Junction Canyon, 2.7 miles SSE Durango, 6600', COLORADO: La Plata County. Todd L. Stout leg. | Anthocharis julia nr. prestonorum female, Ex female 13 May 2009, Emerged 17 Feb 2010, Lower Wildcat Canyon, 2.5 miles WSW Durango, 6800', COLORADO: La Plata County. Todd L. Stout leg. | n/a |
| 22 | 2 | Anthocharis thoosa colorado male, Ex ovum 29 Apr 2009, Emerged 10 Feb 2010, Carbon Junction Canyon, 2.7 miles SSE Durango, 6600', COLORADO: La Plata County. Todd L. Stout leg. | Anthocharis julia nr. prestonorum male, Ex female 13 May 2009, Emerged 17 Feb 2010, Lower Wildcat Canyon, 2.5 miles WSW Durango, 6800', COLORADO: La Plata County. Todd L. Stout leg. | n/a |


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| 24 | 1 | Anthocharis julia nr. prestonorum male, Ex females 5 May 2011, Emerged 6 Mar 2012, Lower Piedra Campground, SSW of Mule Mountain, 6600', COLORADO: Archuleta County. Todd L. Stout leg. (same data as pupa) | Anthocharis julia nr. prestonorum female, Ex females 5 May 2011, Emerged 3 Mar 2012, Lower Piedra Campground, SSW of Mule Mountain, 6600', COLORADO: Archuleta County. Todd L. Stout leg. (same data as pupa) | n/a |
| 24 | 2 | Anthocharis julia nr. prestonorum male, 5 May 2011, Lower Piedra Campground, SSW of Mule Mountain, 6600', COLORADO: Archuleta County. Todd L. Stout leg. | Anthocharis julia nr. prestonorum female, Ex females 5 May 2011, Emerged 5 Mar 2012, Lower Piedra Campground, SSW of Mule Mountain, 6600', COLORADO: Archuleta County. Todd L. Stout leg. (same data as pupa) | $\mathrm{n} / \mathrm{a}$ |
| 24 | 3 | Anthocharis julia nr. prestonorum male, 5 May 2011, Lower Piedra Campground, SSW of Mule Mountain, 6600', COLORADO: Archuleta County. Todd L. Stout leg. | Anthocharis julia nr. prestonorum female, Ex ovum 5 May 2011, Emerged 29 Feb 2012, Lower Piedra Campground, SSW of Mule Mountain, 6600', COLORADO: Archuleta County. Todd L. Stout leg. (same data as pupa) | n/a |
| 24 | 4 | Anthocharis julia nr. prestonorum male, Ex females 5 May 2011, Emerged 1 Mar 2012, Lower Piedra Campground, SSW of Mule Mountain, 6600', COLORADO: Archuleta County. Todd L. Stout leg. (same data as pupa) | Anthocharis julia nr. prestonorum female, Ex females 5 May 2011, Emerged 3 Mar 2012, Lower Piedra Campground, SSW of Mule Mountain, 6600', COLORADO: Archuleta County. Todd L. Stout leg. (same data as pupa) | n/a |
| 25 | 1 | Anthocharis julia nr. prestonorum male, Ex female 5 May 2011, Emerged 25 Feb 2012, 0.5 miles NW Dulce Lake, West side NM Hwy 74, 7100', NEW MEXICO: Rio Arriba County. Todd L. Stout leg. (same data as pupa) | Anthocharis julia nr. prestonorum female, Ex female 5 May 2011, Emerged 28 Feb 2012, 0.5 miles NW Dulce Lake, West side NM Hwy 74, 7100', NEW MEXICO: Rio Arriba County. Todd L. Stout leg. (same data as pupa) | n/a |
| 25 | 2 | Anthocharis julia nr. prestonorum male, Ex female 5 May 2011, Emerged 27 Feb 2012, 0.5 miles NW Dulce Lake, West side NM Hwy 74, 7100', NEW MEXICO: Rio Arriba County. Todd L. Stout leg. (same data as pupa) | Anthocharis julia nr. prestonorum female, Ex female 5 May 2011, Emerged 1 Mar 2012, 0.5 miles NW Dulce Lake, West side NM Hwy 74, 7100', NEW MEXICO: Rio Arriba County. Todd L. Stout leg. (same data as pupa) | n/a |


| in in | 3 | Column 1 | Column 2 | Column 3 |
| :---: | :---: | :---: | :---: | :---: |
| 25 | 3 | Anthocharis julia nr. prestonorum male, Ex female 5 May 2011, Emerged 25 Feb 2012, 0.5 miles NW Dulce Lake, West side NM Hwy 74, 7100', NEW MEXICO: Rio Arriba County. Todd L. Stout leg. (same data as pupa) | Anthocharis julia nr. prestonorum female, Ex female 5 May 2011, Emerged 1 Mar 2012, 0.5 miles NW Dulce Lake, West side NM Hwy 74, 7100', NEW MEXICO: Rio Arriba County. Todd L. Stout leg. (same data as pupa) | $\mathrm{n} / \mathrm{a}$ |
| 25 | 4 | Anthocharis julia nr. prestonorum male, Ex female 5 May 2011, Emerged 27 Feb 2012, 0.5 miles NW Dulce Lake, West side NM Hwy 74, 7100', NEW MEXICO: Rio Arriba County. Todd L. Stout leg. (same data as pupa) | Anthocharis julia nr. prestonorum female, Ex female 5 May 2011, Emerged 28 Feb 2012, 0.5 miles NW Dulce Lake, West side NM Hwy 74, 7100', NEW MEXICO: Rio Arriba County. Todd L. Stout leg. (same data as pupa) | $\mathrm{n} / \mathrm{a}$ |


[^0]:    Stout, Todd L., "A review of three species-level taxa of the Anthocharis sara complex (Lepidoptera: Pieridae: Pierinae: Anthocharidini)" (2018). Insecta Mundi. 1133.
    https://digitalcommons.unl.edu/insectamundi/1133

