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A REVIEW OF THE *THESSALIA LEANIRA* COMPLEX IN THE SOUTHWESTERN UNITED STATES (NYMPHALIDAE: MELITAEINAE), WITH A DESCRIPTION OF TWO NEW SUBSPECIES OF *THESSALIA FULVIA*

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The checkerspot butterflies of the *Thessalia leanira* (Felder & Felder) complex are distributed over a large area of the southwestern United States and Mexico. Bauer's revision (in Howe, 1975) recognized three closely related species involved in the complex in the United States: *Thessalia leanira*, *Thessalia fulvia* (Edwards), and *Thessalia cyneas* (Godman & Salvin). Ecological and biological data clearly verify the separation of *T. cyneas* as a species; however, the relationship between *T. leanira* and *T. fulvia* remains confused. Populations of this complex are found from southern Oregon into Baja California, Mexico; east to south-central Nebraska, south through Texas, into northern Mexico. *T. cyneas* is also found further south into southern Mexico (Fig. 1). W. G. Wright (1905), Ferris & Brown (1981), Hodges (1983), and Scott (1986) have treated the *T. leanira* group with varying points of view. The confusing relationship between *T. leanira* and *T. fulvia* apparently demonstrates few of the classic criteria which permit clear assignment to separate species status as opposed to subspecies or semi-species.

Thessalia cyneas (Godman & Salvin), 1878

The Cyneas Checkerspot is a very distinct species that is distributed in the United States in a very restricted portion of the southwest, in a few mountain ranges of southeastern Arizona. To date, it has only been recorded in the Huachuca Mts., Mule Mts., and the Chiricahua Mts., all in Cochise County, Arizona. *T. cyneas* (Figs. 8-10) is distinguished dorsally by a solid brown-black wing surface, with creamy-yellow median and submarginal bands, and orange-red spots along the margin of the DHW. The VHW is creamy-yellow with no other markings except for black along the veins and checkering along the submarginal band. It shows little sexual dimorphism, except for the larger size of the female specimens. There is relatively little variation within a series of Arizona and Sonora, Mexico, specimens. *T. cyneas* occurs at higher elevations than *T. fulvia*, with the former

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species found more commonly in the upper Madrean (Oak) Evergreen Woodland and Madrean Conifer Forest habitats (or biotic communities [Brown, 1982]), and along the upper ridges within these mountains. In Sonora, Mexico, it occurs in the same habitats and tends to patrol the dirt roads there. Its distribution through Mexico extends to the state of Durango and beyond. The mountains of southwestern New Mexico can be expected to contain *T. cyneas* colonies. Males patrol along the upper rocky ridges and dirt roads, and both sexes are drawn to moisture and nectar in the higher canyon bottoms.

The life history of *T. cyneas* is fairly well known in both the United States and Mexico. Females readily oviposit in captivity on various species of *Castilleja* (Indian Paintbrush) and the resulting larvae feed to pupation on the same plants. Larvae have also been found in nature on *Brachystigma wrightii* (Gray) (Roever, pers. comm.) and on a *Castilleja* species (Mullins, pers. comm.), both in the Huachuca Mts. In Mexico, larvae have been found on other species of Scrophulariaceae (Mori, Mullins, in litt.). Larval appearance is similar to that of *T. fulvia*, but the body color of *T. cyneas* is more lemon-yellow with black around the base of the spines, giving a much brighter appearance to the larvae than in the yellow-patched *T. fulvia*. The head capsule is orange-red.

T. cyneas adults have been collected from April through November in Arizona, which suggests a series of continuous broods throughout the season, with rainfall the primary controlling factor. The butterfly is usually most common in the fall, after the summer rainy season. All United States records to date are from Cochise County, Arizona. Most of the recent records have been from the canyons on the eastern slope of the Huachuca Mts., especially in Miller, Carr and Garden canyons. One recent record was from the Mule Mts., north of Bisbee (Bailowitz, pers. comm.). There are several old museum records from the Chiricahua Mts., but no recent sightings of *T. cyneas* have been documented in this well-collected mountain range. The existing colonies in the Huachuca Mts. seem to be well established, but this species should be closely monitored in Arizona to see if it disappears as apparently did *Speyeria nokomis coerulescens* (Holland) and *Apodemia phyciodoides* (Barnes & Benjamin). *T. cyneas* is obviously an essentially Mexican species that barely occurs in southeastern Arizona, as do so many other species.

The Taxonomic Status of *T. leanira* and *T. fulvia*

The relationship between *T. leanira* and *T. fulvia* has been the topic of discussion by several workers. *T. fulvia* has been variously designated a distinct species by some, and a subspecies of *T. leanira* by others. As discussed by Bauer (1975), *T. leanira* has applied to the western population and *T. fulvia* has applied to the eastern portion of the range (Fig. 1). Bauer considered the two forms as separate species, based on consistent adult differences. More recently, Ferris and Brown (1981) and Scott (1986) considered *T. fulvia* to be a subspecies of *T. leanira*, partly as a result of the revision of the Melitaeinae by Higgins (1960). The current disagreements over what exactly a species is (e.g. interbreeding vs. no interbreeding, etc.) further aggravate the dilemma (Angevine and Brussard, 1979; Brussard, et. al, 1985; Burns, 1964; Burns, 1975; Ehrlich and Murphy, 1983; Geiger and Shapiro, 1986; Peigler, 1985; Scott, 1980; Scott, 1986; Shapiro, 1975; Shapiro, 1983; Vawter and Wright, 1986). *T. leanira* and *T. fulvia* understandably could be called either species or subspecies based on the evolving concepts. The adults of each have consistent characteristics that remain constant throughout their ranges (Figs. 2-7). *T. leanira* is characterized by a black mark in the VHW costal margin discal area (above the discal cell); is only weakly sexually dimorphic; has the presence of black scaling enclosing the VHW discal cell, without an inverted "Y" mark; has red-orange palpi with minimal black shading dorsally; has a black body color with no orange scaling; and is essentially single brooded with adults flying in the late spring (some fall specimens have been taken in years of unusually heavy summer rains). *T. fulvia* is distinct from *T. leanira* due to the absence of the black mark on the VHW costal margin space; is more sexually dimorphic with the females consistently lighter than the males; has an absence of the black scales enclosing the VHW discal cell, with an inverted "Y" mark in that area; has black palpi with white on the ventral surface; has orange scaling over the black body color; and is multiple brooded

throughout most, or all, of its range. The larval stages of the two species are also distinctly different. The mature larvae of *T. leanira* have black head capsules, while those of *T. fulvia* have red-orange head capsules. These characteristics are summarized for each species in Table 1. Based on these factors, and the stability of these differentiating characteristics throughout the range of the complex, we consider *T. leanira* and *T. fulvia* to be separate, distinct species.

