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Cover illustration: *Idea leuconoe* (Large Tree Nymph) mating. Photo taken by Carol Butler at the American Museum of Natural History butterfly conservatory.

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A REVIEW OF *CALLOPHRYS AFFINIS* (W. H. EDWARDS), WITH DESCRIPTIONS OF TWO NEW SUBSPECIES FROM NEW MEXICO AND MEXICO

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ABSTRACT: The subspecies of *Callophrys affinis* (W.H. Edwards) are discussed, with emphasis on biosystematics, ecology and distribution. *C. apama* (W.H. Edwards) is treated as a subspecies and two new subspecies are figured and described from New Mexico and Mexico.

Additional key words: allopatric, sympatric, submesial band (=macular band; postmedian line), ecotype

The holarctic genus *Callophrys* Billberg, thecline lycaenids recognized by the absence of a tail and green scaling on the undersides of the wings, is widely represented in western North America by the *C. affinis* (W. H. Edwards) and *C. sheridanii* (W. H. Edwards) complexes. Species of the *C. sheridanii* complex are characterized by a complete or nearly complete submesial band of predominantly white-scaled maculations on the hindwing undersides. This complex includes nominate *C. sheridanii* (W.H. Edwards), *C. lemberti* Tilden, and *C. comstocki* Henne. Members of the *C. affinis* complex, on the other hand, are recognized by significant intrapopulation variation in the shape and relative completeness of the submesial band on the ventral hindwings. This complex includes *C. affinis* (W.H. Edwards); *C. apama* (W.H. Edwards), treated here as a subspecies of *C. affinis*; *C. dumetorum* (Boisduval), synonymous with *C. viridis* (H. Edw.) (Emmel *et al* 1998); and *C. perplexa* (Barnes & Benjamin), formerly *C. dumetorum* (Bdv.) (Emmel *et al* 1998). Gorelick (1971) treated the members of these complexes as a superspecies (as defined by Mayr 1965) although the study described herein suggests otherwise.

Populations of *Callophrys affinis* (W. H. Edwards) occur throughout western North America as shown by Stanford & Opler (1993). Life histories of the described subspecies were published by Scott (1986). They typically occur in the Transition zone, including steppe habitats. The localities of adult specimens used in this study are depicted in Figure 1. These butterflies are on the wing between April and September, typically in mountain or steppe habitats between 1372–2500m throughout the species range. Like other *Callophrys* (s. str.), some variation may exist in the iridescent color of the green scaling on the ventral surfaces of the hindwings. This variation relies on light interaction with detailed scale architecture to yield the green color, rather than pigment (Ghiradella 1989). The function of this appears to be thermoregulatory (Gorelick 1971).

The most readily chosen diagnostic characteristic examined in the *C. affinis* complex has typically been the number and arrangement of the white maculations composing the submesial band (Clench 1944, Tilden 1963, Ferris 1971a). Owing to substantial adult variation (intrapopulation, ecotypic and clinal), the most revealing taxonomic studies of *Callophrys* also include life cycle observations, flight period(s), mating and oviposition behavior, as well as habitat and hostplant descriptions (Gorelick 1971, Emmel *et al* 1998). First instar and mature larvae of *Callophrys* taxa and other closely related thecline lycaenids are described and figured by Ballmer and Pratt (1988, 1992).

Biological and systematic studies of *Callophrys* species are limited in number, perhaps due to the dearth of exploration in geographically isolated mountain ranges in both the southwestern United States and northern Mexico. Since the 1960s, searches in these areas have resulted in new *Callophrys* distribution records (Clench 1965, Gorelick 1971, Ferris and Brown, 1981, Mueller 1982, Cary and Holland 1992, Brown *et al* 1992, Hinchliff 1994, 1996). Bailowitz and Brock (1991) mention the occurrence of