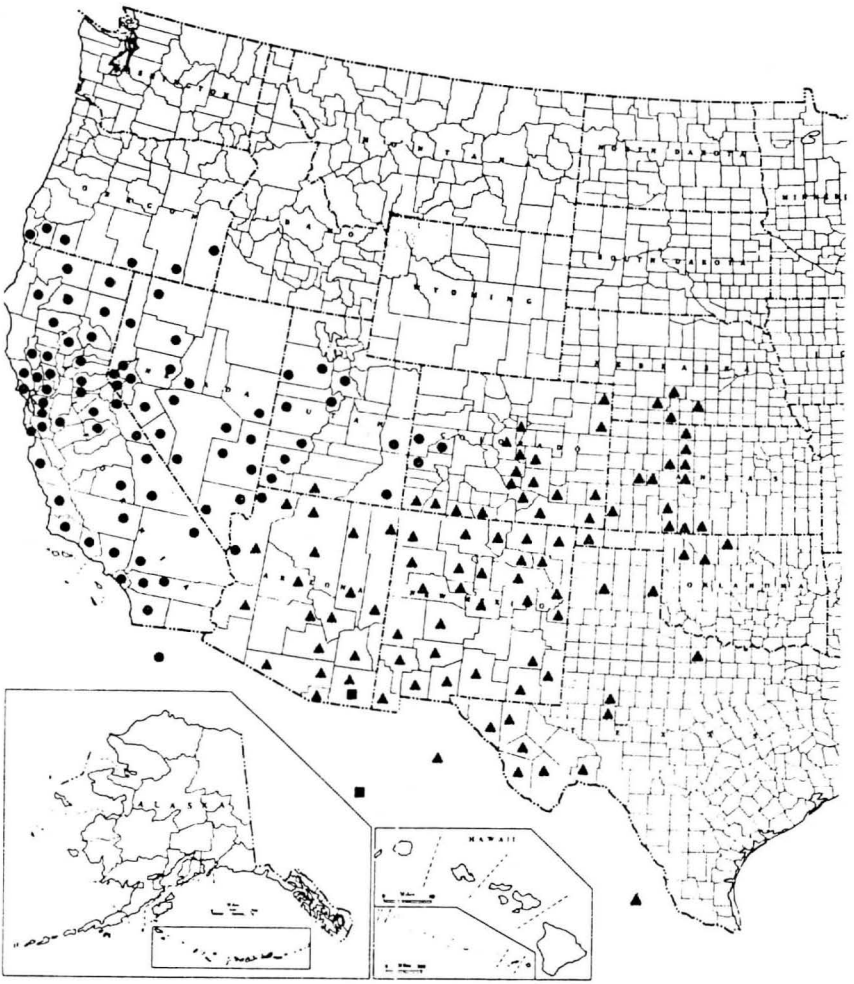
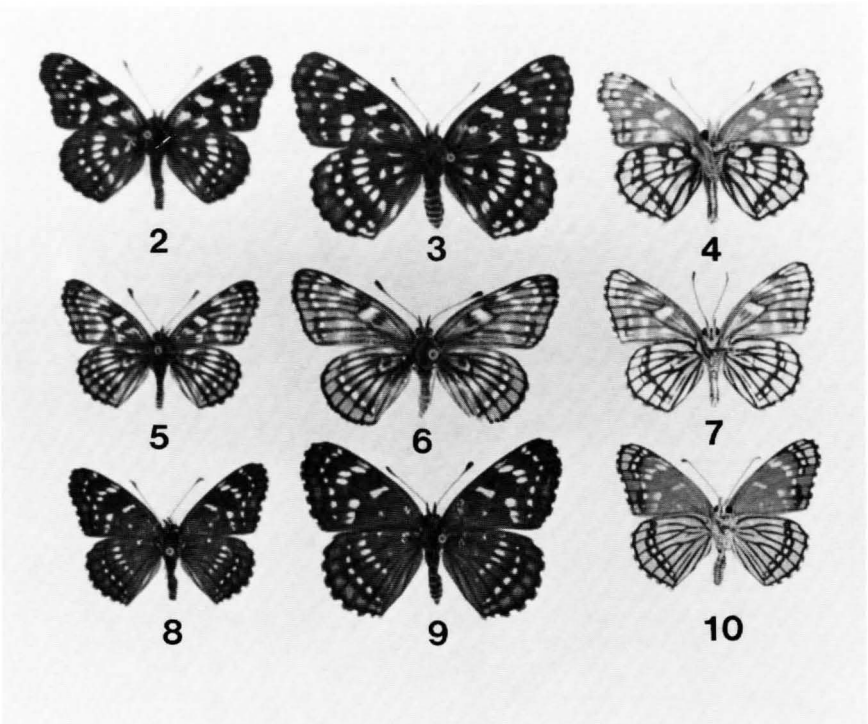


Figure 1: Distribution of species of the *Thessalia leanira* complex. ● = *Thessalia leanira*; ► = *Thessalia fulvia*; ■ = *Thessalia cyneas*,

Thessalia fulvia (Edwards), 1879

The Fulvia Checkerspot is distributed from southern Utah (Kane County) through Arizona, New Mexico, Colorado and into west Texas. Populations also occur in Nebraska, Kansas and Oklahoma (Fig. 19). Its distribution is known to extend into northern Mexico as well. At least three distinct taxa can be recognized within the *T. fulvia* group and we name here two of these taxa as new subspecies. There is also a large area of populations in northern Arizona and northern New Mexico that we refer to as a region of unassigned populations awaiting further study for assignment to a particular subspecies. It appears that a fourth taxon may be named from this region. The three recognized subspecies can be separated from each other by characteristics which are discussed below and which remain fairly constant for each taxon. Available distribution data indicate that there may be geographical separation of the subspecies as well. *T. fulvia* is most often found flying along hilltops and ridges on the edges of mountain ranges, or on the higher knobs in less mountainous terrain. Males have also been observed patrolling along hillsides and in forests in the vicinity of the larval foodplants. Females fly around the larval foodplant. Larvae are distinctive with orange to yellow-orange patches on each segment, satiny-black spiny bodies, and red-orange head capsules. The only documented larval foodplants are several



Figures 2-10: Species in the *Thessalia leanira* complex. **2-4**: *Thessalia leanira*, male upperside (**2**), female upperside (**3**), and male underside (**4**). **5-7**: *Thessalia fulvia*, male upperside (**5**), female upperside (**6**), and male underside (**7**). **8-10**: *Thessalia cyneas*, male upperside (**8**), female upperside (**9**), and male underside (**10**).

Table 1. Physical and physiological characteristic differences between *T. leanira* and *T. fulvia*.

Characteristic	*Thessalia leanira*	*Thessalia fulvia*
space above the discal cell, VHW	has a black mark	no black mark
sexual dimorphism	essentially none	sexually dimorphic
VHW discal cell	cell is enclosed by black scaling, no inverted "Y"	cell is open, with inverted "Y"
abdomen color	black, no orange scaling	orange scaling over the black body color
palpi	red-orange palpi	black palpi with white ventrally
mature larval head color	blackish heads	red-orange heads
broods	single brooded	multiple brooded

species of *Castilleja*, except for recent records of *Cordylanthus wrightii* Gray from Cochise County, Arizona by Greg Balmer (Mullins, pers. comm.) and Apache County, Arizona by the senior author, Pat Savage, Ken Hansen, and Douglas Mullins. These recent discoveries are the first record of a larval foodplant other than species of *Castilleja* and seem to represent an alternate foodplant used by larvae of subsequent broods when the available *Castilleja* is dormant. In the southern part of its range, *T. fulvia* frequently flies in association with *Thessalia theona thekla* (Edwards), *Thessalia theona bolli* (Edwards), or *Thessalia chinatiensis* (Tinkham).

A large portion of the range of *T. fulvia* consists of populations which cannot yet be assigned to any subspecific status. This area extends from north of the Mogollon Rim in central Arizona (including populations in the Hualapai Mts. of Mohave County in western Arizona), northeast into southern Colorado (Archuleta County), and into northwestern New Mexico. A long series from the Sandia Mts., Bernalillo County, New Mexico, appear to be nominate *T. f. fulvia*, so the Rio Grande River provides an eastern boundary to the unassigned population at this point. When a longer series of specimens from throughout this area is available, comparison will be made with specimens of the three described taxa, and a clearer picture of this form should appear. Review of the limited series currently available for study indicate that a more brown, more evenly suffused, less checkered taxon occurs over this region. The lack of yellow below the DFW discal cell and the increased amount of basal suffusion on the dorsal surfaces create the browner, smoothly suffused appearance that differs from the other taxa. Female specimens from this unassigned group of populations vary in appearance from those with a medium amount of suffusion dorsally to those with little suffusion and therefore a very orange appearance.

Thessalia fulvia fulvia (Edwards), 1879: type locality, restricted to Archer County, Texas, (Brown, 1966). Populations are nominate *T. fulvia* that are found in eastern Colorado, southcentral Nebraska, west and central Kansas, northcentral and extreme western Oklahoma, west Texas, and eastern New Mexico (east of the Rio Grande River). The nominate subspecies is distinguished by its relatively small adult size and its lighter, more orange, dorsal surface. This is due to a reduction of suffusion on the upper wing surfaces. Females have almost no suffusion and present a very orange dorsal appearance. Adults emerge in early April and May, and are continuously brooded throughout the season, depending upon elevation and climatic factors. In Colorado, *T. f. fulvia* occurs in populations along the eastern slope of the Rocky Mts., and in the plains to the east.

Recent collecting efforts in Kansas, Oklahoma, New Mexico, and west Texas have closed the gap between the Rocky Mts. and central plains populations that once seemed disjunct (Ely, Harp, pers comm; Cary, Stanford, Scott, Lep. Soc. Season Summary). No records are known from the immediate vicinity of the type locality in north central Texas, but *T. f. fulvia* was recently discovered in Nebraska by James Scott and Steve Spomer separately. Examples from the Sandia Mts., near Albuquerque, New Mexico, have affinities with *T. f. fulvia* and are assigned to the nominate subspecies. It appears that colonies east of the Rio Grande River are *T. f. fulvia*, since populations from Dona Ana County and Otero County, New Mexico, are also best assigned to the nominate subspecies. Blending between populations of the various *T. fulvia* subspecies has not been observed to date, largely due to the lack of understanding of the distribution of each subspecies, and perhaps the relatively effective geographical boundaries that appear to separate the recognized subspecies.

Thessalia fulvia coronado Smith & Brock, new subspecies

(Figs. **13-14**).

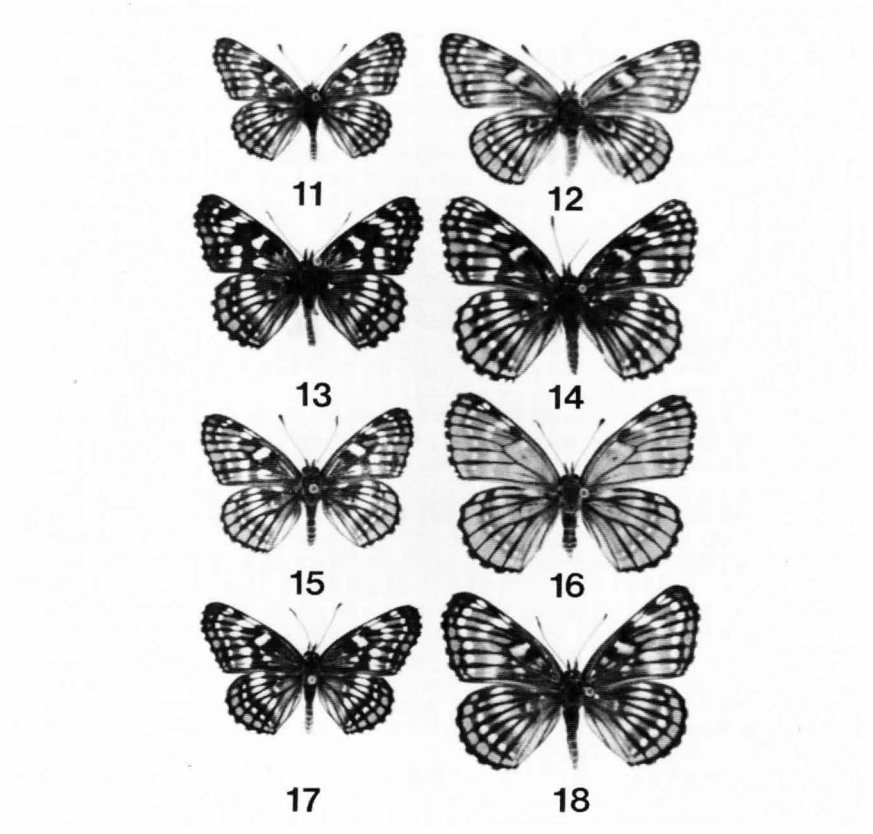
MALE: Forewing length X = 18.6 mm (range 17.0 -20.0 mm, N = 20). Head, thorax and abdomen are black dorsally and light yellow ventrally. Abdomen has red-orange suffusion on dorsal surface, and narrow yellow rings around the body. Legs are red-orange. Antennae are black, checkered with narrow white rings, tips are black. Palpi are black with white ventrally. *Dorsal forewing*: dark black-brown, more heavily so in the basal half. Outer portion of discal cell has a prominent light yellow rectangular patch, and there is a yellow spot postbasally in cell Cu^2. The distal half of the forewing is primarily red-orange. The median yellow band is interrupted in cell M^3 by red-orange. Major veins are black. *Dorsal hindwing*: basal area and discal cell area are black suffused with brown hairs. The yellow median band crosses the wing in a slightly curved line, bordered distally by red-orange, A narrow subterminal band is faintly shadowed by black. The marginal band is red-orange with a solid black line along the outer margin, Major veins are black. Dorsally, the fringe of both wings is checkered black and white. *Ventral forewing*: base color is a deep red-orange, with yellow suffusion in the basal area of the discal cell. The yellow median band is also very prominent. The apical and subapical regions are light yellow; the veins are black and the outer margin is a solid black line. *Ventral hindwing*: base color is chalky-white, with a faint yellow shading. Veins and the inverted "Y" mark near the cell (typical mark of *T. fulvia*) are black. A subterminal black band is centered with a yellow spot in each cell, creating a checkered appearance. Fringe ventrally is checkered the same as the dorsal surface.

FEMALE: Forewing length X = 22.5 mm (range 21.0 -24.0 mm, N = 10). Wing and body patterns are the same as in the male, although the female is distinguished by a much lighter overall appearance, *Dorsal forewing*: orange base color and with black suffusion basally. Discal cell has a yellow patch identical to the male, except the color is a darker yellow. The black suffusion is limited to three conspicuous patches around the cell, creating an overall effect of highlighting the yellow patch in the cell. The median yellow band is relatively small and suffused with the orange outer wing color. A row of yellow subterminal spots is shadowed distally by black; the marginal band is orange and very prominent. *Dorsal hindwing*: similar to forewing but with very little basal suffusion. The limited suffusion is located primarily along the costal margin. The yellow bands are more orange suffused and therefore less contrasting. The orange marginal band is prominent. Ventral surfaces are essentially the same as in the male.

TYPES: Holotype, male, Arizona: Pima County, summit of Redington Pass, 20 km ENE of Tucson, Santa Catalina Mts., ex-larva found on 20-II-1982, emerged on 10-III-1982 (leg. Smith). Allotype, female, same locality as holotype, ex-larva found on 22-II-1983, emerged on 14-III-1983 (leg. Brock). Described from a series of 29 male and 24 female

specimens all collected or reared from the type locality as follows: 7 males, 7 females, ex-larvae found on 8-III-1982, emerged 20-25-III-1982 (leg. Brock); 7 males, collected on 28-III-1981 (leg. Smith); 8 males, 9 females, ex-larvae found on 15-II-1984, emerged 1-6-III-1984 (leg. Brock); 3 males, 3 females, ex-larvae found on 20-II-1982, emerged on 7-10-III-1982 (leg. Smith); 1 male, collected on 22-III-1981 (leg. D. Mullins); 3 males, collected on 30-III-1981 (leg. Mullins); 2 females, ex-larvae found on 22-III-1981, emerged on 10-IV-1981 (leg. Mullins); 3 females, ex-larvae found on 20-II-1983, emerged on 8-III-1983 (leg. Mullins).

DISPOSITION OF TYPES: The holotype male and allotype female have been deposited in the collection of the Los Angeles County Museum, Los Angeles, California. Paratype specimens have been deposited in the following institutions: Allyn Museum of Entomology/FSM, Sarasota, Florida; California Academy of Sciences, San Francisco, California; San Diego Natural History Museum, San Diego, California; United States



Figures 11-18: Subspecies of *Thessalia fulvia*. 11-12: *T. f. fulvia*, male (11), female (12): west Texas. 13-14: *T. f. coronado*, male (13), female (14); Redington Pass, Pima Co., Arizona. 15-16: *T. f. pariaensis*, male (15), female (16); Cockscomb Ridge, Kane Co., Utah. 17-18: *T. fulvia* (undetermined), male (17), female (18); southeast of Holbrook, Navajo Co., Arizona.

National Museum, Washington D. C.; American Museum of Natural History, New York City, New York; and Instituto de Biologia, Mexico City, Mexico. Other paratype specimens will be maintained in the collection of Doug Mullins, Tucson, Arizona; and the collections of the authors.