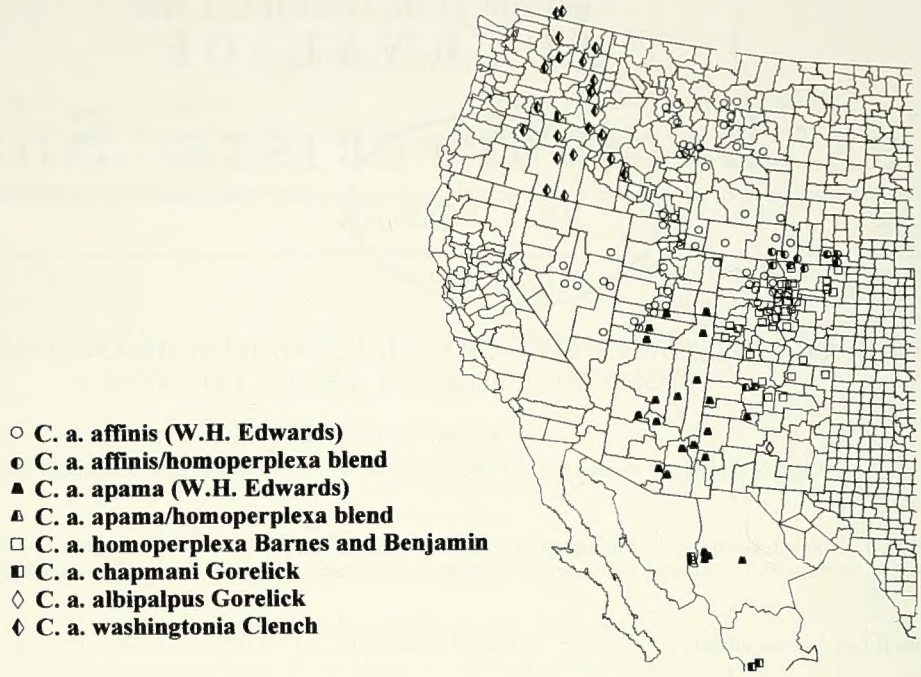


FIG. 1. Distribution of *Callophrys affinis* (W. H. Edwards)

C. affinis apama in the Santa Catalina Mountains of southeastern Arizona with respect to this apparent isolation. Such isolation is also seen in such areas as the La Sal Mountains of eastern Utah, shrub-laden arroyos and prairie breaks of Huerfano, Lincoln/Washington and Crowley counties in eastern Colorado (Stanford 1994), southwestern Nebraska, the Sacramento Mountains of southern New Mexico, and the Sierra Madre Occidental of northern Mexico. Adult populations of this species were found to be relatively abundant with considerable variation in the northern and central portions of its range, but scarcity and relative loss of variation were observed in the southernmost montane portion of its range in northern Mexico.

SYSTEMATICS

First in the *C. affinis* species group to be described was *Thecla dumetorum*, named by Boisduval (1852). He believed *C. dumetorum* to be a local race of the European species, *T. rubi* L. (Gorelick 1971). The taxa *Thecla affinis* and *Thecla viridis* were described by William Henry Edwards in 1862. In 1882, William Henry Edwards described *Thecla apama* on the basis of white maculations of the ventral hindwings (VHW) lined with a reddish brown band. F.M. Brown (1970) designated a lectotype for this species and referred to five specimens deposited in the AMNH that are probably paratypes. After incorporation into the genus *Callophrys*, a second subspecies, *C. apama homoperplexa*, was named by Barnes and Benjamin (1923) from Colorado on the basis of significant "reduction of white lines and their corresponding black and brown bands, the spots being usually quite disconnected." Barnes and Benjamin correctly pointed out that the total absence of these white spots or maculations on the wing undersides in females renders them quite similar to *Callophrys dumetorum perplexa* from San Diego, described by them in 1923. Unlike other *C. affinis* complex members, females of *C. perplexa* are distinct in their dorsally brown to golden brown wing scaling and grass green to golden green-scaled ventral hindwings. They also implied the necessity of examining a significant number of specimens from each locality to best insure proper identification of *C. apama* subspecies due to the existence of "intermediates to typical *C. apama*."

Haskin and Grinnell (1912) treated *Thecla dumetorum* (Bdv.), *T. viridis* (W. H. Edw.), & *T. affinis* (W. H. Edw.) as synonyms. Succeeding publications list these species as separate taxa (Klots 1951, dos Passos 1964, Howe 1975, Miller & Brown 1981). In his study on the genus *Callophrys* in North America, Clench (1944)) presented a key to the species wherein he separated *C. apama* from *C. perplexa* (formerly *C. dumetorum*) (Emmel *et al* 1998) on the basis of the

convexity of the outer margin of the forewing. Subspecies were principally identified by use of these white maculations on the hindwing undersides, and a new taxon, *C. affinis washingtonia*, was described from Washington. More recently, Pyle (2002) treats *C. perplexa* and *C. affinis* as separate taxa, as do Brock & Kaufmann (2003), and Opler & Warren (2003).

The variability of *Callophrys affinis* adults is well described by Ferris and Brown (1981), who treated *C. apama* as a separate species. The diagnostic characteristics and intrapopulation variation discussed sufficiently separate *C. apama* from closely allied *C. affinis*. They also described the appearance of the submesial band of white spots on the ventral hindwing (VHW) in some Rocky Mountains specimens as varying from a nearly continuous irregular line to those in which such white spots are virtually absent. This description applies to specimens from large populations that were studied from Boulder and Jefferson counties, Colorado, which are treated here as *C. affinis homoperplexa*. Using ventral hindwing features, phenotypic intermediates between *C. affinis affinis* and *C. affinis homoperplexa* in Wyoming, Colorado and Nebraska suggest intergradation. Recognizing this intergradation, Scott (1986) was the first to treat both *homoperplexa* and *apama* as subspecies of *C. affinis*.

In their treatment of the butterflies of New Mexico, Toliver *et al* (1994), Cary and Holland (1992), Holland and Cary (1996) list *C. apama* from the Jemez and Sangre de Cristo ranges of northern New Mexico as *C. apama homoperplexa*. This was confirmed by eight specimens collected by the author in late May and early June of 1996. Nevertheless, all four specimens reared from four second generation larvae taken from the Jemez Mountains emerged in August 1997 with a nearly complete submesial band more typical of *C. affinis apama* (Fig. 2), also suggesting intergradation. Two paratypes of "*Thecla apama homoperplexa*" also have a nearly complete submesial band with abundant brown scaling on the mesial side of the white maculations on the VHW, like that shown in figure 3.