OTHER SPECIMENS EXAMINED: 78 male and 38 female specimens from the following localities were examined and categorized as *T. fulvia coronado*: ARIZONA — *Cochise County*: Guadalupe Canyon, Peloncillo Mts., 11-IV-1976 (1 male, leg. Warner); summit west of Leslie Canyon, Swisshelm Mts., ex-larvae found on 27-II-1982, emerged 15-21-III-1982 (3 males, 5 females, leg. Mullins & Smith); ridge above French Joe Canyon, Whetstone Mts., ex-larvae found 2-V-1981, emerged 21-24-V-1981 (3 males, 3 females, leg. Mullins); mouth of Ash Canyon, Huachuca Mts., ex-larvae found 27-II-1983, emerged 16-25-III-1983 (5 males, 3 females, leg. Smith); hill at mouth of Carr Canyon, Huachuca Mts., ex-larvae found 27-II-1983, emerged 14-24-III-1983 (14 males, 7 females, leg. Brock & Smith); same locality, 27-III-1982 (6 males, leg. Smith); same locality, 3-IV-1982 (6 males, leg. Mullins); *Graham County*: Hwy 366 at Noon Creek, Penaleno Mts., 14-IV-1979 (3 males, leg. Brock); *Gila County*: Hwy 60 at Gila River, 24-VI-1979 (1 male, leg. Brock); canyon north of Roosevelt Dam, ex-larvae found 21-II-1982, emerged 8-15-III-1982 (4 males, 3 females, leg. Smith); same locality, ex-larvae found 10-III-1979, emerged 29-III-1979 (2 females, leg. Brock); *Maricopa County*: Hwy 87, 3 mi. north of Sunflower, 5-IV-1969 (1 male, leg. K. Roever); *Pima County*: ridge east above Helvetia, Santa Rita Mts., 2-V-1981 (1 male, leg. Brock); same locality, ex-larvae found 5-III-1982, emerged 21-30-III-1982 (6 males, 5 females, leg. G. Tyler, Jr. & Smith); Molino Basin, Santa Catalina Mts., 31-III-1981 (1 male, 1 female, leg. Smith); same locality, ex-larvae found 31-III-1981, emerged 17-25-IV-1981 (1 male, 1 female, leg. Smith); same locality, 22-IX-1984 (1 male, leg. Mullins); ridge south above Alamo Canyon, Ajo Mts., 2 & 9-IV-1983 (10 males, leg. Mullins & Smith); *Pinal County*: Peralta Canyon, Superstition Mts., ex-larvae found 13-II-1983, emerged 6-III-1983 (2 females, leg. Mullins); Peppersauce Canyon, Santa Catalina Mts., ex-larvae found (date unknown), emerged 30-III-1972 (6 males, leg. J. Mori); same locality, 8-IV-1979 (1 male, 1 female, leg. Brock); same locality, ex-larvae found 21-II-1983, emerged 16-23-III-1983 (3 males, 5 females, leg. Smith); *Yavapai County*: Fossil Creek Road, 17 km south of Camp Verde, 21-VIII-1977 (1 male, leg. Roever).

ETYMOLOGY: The name *coronado* is derived from the Coronado National Forest, which encompasses the forests of southern Arizona, and is in the vicinity of many of the populations identified as *Thessalia fulvia coronado*, including the type locality.

DISTRIBUTION: As reflected in the distribution map (Fig. **19**), *T. f. coronado* has been recorded throughout southern Arizona, north as far as Yavapai County. It is expected that this phenotype will include colonies in southwestern New Mexico. Populations in Catron Co., New Mexico and north require additional study before they can be assigned to any subspecific entity. Specimens from southeast of Kingman, Hualapai Mts., Mohave Co., Arizona, collected by George Austin have been reviewed and determined to fall into the unclassified range of *T. fulvia*, rather than into *T. f. coronado*.

DISCUSSION: A degree of variation has been observed in examples of *T. f. coronado*, and the same degree of variation seems to occur within each population. The variation consists of differing amounts of black suffusion on the dorsal surfaces, giving a lighter or darker appearance. Examples from a population at the mouth of Carr Canyon, Huachuca Mts., Cochise Co., Arizona have a greater percentage of light specimens than other populations. This trend has not been observed to that extent elsewhere, even in a population from a few miles south of this locality. A series of males from Alamo Canyon, Ajo Mts., Pima Co., Arizona are slightly darker than the norm, with a more consistent increase of black suffusion on the upper surfaces. Examples collected by Clifford Ferris in mid-summer 1985 near Portal, Chiricahua Mts., Cochise Co., Arizona, showed the greatest

degree of variation seen to date, with some specimens nearly orange and other very dark. Review of slides of these specimens sent by Ferris indicate that the population is *T. f. coronado* without any influence by *T. cyneas*, although this unusual degree of variation warrants further study.

When compared to specimens of nominate *T. fulvia* (Figs. 11-12), two primary differences are obvious. *T. f. coronado* is larger than *T. f. fulvia*, with a male forewing length of X

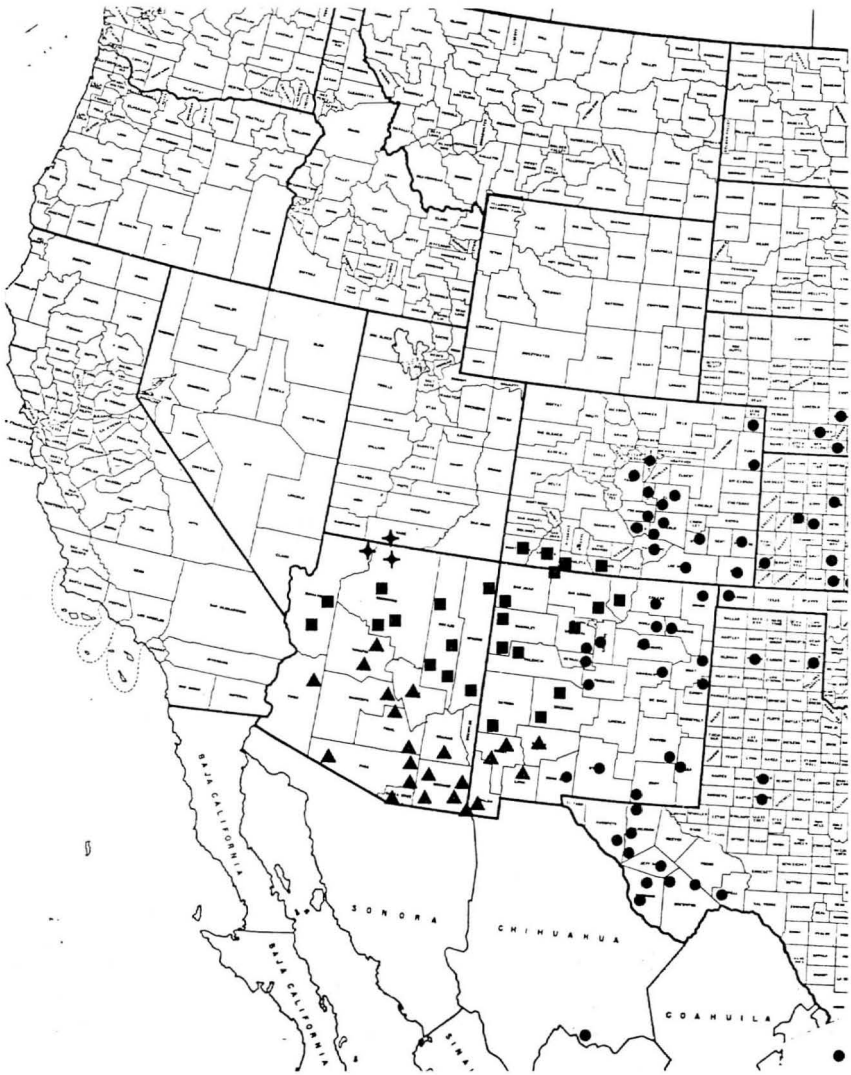


Figure 19: Distribution of subspecies of *Thessalia fulvia*. ● = *Thessalia fulvia fulvia*. ► = *Thessalia fulvia coronado*. ✚ = *Thessalia fulvia pariaensis*. ■ = *Thessalia fulvia* (undetermined).

= 18.6 mm (N = 20) versus X = 16.2 mm (N = 20). This same ratio also exists for the female specimens. The other trait is the increased dorsal black suffusion in *T. f. coronado* which is most prominent in the three dark patches around the DFW yellow cell spot. This creates a much more contrasting, checkered appearance than in *T. f. fulvia*. This trait is apparent in both male and female specimens, and remains consistent in even the lightest examples of *T. f. coronado*.