MATERIALS AND METHODS

Ecological and behavioral observations were conducted in the state of Durango (Mexico), and in selected localities in Coconino Co., Arizona, Lincoln Co., New Mexico, Albany Co., Wyoming and Cheyenne Co., Nebraska, between 1981 and 1997 to gather comparative biosystematic information. On these trips, adults, immature stages, larval hostplants, and soil samples were collected. Field notes and photos were taken, including habitat descriptions and hostplant selections, as well as mating and ovipositional behaviors. Live immature stages were transported in an ice chest by automobile and live females were shipped by overnight express within twelve hours of their capture to Dr. John Emmel, Hemet, California. In this manner, newly-eclosed adults emerged from ova obtained by oviposition in a lab setting using closely related hostplants. In addition to the rearing of immature stages, 12 *C. a. apama* ova and first instar larvae were examined using a stereoscopic microscope.

No fewer than 12 first instar larvae of *C. a. apama* were collected and preserved in a larval fixative solution, along with a similar number of mature larvae. These and the field-collected adults are currently housed in the author's personal collection.

In most cases, observations were made on flights of a minimum of 12 individual adults at a given roadside or trailside locality, mostly during 2nd generation flight periods. Such observations of *C. affinis* were conducted on both sides of the Continental Divide. On the west side of the Mogollon Plateau, a portion of the Colorado Plateau characterized by Hubbard (1965), *C. affinis* populations were studied at four localities: base of San Francisco Peaks, north of Flagstaff in north-central Arizona, 2287m; the vicinity of Rose Peak, Apache National Forest in southeastern Arizona, 2287–2439m; the Zuni Mountains of western New Mexico, 2287–2317m; and the Sierra Madre Occidental west of Durango, Mexico, 2287–2439m.

On the east side, studies were conducted on isolated limestone outcrops with silt-laden sandstone layers and in cherty limestone/volcanic ash arroyos that occur in northeastern Colorado and southwestern Nebraska, 1372–1524m, and in the Sacramento Mountains of south-central New Mexico, 2287–2317m.

Using both field-collected and reared adult specimens, selected body and wing characteristics were compared. The characteristics chosen for comparison generated the nominal data entered in Table 1.

RESULTS

Ova are disc-shaped with abundant, variably shaped trabeculae. Green in color, the ova were found to be similar in size and texture to those described for *Callophrys perplexa* (=*dumetorum*) and *C. dumetorum* (=*viridis*) (Gorelick 1971, Emmel *et al* 1998) and for *C. sheridanii* (Ferris 1973). No changes in color occurred up to the day of eclosion.

Intrapopulation variation in the submesial band of ventral hindwing maculations was found to conform to the following generalizations along a north to south gradient:

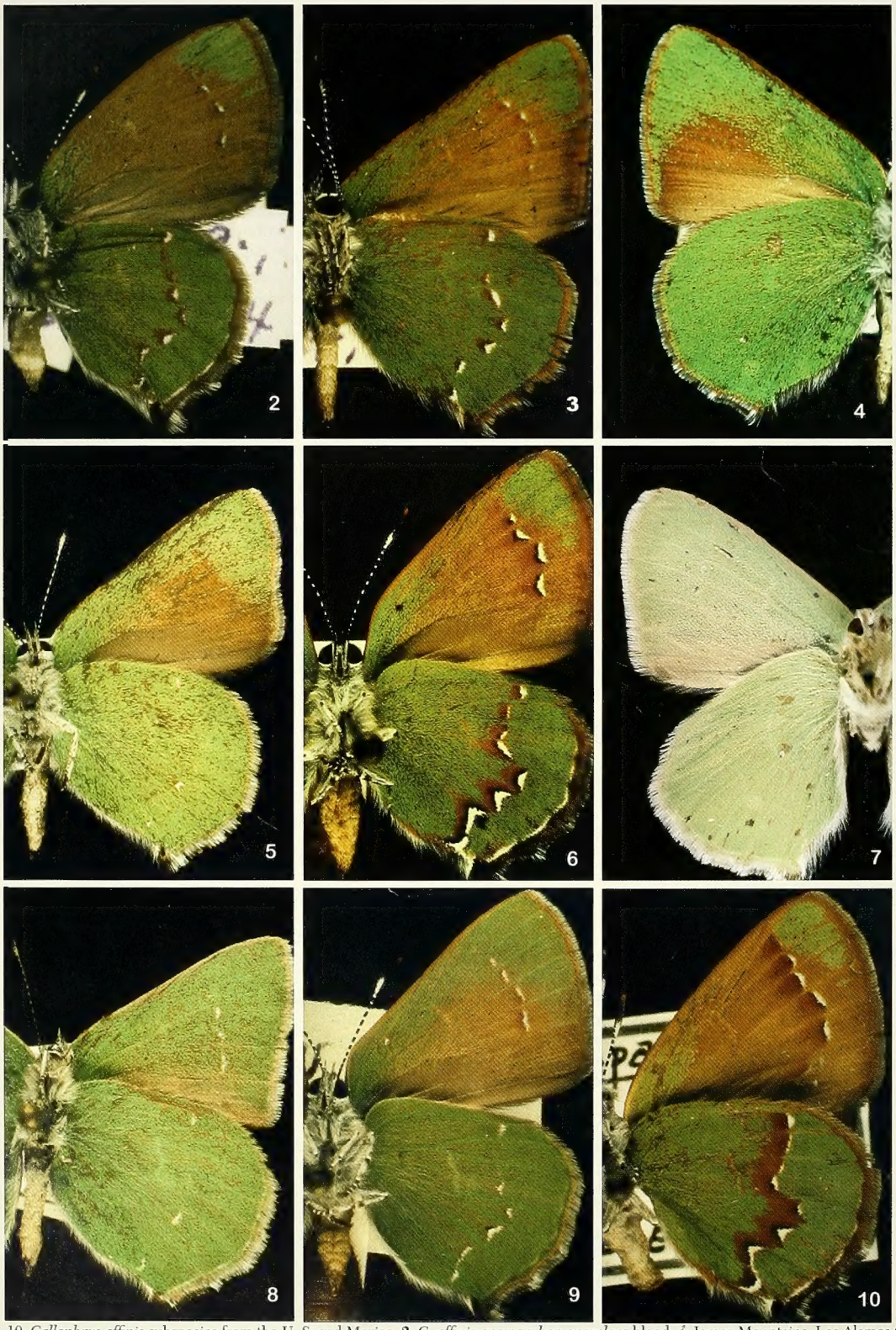
1. Specimens taken in northern Colorado (Larimer, Weld counties), southwestern Nebraska (Banner and

TABLE 1: Characters used in the analysis of the *Callophrys affinis* complex in the western United States and Mexico

CHARACTER	Subspecies of *Callophrys affinis*:							
	apama	*chapmani*	*apama* x *homoperplexa*	*homoperplexa*	*albipalpus*	*affinis* x *homoperplexa*	*washingtonia*	*affinis*
1. VHW vein tips: M3-2A	outer-brown; mesial-black; inner-white	outer-brown; mesial-dark brown; inner-white	uniform brown	uniform brown	outer-brown; inner-white (very weak)	uniform light brown	uniform pale to light brown	uniform pale to light brown
2. VHW margin - females	prominent intervenous white line; outside green scaling, M3 to 2A	prominent intervenous white line; outside green scaling, Cu1 to 2A	intervenous white line outside green scaling, Cu1 to 2A	white line typically absent	white line thin; weakly developed	intervenous white line absent	intervenous white line absent	intervenous white line absent
3. Wing fringes: VFW	basally gray brown; mesially light brown; distally pale-tipped	basally light brown; mesially gray brown; distally pale	basally dark brown; distally pale	basally brown; distally pale	basally brown; distally pale	basally light brown; distally pale	basally light brown; distally white	basally brown; distally pale to white
VHW: M1-Cu2	basally brown; mesially dark brown; distally pale to white	basally brown; mesially gray brown; distally mixed pale	basally brown; distally pale	basally brown; distally pale to white	basally brown; distally pale to white or mixed	basally light brown; distally pale	basally light brown; distally pale	basally brown; distally pale to white
VHW: 2A-3A	distally dark brown; mesially white; distally dark brown; elongated white scales at vein tips	distally brown; mesially white; distally dark brown; elongated white scales at vein tips	basally brown; mesially white; distally dark brown	basally brown; mesially white; distally dark brown	basally brown; mesially white (reduced); distally dark brown	basally light brown; mesially white (prominent); distally dark brown	basally light brown; mesially white; distally mixed	basally light brown; mesially white; distally light brown
4. FW apex	obtuse-angled	obtuse-angled	obtuse-angled	obtuse-angled	obtuse-angled	slightly obtuse-angled	nearly pointed	nearly pointed
5. FW outer margin: male	slightly crenated between Cu1 & M3	as in *apama*	as in *apama*	as in *apama*	as in *apama*	as in *apama*	nearly right-angled	nearly right-angled
female	slightly rounded	slightly rounded	slightly rounded	slightly rounded	slightly rounded	nearly right-angled	nearly right-angled	nearly right-angled
6. VFW costa	pale brown to yellowish, concolorous	brown to yellowish, concolorous	light brown	light brown	light brown	light brown	gray	grayish
7. VFW coloration inner margin	light brown to Cu2; brown above	light brown to Cu2; brown above	light brown to Cu2; brown above	typically grayish to Cu2; light brown above	grayish to Cu2; light brown above l	grayish to M2	gray to Cu2; mostly green	gray from inner margin to Cu2; mostly green
8. Antennal annuli	15-16	16-17	16-17	17-18	16-17	16-17	17 mostly white	17
9. Facial hair tuft	typically bent forward; thicker laterally	as in apama	as in apama	as in apama	as in apama	sparse; bent forward	sparse; bent forward	sparse; prostrate
scale color	mixed gray and brown	as in apama	light gray	light gray	light gray to white	light gray	white to gray	white to gray
10. FW stigma - male	lighter than ground color	lighter than ground color	typically concolorous	typically concolorous	lighter than ground color	typically concolorous	typically concolorous	typically concolorous