T. f. coronado has a major emergence in the spring, after diapausing larvae complete their feeding on the larval foodplants, which are primarily species of *Castilleja* (Indian Paintbrush). In addition, larvae were found and reared to adults on *Cordylanthus wrightii* Gray (Bird's Beak) in the summer of 1985 from the Chiricahua Mts., Cochise Co., Arizona, by Greg Balmer (Mullins, pers comm). Larvae were again found on *Cordylanthus* in Apache Co., Arizona, in July 1987 by Smith and Pat Savage, and Mullins and Ken Hansen on separate occasions. These records apparently represent an alternate summer foodplant for *T. fulvia*, which is used when the *Castilleja* growth ceases during the early summer drought. This shift of foodplant choices is the first verified for *T. fulvia* or *T. leanira*, and requires further research. This also lends credence to the report in Comstock (1927) of *T. leanira* larvae on *Cordylanthus* in California. Previously, this report was thought to represent a moulting larvae rather than a foodplant record. After the spring emergence, several smaller broods have been recorded sporadically into September. Laboratory rearing of first brood *T. fulvia* indicate that a percentage (usually less than 40%) of the larvae continue to feed to maturation, while the majority enter a period of aestivation in the middle instars. Seasonal rainfall patterns and larval foodplant condition seem to determine the percentage of larvae continuing through to pupation. It is also likely that aestivating larvae will break diapause throughout the year whenever environmental conditions are favorable. Populations are most frequently located in the foothill regions of the major mountain ranges, along gullies and ridgetop areas where the larval foodplant grows. Adult males patrol at or near the ridgetops, and females are usually found near the larval host plants. *Castilleja* is partially root-parasitic (Kearney and Peebles, 1960) and often grows under Oak (*Quercus*) and Manzanita (*Arctostaphylos*) species. Larvae compete with *Thessalia theona thekla* (Edwards) and *Occidryas anicia hermosa* (Wright) or *Occidryas chalcedona klotsi* (dosPassos). On the east slopes of the Huachuca Mts., Cochise Co., Arizona, *T. f. coronado* occurs in the proximity of *T. cyneas*. However, no interaction has been observed, possibly due to the elevational and habitat separation of the two species. The former species flies on the xeric foothill hilltops and ridges at the base of the Huachuca Mts., while the latter species flies higher in the rocky ridges of the upper reaches of the Huachuca Mts.

Thessalia fulvia pariaensis Smith & Brock, new subspecies

(Figs. **15-16**)

MALE: Forewing length X = 17.1 mm (range 15.0 - 19.0 mm, N = 20). Head, thorax, and abdomen are black with red-orange hairs. Abdomen segments are suffused with orange and narrowly ringed by yellow. The ventral surface of the body is light yellow and the legs are orange. Antennae are black with very narrow yellow rings, and faint yellow scaling on the club ends. Palpi are black dorsally and white ventrally. *Dorsal forewing*: base color is a rich dark orange, with the basal half suffused with black-brown. The discal cell is completely suffused except for a yellow rectangular patch at the distal end of the cell. A yellow spot is located below the cell in space Cu^2. The median yellow band is interrupted at cell M^3 by an intrusion of the orange postmedian band. A narrow line of yellow spots occurs subterminally, bordered distally by faint black shadowing. The apical area is orange with heavy black suffusion, and the marginal band is orange. The outer margin line is black and the fringe is black and white checkered. Major veins are black. *Dorsal hindwing*: similar to the forewing, except only the basal one-third is suffused by black. The median band is yellow, with increasing orange suffusion toward the inner margin. The postmedian

band is yellow with orange suffusion and no shadowing of black. A black patch is located at the outer margin. *Ventral forewing*: base color is red-orange with black on the veins only. The discal cell patch is bright yellow, and the median and subterminal yellow bands come through from the dorsal surface. The apical areas is light yellow, and the tornus margin spots are yellow. *Ventral hindwing*: base color is chalky-white with a very faint tinge of yellow. Veins are black, as is the discal cell "Y' mark. The postmedian black band has a yellow dot in each space, creating a double checkered line.

FEMALE: Forewing length X = 20.0 mm (range 18.0 - 21.0, N = 7). Body description same as male. *Dorsal forewing*: pattern similar to male, but with much less dark suffusion basally; the majority of the suffusion is in the discal cell. The cell yellow patch and the yellow median band are suffused with orange and are not as contrasting as in the male. The yellow subterminal band is narrower and without the distal black shadowing. Along the costal margin, the spots are a bright dark orange. Major veins are black. *Dorsal hindwing*: similar to male but again with very little black suffusion, most of which is along the costal margin. The yellow bands are almost totally obscured by the orange base color. The narrow postmedian band is yellow. *Ventral forewing*: similar to male except the base color is a darker red-orange with essentially no yellow banding. The apical region is bright yellow, as are the postmedian band and tornus region. Major veins are black, although some veins are nearly obscured by the red-orange suffusion. *Ventral hindwing*: same as that of the male.

TYPES: Holotype, male, Utah, Kane County, the Cockscomb Ridge, ca. 61 road km east of Kanab, 20-V-1979 (leg. Brock). Allotype, female, same locality as holotype, ex-larva found 11-IV-1980, emerged on 23-IV-1980 (leg. Brock). Described from a type series of 27 male, 7 female specimens collected or reared from the type locality as follows: 15 males, 1 female, collected on 16-17-V-1980 (leg. Brock); 2 males, ex-larvae found on 11-IV-1980, emerged on 26-IV-1980 (leg. Brock); 3 females, ex-larvae found on 11-IV-1980, emerged on 29-IV-1980 (leg. Brock); 2 females, ex-larvae found on 12-IV-1981, emerged on 24-IV-1981 (leg. Smith); 1 male, collected on 27-V-1980 (leg. Brock); 8 males, collected on 20-V-1979 (leg. Brock).

DISPOSITION OF TYPES: The holotype male and allotype female are deposited in the collection of the Los Angeles County Museum, Los Angeles, California. Paratype specimens have been deposited in the following institutions: Allyn Museum of Entomology/FSM, Sarasota, Florida; California Academy of Sciences, San Francisco, California; San Diego Natural History Museum, San Diego, California; United States National Museum, Washington D.C.; and the American Museum of Natural History, New York City, New York. Other paratype specimens will be maintained in the collection of the senior author.

OTHER SPECIMENS EXAMINED: 4 male and 1 female specimens from the following localities were examined and determined to be *T. fulvia pariaensis*: ARIZONA — *Coconino County*: Hwy 89A, 18 km east of Jacob Lake, 13-V-1982 (1 male, 1 female, leg Roever); *Mohave County*; 30 km southwest of Fredonia, 20-VI-1977 (1 male, leg. R. Bailowitz); Tuweep Road, ca. 35 km southwest of Hwy 389, 14-V-1982 (1 male, leg. Roever); UTAH — *Kane County*: Hwy 89, 15 km east of Kanab, 21-VI-1967 (1 male, leg. Roever).

ETYMOLOGY: The name *pariaensis* is derived from the Paria River and Paria Plateau, both of which are major geographical features in the vicinity of the type locality.

DISTRIBUTION: *T. f. pariaensis* is known only from localities along the Cockscomb Ridge of southern Utah, and along both slopes of the Kaibab Plateau of northern Arizona (Fig. **19**). The known colonies of *T. f. pariaensis* occur on the edges of the Kaibab Plateau and extend along the Cockscomb Ridge complex into southern Utah. The population located 15 km east of Kanab is located along the Vermilion Cliffs, which are connected to the Cockscomb Ridge complex to the northeast of this population. As reflected on the distribution map (Fig. **1**), these colonies are surrounded on three sides by populations of *Thessalia leanira alma* (Strecker). Further field work in northern Arizona and southern

Utah is necessary to clarify the distribution of *T. f. pariaensis* more accurately, and to define the transition to *T. l. alma*.

DISCUSSION: Very little variation occurs in the type series. There is some slight degree of difference in the amount of dark suffusion on individual specimens. Some female specimens have the suffusion in the DFW discal cell totally absent. It was initially thought that this phenotype represented a blend zone between *T. fulvia* and *T. leanira*; but as a longer series of examples was obtained, several consistent factors in the taxon indicated that this was a *T. fulvia* phenotype. These factors include the lack of variation in adults in the population compared to the extensive variation observed in blend zone colonies of *T. leanira* subspecies; and the typical *T. fulvia* characteristics described above. As shown in a comparison of the two taxa (Figs. **29-34**), *T. f. pariaensis* can be consistently separated from *T. l. alma* by the traits described for each species above. These traits remain constant for all specimens reviewed. Females specimens of *T. f. pariaensis* are much lighter than the males, differing in this regard from the more similar sexes of *T. l. alma*. The two small veins in the VFW discal cell are black in *T. f. pariaensis*. The light orange dorsal surface of this subspecies will easily separate it from the dark brown dorsal surfaces of central and northeastern Arizona *T. fulvia* populations (Figs. **11-18**).