TABLE 1: Continued

CHARACTER	Subspecies of *Callophrys affinis*:							
	apama	*chapmani*	*apama* x *homoperplexa*	*homoperplexa*	*albipalpus*	*affinis* x *homoperplexa*	*washingtonia*	*affinis*
11. Labial palp scaling	black dorsally; white laterally	black dorsally; white laterally	black dorsally; white laterally	black dorsally; white laterally	black dorsally; white laterally	some black; mostly white	mixed black and white	thin; mixed black and gray
ventral setae	thick; black; abundant	thick; black; abundant	thick; black; abundant	thick; black; abundant	black; abundant	black; mixed with white scales	black; mixed with white scales	black; mixed with white scales
distal segment	black; white-tipped	typically tricolored: black with 4-5 brown scales ventrally; white-tipped	black; white-tipped	typically black; white-tipped	typically white; white-tipped	mostly black; white-tipped	white; white-tipped	mixed black and white
12. Green scaling-VHW (Kelly & Judd, 1976)	bright (emerald) green	typically olive green in males; strong (dark) green in females	1st generation: bright green 2nd generation: bright to yellow green	bright green	1st generation: moderate to bright green 2nd generation: bright green	slightly yellowish green	light green	pale to yellow green
13. Maculations VHW	complete band; maculations in Cu1 & Cu2 displaced laterally; tricolored-white, black, and brown	complete band & tricolored as in apama; mesial brown scaling also forms a contiguous band	nearly complete; maculations in M1-M3 may be absent; black scaling weak (12 or fewer scales)	typially incomplete; variable; mesial black scaling weak or absent	1st generation: absent in females 2nd generation: typically complete or nearly complete - M2 to 3A only 2nd generation (males): inner brown scales reduced to 8 or fewer; black scaling absent	variable; both black and brown scaling absent in males; brown scaling absent in females	typically one spot in cell Cu2; brown scaling absent; black scaling greatly reduced to fewer than 12 scales or absent	typically absent or one spot in cell Cu2; nearly complete-M2 to 3A in some; black scaling reduced to fewer than 12 scales or absent
VFW	4-5 maculations prominent white; black mesially	4-5 maculations weakly black mesially	3-4 weakly developed or absent; contrasting brown scaling mesially	4-5 weakly developed or absent; contrasting brown scaling mesially	4 weakly developed or absent; contrasting brown scaling mesially	4 or fewer; greatly reduced or absent	4 or fewer; greatly reduced or absent	2 or fewer; greatly reduced or absent
14. Dorsal features male	grayish to brown	grayish brown	brown to orange brown	brown to orange brown	brown to orange brown	orange brown	grayish brown	grayish
female	orange brown with dark brown margins	as in *apama*	as in *apama*	as in *apama*	as in *apama*	as in *apama*	uniform orange brown	uniform orange brown



FIGS. 2–10: *Callophrys affinis* subspecies from the U. S. and Mexico. **2**. *C. affinis apama* x *homoperplexa* blend, ♂, Jemez Mountains, Los Alamos Co., NM. **3** *C. affinis homoperplexa*, ♂, Boulder Co., CO. **4**: *C. affinis homoperplexa*, ♂, Jefferson Co., CO. **5**: *C. affinis affinis* x *homoperplexa* blend, Albany Co., WY. **6**. *C. affinis apama*, ♂, Coconino, Co., AZ. **7**. *C. affinis affinis*, ♂, Box Elder Co., UT. **8**: *C. affinis washingtonia*, ♂, Goose Lake, British Columbia, Canada **9**: *C. affinis albipalpus*, **n. ssp**. holotype ♂, Lincoln Co., NM. **10**. *C. affinis chapmani*, **n. ssp**. allotype ♀, Durango, Mexico

Cheyenne counties) and southeastern Wyoming (Laramie Range, Albany County) showed wide variation in the submesial band. Most males examined (31 of 38, 81.6%) exhibited up to six maculations with both brown and black scaling, while 7 (18.4 %) females exhibited a complete band that lacked brown scaling. In the Laramie Range, specimens treated as *C. a. homoperplexa* by Hardesty & Groothuis (1993) had slightly-pointed forewing apices that more resembled those of *C. affinis affinis*. Similarly, the southwestern Nebraska specimens thus appear to be intergrades between these two taxa, as suggested by Scott & Scott (1980) & Scott (1986).

The phenotypic intermediates in Wyoming were studied on the eastern edge of the city of Laramie in a ravine dominated by *Cercocarpus* shrubs along with scattered *Juniperus*. Stands of *Cercocarpus montanus* Raf. were found to be the preferred male perching sites between 1 and 4 PM. Despite numerous stands of the flowering larval hostplant, *Eriogonum flavum* (Table 2) in this ravine, adults of these intermediates do not occur in most years (C. Ferris pers. com.). Their relative scarcity was also noted during this study, a fact that rendered a reliable comparison of macular band scaling between this population and other populations in Albany and Laramie counties, Wyoming, and Weld County, Colorado inconclusive. A total of 12 of 12 males (100%) from these localities lacked brown and black scaling mesial to the white maculations.

2. Only 18 of 221 (8%) specimens examined from localities in Colorado (Denver southward) and New Mexico (Albuquerque northward) possessed a nearly complete white band bearing more than 12 black scales in each maculation (Fig. 3). The majority (203, 92%) possessed six or fewer white maculations that included eight or fewer black macular scales (Fig. 4). Intergradation between *C. affinis apama* (Fig. 6) and *C. a. homoperplexa* in eastern Wyoming and southwestern Nebraska (Fig. 5) also occurs in the Jemez Mountains of northern New Mexico (Fig. 2). A lack of sympatry exists between *C. affinis affinis* (Fig. 7) and *C. a. apama* in Arizona, as shown by Scott (1986). This lack of sympatry probably led to earlier treatments of the two taxa as separate species. Sympatry with *C. a. affinis* is also absent within the known range of *C. affinis washingtonia* in the Pacific Northwest (Guppy and Shepard 2001) (Fig. 8) yet *C. a. affinis* is narrowly sympatric with *C. perplexa* in Washington (Hinchliff 1996).

3. In southwest Colorado, sharp VHW maculation differences were found to occur within and between populations. These varied from only a few VHW white maculations typical of *C. affinis homoperplexa* (16 of 23 specimens, 70%) to those with more prominent brown-bordered maculations, indicative of *C. affinis apama* (7 of 23 specimens, 30 %).

4. In New Mexico (southwest of Albuquerque), Utah, and Arizona, most of the specimens examined (142 of 145, 98%) possessed a complete or nearly complete black-and brown-bordered macular band that exhibited little variation, typical of *C. affinis apama*.

5. Specimens from a population in the Sacramento Mountains near Ruidoso (Lincoln County, New Mexico), lacked hindwing maculations or exhibited an incomplete, curved macular band lacking in brown scaling or containing 12 or fewer brown scales in each. This was seen in 15 of 20 (75%) specimens (Fig. 9). This brown macular scaling was very greatly reduced or absent in both sexes, as were black macular scales in 19 of 20 specimens (95%). One male and one female examined from two localities in the southern portion of the Sacramento Mountains (Otero County, New Mexico) possessed a complete macular band typical of *C. a. apama* yet its hostplant, *C. fendleri* A. Gray, is absent from these localities. These two specimens from the first decade of the 20th Century bore incomplete collection data and no further sightings or captures of completely banded specimens have been recorded from the Sacramento Mountains.

6. A complete submesial white band was exhibited by all specimens seen from the Sierra Madre Occidental range of Sonora, Chihuahua, and Durango states (21 of 21, 100%). This feature was also accompanied by a darker green scale color on the VHW surfaces (Fig. 10) except on Chihuahua specimens, which exhibited a VHW green color similar to that seen in typical *C. affinis apama* from Arizona and New Mexico (15 of 15, 100%). The contiguous brown scale border of the submesial band was notably wider, more like that seen in specimens from the state of Durango. These specimens suggest discontinuous distribution in *C. a. apama*.

In summary, populations west of the Continental Divide and south of Utah should now be treated as *C. affinis apama* with a complete macular band and a nearly complete brown border to this band. These tend to exhibit a relative loss of maculations east of the Continental Divide suggesting possible clinal variation from west to east. Variable specimens from southwestern Nebraska, southeastern Wyoming and northern Colorado suggest local breakdown of this pattern. The populations of *C. affinis* studied east of the Continental Divide with respect to the VHW submesial band appear to be local adaptations (ecotypes) that most closely resemble *C. affinis homoperplexa*. Using both reared and field-collected specimens, consistent

structural differences were found to exist in adult specimens of *C. affinis* from the Sierra Madre Occidental in the states of Sonora and Durango and the Sacramento Mountains of New Mexico. Such differences were noted in the labial palps as well as on the ventral hindwings. These character differences suggest two rather distinct populations that are now, using both structural and biological features, designated as new subspecies:

Callophrys affinis albipalpus ssp. nov.

(Figs. 13, 14)

Description: **holotype male**: **Head**: Antennae black with 16 white annuli; distal three white annuli contiguous ventrally; club annuli black, orange brown distally; basal segment black with a single white maculation laterally; labial palp scaling black dorsally, white laterally, with distal segment predominantly white with white tip. **Dorsal surface of forewing:** FWL = 12.1 mm. Ground color uniform orange brown with contrasting brown venation and light brown stigma; outer margin dark brown with bicolored wing fringe (basally brown, distally white). **Dorsal surface of hindwing**: Ground color, outer margin and fringe as in forewing; fringe tricolored between vein 2A and 3A (basally brown, mesially white, distally dark brown).Ventral surface of forewing: Ground color grayish from posterior margin to vein Cu2; light brown to vein R5; abundant scattered bright green scaling between vein R5 and costa; incomplete band of five laterally-displaced submesial white maculations between veins R4 and Cu1; two maculations with very weak black scaling mesially; apical region to vein Cu1 lateral to submesial maculation with bright green scaling; outer margin brown with bicolored fringe (basally gray brown, distally pale). **Ventral surface of hindwing**: Ground color bright green with an incomplete submesial band of six white maculations displaced laterally between veins Cu1 and 2A; basal brown scaling in each maculation weakly developed; mesial black scaling significantly reduced to three or fewer scales or absent; outer margin as in forewing; anterior portion of fringe bicolored (basally light brown, distally pale); tricolored between veins 2A and 3A (basally light brown, mesially white, greatly reduced, & distally dark brown).