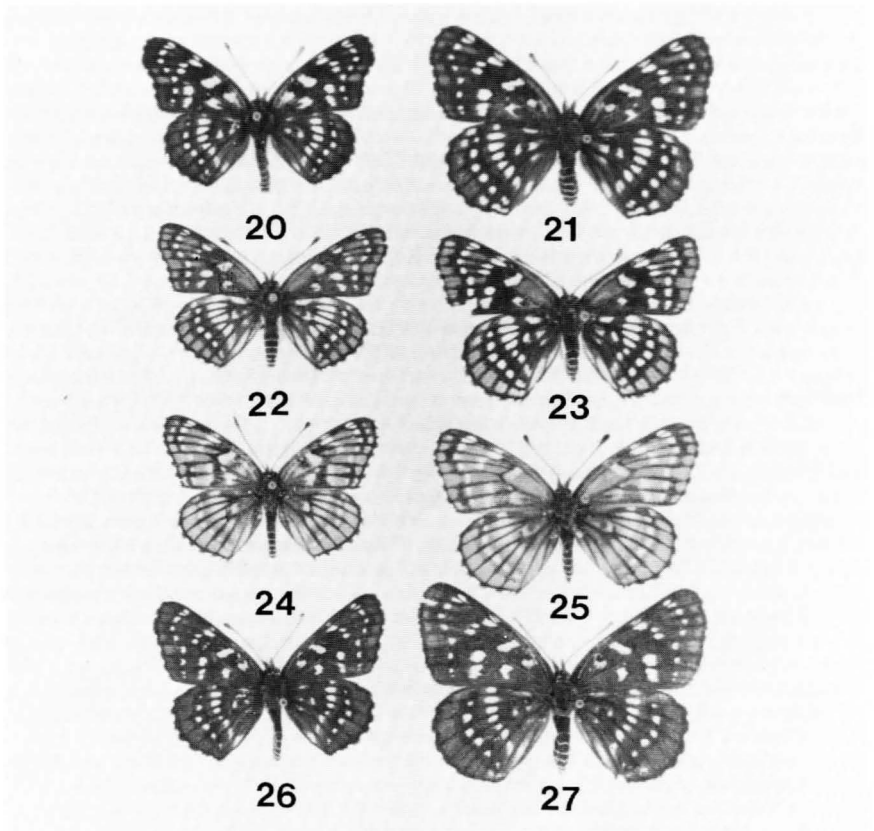
To date, only one brood has been recorded for *T. f. pariaensis*, occurring in mid-May to June. The type locality has not been collected extensively in the summer, when the subsequent broods would be in flight, and further field work is necessary to verify the number of broods for this form. Larvae have been found on the larval foodplant, Desert Paintbrush (*Castilleja chromosa*), in early April. The mature larvae have orange-red heads and the body is spiny and black, with orange patches on each segment. In the limited laboratory rearing efforts to date, all larvae have entered diapause in the middle instars.

Thessalia leanira (Felder & Felder), 1860

The Leanira Checkerspot is distributed from western Colorado, Utah, through northwestern Arizona, Nevada, into southern Oregon, California, and Baja California (Fig. **28**). It is represented by four described subspecies: *T. l. leanira*, *T. l. wrighti* (Edwards) *T. l. alma*, and *T. l. oregonensis* Bauer (Figs. **20-27**). Other taxa potentially deserving of subspecific rank also occur and require further research to properly clarify their status. Populations where two or more subspecies blend have yielded some impressive variations in individual specimens. *T. leanira* occurs in a great variety of habitats, from the redwood forests of Oregon and northern California to the arid deserts of Death Valley, and the subtropical hills of Baja California Norte. It is most often found in the transition zone between forest and chaparrel, or at lower elevations within the chaparral, and along desert ridges. Three of the four described taxa are very distinct and can easily be separated by range and adult appearance. The least distinct subspecies is the very dark *T. l. oregonensis*, and while it appears to be a legitimate subspecific race, more understanding of its range is necessary to clarify its relationship with *T. l. leanira*, especially to the dark coastal populations of the nominate subspecies.

Thessalia leanira leanira (Felder & Felder), 1860: type locality, vicinity of San Francisco, California (Bauer, in Howe, 1975). The nominate race is found throughout northern and central California, from Monterey and Tulare counties in the south to Shasta and Trinity counties in the north. It is found along the western slope of the Sierra Nevada Mts. and on both slopes of the Coast Range. *T. l. leanira* flies primarily in the chaparral and transition zones, and is often found in association with serpentine ridges. Unlike many other members of the *Thessalia* complex in the United States, males of nominate *T. leanira* do not hilltop but tend to patrol along paths or roads, where they are very attracted to available nectar. Several species of *Castilleja* are utilized by the larvae of this subspecies, and no other genus of foodplant has been verified. The reference in Comstock (1927) to *Cordylanthus* as a larvae foodplant was considered unlikely until the 1985 discovery of *T. fulvia coronado* larvae on *Cordylanthus wrighti* in Cochise Co., Arizona; and the successful rearing of

those larvae to adults on the same foodplant. The habit of the larvae to utilize many adjacent plants to moult may lead to erroneous foodplant records (pers. obv.). The adult flight period is in a single brood in late spring, from early May to early July. *T. l. leanira* has been found in northern Shasta County near Lake McCloud, and is replaced by *T. l. oregonensis* on the Mt. Shasta plateau in Siskiyou County. The type locality for the form *daviesi* (Wind) at Strawberry Lake, Tuolumne County, is a relatively high elevation locality in the Sierra Nevada Mts. The name has been applied to all Sierra Nevada west slope populations, but examples reared from late instar larvae from the Sierra Nevada (Mariposa County) and the Coast Range (Stanislaus County) are indistinguishable. In addition, the characteristics described by Wind (1947) to recognize *daviesi* ("the bright orange russett fore wings and very dark black hind wings,") can be observed on specimens from both mountain ranges. The name *daviesi* is best assigned as a synonym of *T. l. leanira* unless further field work establishes that populations from the higher elevations of the Sierra Nevada Mts. are representative of a legitimate taxon. Specimens from coastal colonies



Figures 20-27: Subspecies of *Thessalia leanira*. **20-21**: *T. l. leanira*, male (**20**), female (**21**); Santa Clara Co., California. **22-23**: *T. l. wrighti*, male (**22**), female (**23**); San Diego Co., California. **24-25**: *T. l. alma, male* (**24**), female (**25**); Death Valley Natl Mon., Inyo Co., California. **26-27**: *T. l. oregonensis*, male (**26**), female (**27**); Mt. Ashland, Jackson Co., Oregon.

in the fog belt of central California are very dark, similar in appearance to *T. leanira oregonensis*. This apparent reaction to the cool, wet coastal environment requires further study to determine its relationship to the northern subspecies. The unusual form *obsoleta* (H. Edwards) from Marin County has totally immaculate ventral hindwing surfaces, except for the wing vein markings. It is considered a form or aberrant of nominate *T. leanira*, but the consistency of these extreme markings over a very large series suggest that *obsoleta* may prove to be a unique subspecific race. This form has not been collected since the 1950's, and suburban growth in Marin County may have eliminated the ecological niche occupied by *T. leanira* form *obsoleta*. However, the long series available for study in major museum collections will help to properly define this taxon's relationship to nominate *T. leanira*.