Allotype female: **Head**: Antennae as in holotype male with 17 white annuli; labial palp scaling mostly white; distal segment predominantly white with white tip. **Dorsal surface of forewing**: FWL = 12.5 mm. Ground color orange brown with 1.2 to 1.5 mm wide dark brown outer margin; wing venation and fringe as in holotye male. **Dorsal surface of hindwing**: Ground color as in forewing, with dark brown outer margin narrower than 0.5 mm; venation and fringe as in forewing; mixed brown and white scales between veins 2A and 3A. **Ventral surface of forewing**: Ground color as in holotype male, with brown scaling reaching the costal vein; submesial maculations absent; apical and subapical region very weakly green; fringe light brown basally; pale distally. **Ventral surface of hindwing**: Ground color as in forewing; incomplete submesial band with five white maculations; maculations with reduced brown scaling basally; mesial black scaling greatly reduced to three or fewer scales per maculation; outer margin brown with white scales forming a line between veins Cu1 and 2A; fringe as in holotype male.

Types. All type specimens were collected in the Sacramento Mountains of Lincoln County, New Mexico. The holotype male and allotype female were reared from a 1st generation female taken at the New Mexico State University's Montgomery Biological Research Laboratory (now privately owned property), 10 km north of Ruidoso, 2134m, Sacramento Mountains on June 28, 1982. They emerged in August 1982. Twelve paratypes (6 ♂, 6 ♀) bear the same data as the holotype male and allotype female. Additional paratypes were collected at the type locality on VII-4-1981 by the author (2♂, 4♀) and 1♂ reared *ex ovum* in 1982. Other field-collected paratypes include 2 males from Cedar Creek Camp, 10 km north of Ruidoso, 2134m, Sacramento Mountains, VI-30-1961, F., P. & J. Rindge, collectors (Carnegie Museum). The holotype male and allotype female and seven paratypes will be deposited in the Natural History Museum of Los Angeles County, Los Angeles, California. Two paratypes will be deposited at each of the following institutions: Florida Museum of Natural History, American Museum of Natural History, California Academy of Sciences, Carnegie Museum of Natural History, National Museum of Natural History, Essig Museum of Entomology (University of California, Berkeley). One paratype has been placed in the Entomology Research Museum (University of California, Riverside) and one remains in the collection of the author.

Etymology. The name given to this new taxon describes the dominant white scaling on the distal segment of the labial palpi observed in 18 of 20 (90%) specimens of both sexes, both reared and field-collected.

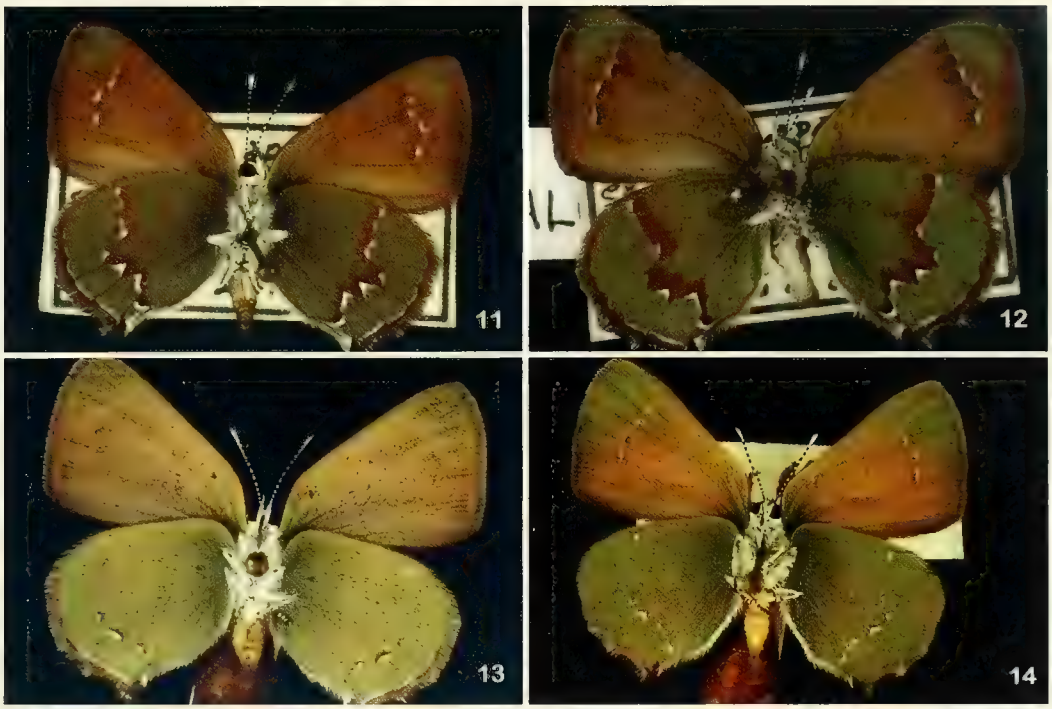
Diagnosis. Males and females of *C. a. albipalpus* typically exhibit predominantly white scaling along the labial palps. The distal segment is entirely white. This trait, along with the absence of black scaling along the submesial band of the ventral hindwing, distinguishes this taxon from its closest allies, *C. a. apama* and *C. a. homoperplexa*.