Thessalia leanira wrighti (Edwards), 1886: type locality, San Bernardino County, California. This subspecies is found in coastal southern California and northern Baja California Norte, Mexico. Specimens from the vicinity of El Rosario and south to below Catavina have much more red-orange on the upper wing surfaces, replacing the black in *T. l. wrighti* and probably represent an undescribed subspecies in response to the change to the Vizcaino Subdivision of the Sonoran Desertscrub habitat (Brown, 1982) of that region, Colonies along the desert edges of Riverside and San Diego counties are representative of *T. l. wrighti* and not of the Mojave Desert taxon *T. l. alma*. *T. l. wrighti* is characterized by the bright orange-red marginal band on the upper hindwing surface. This band is yellow with black suffusion in *T. l. leanira*, and *T. l. alma* is completely bright orange dorsally. Brown (1966) commented that Edwards indicated Wright took the type specimens flying with nominate *T. leanira*, but this cannot be validated by the hundreds of specimens reviewed in museums. Typical examples of *T. l. wrighti* can be found along coastal California and Baja California from Santa Barbara County through San Diego County to the vicinity north of El Rosario in Baja California Norte. Intergradation with *T. l. leanira* occurs in Monterey County and blending with both nominate *T. leanira* and *T. l. alma* occurs in Tulare and Kern counties in the Kern River basin. *T. l. wrighti* also blends with *T. l. alma* on the desert slopes of the Transverse Ranges of southern California at locations such as Mint Canyon, southwest of Palmdale, Los Angeles County; Sheep Creek, near Phelan, San Bernardino County; and east of Hesperia above the Mojave River, San Bernardino County. Specimens from these blend zone colonies with *T. l. alma* are extremely variable and spectacular and will be discussed in a future paper. A distinctive form currently carried as *T. l. wrighti* was discovered in the sand dune habitat around Oso Flaco Lake, San Luis Obispo County, by Robert Langston and William Swisher in separate records. Adults are very brightly marked, and while maintaining the *T. l. wrighti* markings on the DHW, also have a distinctive black and yellow checkering on the dorsal surface that is more contrasting than in other *T. leanira* populations. This form also has less red in the DFW discal cell than in other *T. l. wrighti* populations. Examples from Pozo, in eastern San Luis Obispo County, also exhibit this appearance. Despite the cool coastal location, the population does not reflect the heavy black obscuration observed in coastal populations to the north in Monterey and Santa Cruz counties. This unique taxon requires further study and may prove to be a unique subspecies. *T. l. wrighti* flies in a single brood from March to June. Occasional specimens have been collected in the fall after unusually heavy summer rains in the southern California deserts. Several species of *Castilleja* are the only documented larval foodplants, with *C. foliolosa* (Hooker & Arnott) most frequently used. Unlike the nominate subspecies, *T. l. wrighti* males are commonly found on hilltops, similar to *T. l. alma* and *T. fulvia* subspecies. Males patrol immediately below hilltops and nectar in the vicinity. They also fly in the area of the larval foodplant. *T. l. wrighti* seems to have a more stable population size than *T. l. alma*, without the periodic population explosions observed with the latter. Many of the historic *T. l. wrighti* locations in southern California have been destroyed by construction or range fires (e.g. Mint Canyon, Dictionary Hill, San Gabriel Canyon). The most consistently producing colonies currently are in San Diego and Orange counties (McElresh, Mullins, pers. comm.; Orsak, 1977).

Thessalia leanira alma (Strecker), 1878: type locality, vicinity of St. George, Utah. *T. l. alma* is distributed over a wide area of the Great Basin and Mojave Desert, from eastern California to western Colorado. It is found throughout most of Nevada and Utah, and has been collected in the northwestern corner of Arizona (Mohave County: Virgin Mts.,

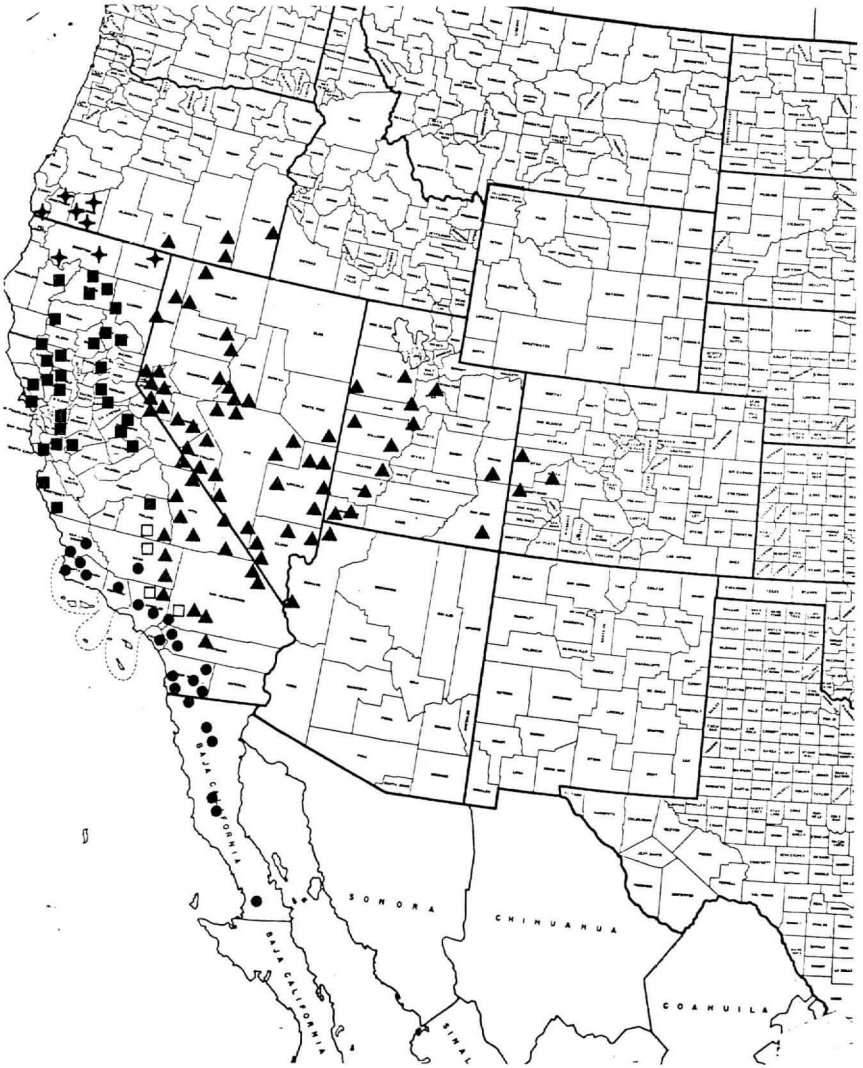


Figure 28: Distribution of subspecies of *Thessalia leanira*.
■ = *Thessalia leanira leanira*. ● = *Thessalia leanira wrighti*.
► = *Thessalia leanira alma*. ✚ = *Thessalia leanira oregonensis*.
□ = *Thessalia leanira* blend zones.

Seegmuller Mtn.). Recently, this taxon was also recorded from southeastern Oregon (Dornfeld, 1980). This phenotype remains relatively constant in appearance throughout its range, with limited variation in the dark suffusion of the basal regions of the dorsal surfaces. Extensive field work by George Austin, Nevada State Museum, indicates that there may be two taxa involved in the range currently classified as *T. l. alma* (Austin, pers. comm.). Although the differences are subtle, review of a long series of specimens indicates that populations from the Great Basin differ consistently from those of the Mojave Desert, with the Great Basin form darker and with heavier markings on the dorsal surface veins. The status of these possible taxa will require further research. Form *cerrita* (W. G. Wright) was described in 1905 from a mixed population with *T. l. wrighti* near Little Mountain, northwest of San Bernardino, California. The populations in that region represent the highly variable blend zone associated with the Cajon Pass discussed above (Sheep Creek, Hesperia), and the form *cerrita* at best represents the variable transition zone specimens between *T. l. wrighti* and *T. l. alma*. Austin (pers. comm.) has evaluated the type specimen for *T. l. alma* and feels that it represents the Great Basin taxon. Thus, if the two taxa prove to be valid subspecies, the Mojave Desert form will require a name. Specimens reported as *cerrita* from the Bodfish area of Kern County, California are actually examples of the interesting and variable blend zone in that region with influences from all three subspecies.

The dorsal surface of *T. l. alma* is almost a solid orange color with brown markings on the wing veins, and some brown suffusion near the basal regions and in the discal cell. The ventral surface of the hindwings is chalky-white, contrasting with the yellow underside shading of the other subspecies of *T. leanira*. The VFW has a red-orange coloration with few dark markings. The increased brown shading in Great Basin populations creates a slight banding effect on the dorsal wing surfaces. Colonies along the desert slopes of the San Bernardino Mts. in California have a yellowish tint to the ventral hindwing surface that differs from the rest of the Mojave Desert populations with their chalky-white under surface. Larvae of *T. l. alma* feed primarily on *Castilleja chromosa*, the common Desert Paintbrush of the Mojave Desert and the Great Basin. The satiny-black color of the larvae differs from the shiny black color of the larvae of *T. l. leanira*, caused by the presence of minute bluish raised dots in the nominate subspecies. *T. l. alma* flies in a single brood from April to June, and occasional specimens have been collected in the fall after unusually heavy summer rains, as with *T. l. wrighti*. Males patrol along the hilltops and ridges of the desert mountain foothills, and the females fly or nectar near the larval foodplant in desert washes, gullies, and hillsides. Adult emergence can be protracted over at least a 30 day period within each population. Occasional emergences of large numbers of adults appear to coincide with years of lush growth of *Castilleja*. The transition from the *T. l. alma* to *T. fulvia* subspecies remains unknown in southwestern Colorado, southern Utah, and northwestern Arizona. Unlike the highly variable California blend zone populations between various *T. leanira* subspecies, no blending or intermediate populations are currently known between *T. leanira* and *T. fulvia*. In Nevada and Utah, *T. l. alma* has been taken in all but the northeastern portions of each state. It is found along the eastern slope of the Sierra Nevada Mts. in California, from Lassen County into San Bernardino County. It flies at low and middle elevations in most Mojave Desert and Great Basin mountain ranges. *T. l. alma* should be looked for in southern Idaho, in the vicinity of the Owyhee Mts.

Thessalia leanira oregonensis Bauer, 1975: This subspecies was named to identify the very dark race that occurs in Siskiyou County, California and north into southern Oregon (Fig. 28). Although no type locality was indicated, Bauer (in Howe, 1975) stated that most specimens of *T. l. oregonensis* were from Jackson County, Oregon. The upper wing surfaces are nearly completely obscured by black, with very small yellow spots remaining. The DFW marginal band is almost 100% obscured. This very dark appearance is possibly a reaction to the cooler and wetter environment in which the butterfly lives. The similarity of *T. l. oregonensis* to central coastal California specimens has been discussed above. This

subspecies is distributed from the Mt. Shasta region of California, north into southern Oregon. A variety of habitats has been observed, from the dry sagebrush area around Mt. Shasta to the lush redwood forests of Mt. Ashland, Oregon. The transition of this subspecies to *T. l. leanira* and *T. l. alma* has not been observed in specimens currently available for study.

KEY TO THE *THESSALIA LEANIRA* COMPLEX

1 Upper surface black with small white submarginal spots on both wings, white median spots on FW and a continuous cream-yellow median band on HW (Oaxaca and perhaps Chiapas, Mexico) ..... *Thessalia cyneas cynisca*

1' Not as above ..... .2.

2 Upper surface dark brown-black with small cream-yellow spots forming median and submarginal bands, occasional dark orange-red spots along margin (southeastern Arizona and Mexico ..... *Thessalia cyneas cyneas*

2' Upper surface not as above ..... .3.

3 Palpi black dorsally and white ventrally; abdomen black with orange overscaling; sexually dimorphic (*Thessalia fulvia*) ..... .4.

3' Palpi red-orange; abdomen without orange overscaling; not sexually dimorphic (*Thessalia leanira*) ..... .7.

4 Dorsal brownish black suffusion on wings limited to basal half; variable; red-orange in limbal area; females with very little basal suffusion (east of Rio Grande/Rocky Mountains) ..... *Thessalia fulvia fulvia*

4' Not as above ..... .5.

5 Very dark insects, fuscous area very prominent around FW discal spot; male with extensive pattern of dark veins and bands; female checkered appearance enhanced by dark basal and yellow to red-orange lighter areas (central and southern Arizona, southwestern New Mexico, always south of Mogollon Rim) ..... *Thessalia fulvia coronado*

5' Much paler insects ..... .6.

6 Male dorsally paler orange than in *T. f. fulvia* with very little darker suffusion; female as in nominate subspecies, but with very little dark basal suffusion; DHW band broader in both sexes (south-central Utah, north-central Arizona). ..... *Thessalia fulvia pariaensis*

6' Upper surface basal suffusion darker and browner than in nominate subspecies; DHW marginal band narrower due to intrusion of brown in paler band; female lighter dorsally, but otherwise as *T. f. coronado*; postmedian yellow band more prominent than in other populations (northern Arizona, north of Mogollon Rim, northwestern New Mexico, northwestern Arizona). ..... *Thessalia fulvia*, unnamed population

7 Upper surface very dark with overall heavy suffusion ..... .8.

7' Upper surface with extensive red-orange areas ..... .9.

8 Upper surface with very small cream-yellow spots (extreme northern California and southern Oregon). ..... *Thessalia leanira oregonensis*

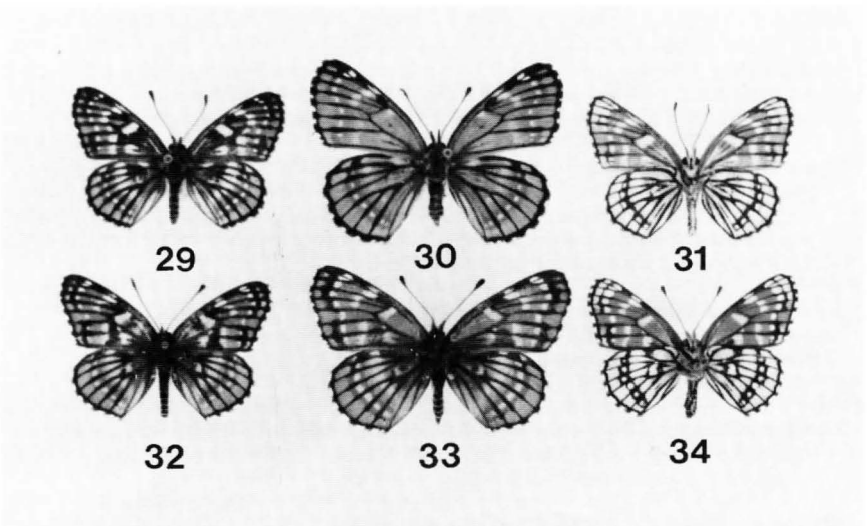
8' Upper surface appearing checkered with black and cream yellow; DHW Marginal cream spotband with or without black suffusion (California: Shasta to Monterey Cos. in Coast range and Tulare Co. in Sierra Nevada). ..... *Thessalia leanira leanira*

9 DFW with extensive red-orange limbally, basally in discal cell and along costal margin; DHW with red-orange marginal band (coastal southern California and Baja California Norte) ..... *Thessalia leanira wrighti*

9' Dorsal surfaces orange with almost no basal suffusion
(Mojave Desert and Great Basin to western Colorado).
..... *Thessalia leanira alma*

CONCLUSIONS

Increasing field work, the accumulation of specimens for study, and the resultant greater knowledge of individual variation within populations in the southwestern United States have provided a better understanding of the *Thessalia leanira* complex in this region, and on the interrelationships between the species of this group. *Thessalia cyneas* is a significantly different species, occupying a unique ecological niche for the complex, and with its affinities toward Mexico to the south. *Thessalia leanira* and *Thessalia fulvia* are not as obviously separated as species, occupying essentially the same ecological niche and replacing each other in distribution; but with a clear separation between the two species, and without intermediate forms or intergradation. These factors, and the consistent characteristic differences between the two taxa, argue that the two phenotypes should best be carried as separate species. Further research will better define this relationship. Continued efforts are also required for better understanding of the natural larval foodplants for *T. cyneas* in the United States, as well as defining the boundary between *T. leanira* and *T. fulvia* populations. Two new subspecies have been identified within the range of *T. fulvia (T. f. coronado* and *T. f. pariaensis*) while further analysis and field work is necessary throughout the distribution of *T. fulvia* to determine if the unassigned populations represent a distinct subspecies. The Great Basin and Mojave Desert populations of *T. leanira* need further study to more clearly define their relationship, as do the southern populations of Baja California Norte and the form in San Luis Obispo County, California. The status of all three species in Mexico is largely unknown. While



Figures 29-34: Comparison of *Thessalia fulvia pariaensis* and *Thessalia leanira alma*. 29-31: *T. f. pariaensis*, male upperside (29), female upperside (30), male underside (31). 32-34: *T. l. alma*, male upperside (32), female upperside (33), male underside (34).

much is known about the distribution and habitat of the *Thessalia leanira* complex, many challenges remain to more clearly establish the true meaning of the relationships within this complex.

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