Range and habits. *C. a. albipalpus* is endemic to the Sacramento Mountains of south central New Mexico. It prefers the sun-exposed canyons and disturbed areas that exist in the vicinity of New Mexico State highways 37 and 48 at or above 2100m. First generation males and females often obtain nectar from the flowers of *Melilotus indicus* (L.), while second generation individuals prefer those of *Eriogonum jamesii*. Bivoltine in most years, it appears to be strongly influenced by ecological succession and thus relocates for both nectaring and oviposition. *E. alatum* appears to be the preferred larval hostplant (Table 2). Male hilltopping has not been observed.

Callophrys affinis chapmani ssp. nov.

(Figs. 11, 12)

Description: **Head**: Antennae black with 17 white annuli basal segment bicolored (black mesially, white laterally); club annuli black, terminally orange brown; labial palp scaling black, white laterally; distal segment black with white tip. **Dorsal surface of forewing**: FWL = 13.2 mm. Ground color uniform gray brown with concolorous venation; stigma gray; outer margin scales dark brown; fringe brown basally, pale distally. **Dorsal surface of hindwing**: Ground color and outer margin as in forewing; fringe tricolored (brown basally, pale mesially, orange brown distally); fringe at tips of veins Cu2, 2A, and 3A with elongated white scales. **Ventral surface of forewing**: Ground color grayish brown from posterior margin to vein Cu2; brown to costa; incomplete band of five submesial white maculations between vein R4 and Cu1, displaced laterally between vein M3 and Cu1; white maculations very weakly black-scaled mesially; basal, apical and subapical regions lateral to submesial maculations with olive green scaling; outer margin brown with tricolored fringe (basally light brown, mesially gray brown, distally pale along anterior margin, with distal portion becoming brown near tornus). **Ventral surface of hindwing**: Ground color olive green, with complete submesial band of white maculations displaced laterally between veins Cu1 and 2A; basal brown scaling of maculations form a contiguous band 0.8 to 1.0 mm wide; prominent black scaling mesially; outer margin brown with white scaling that forms a line between veins 3A and Cu1; fringe



FIGS. 11–14: **New subspecies** of *Callophrys affinis* **11**. *C. affinis chapmani*, holotype male, 38 km east of El Salto, Hwy. 28, 2439 m, collected ex ovum on July 13, 1985 -emerged: August 28, 1985, G.A. Gorelick, collector **12**. *C. affinis chapmani*, allotype female, 38 km east of El Salto, Hwy. 28, 2439 m, Durango, Mexico, collected ex ovum on July 13, 1985 -emerged: August 27, 1985, G.A. Gorelick, collector **13**: *C. affinis albipalpus*, allotype female, 10 km north of Ruidoso, 2134 m, Lincoln Co., NM, ciollected ex female on June 28, 1982 - Emerged: August 15, 1982, G.A. Gorelick, collector **14**: *C. affinis albipalpus*, holotype male, 10 km north of Ruidoso, 2134 m, Lincoln Co., NM, collected ex female on June 28, 1982 - Emerged: August 15, 1982, G.A. Gorelick, collector

tricolored (basally brown, mesially gray brown, distally mixed pale and gray brown); fringe between veins 2A and 3A distally dark brown; elongated white fringe scaling at tips of veins Cu2, 2A and 3A.

Allotype female: **Head**: Antennae with 17 white annuli, the distal three contiguous ventrally; basal and distal segments as in holotype male; labial palps white-scaled laterally; distal segment brown, white-tipped. **Dorsal surface of forewing**: FWL= 13.8 mm. Ground color uniform orange brown with 1.0 mm wide dark brown outer margin; fringe as in holotype male. **Dorsal surface of hindwing**: Ground color as in forewing, with 0.8 mm wide outer margin; fringe as in holotype male; fringe between veins Cu2 and 3A light brown distally; fringe at tips of veins 2A and 3A with elongated white scales. **Ventral surface of forewing**: Ground color as in holotype male; incomplete band of four nondisplaced white submesial maculations between vein R5 and Cu1 with prominent black scaling mesially; basal, apical and subapical area lateral to submesial maculations dark green; outer margin and fringe as in holotype male. **Ventral surface of hindwing**: Ground color dark green; submesial band of white maculations as in holotype male; contiguous brown scaling 1.5 to 1.8 mm wide; outer margin, tips of veins, and fringe as in holotype.

Types. The holotype male and allotype female were both collected and reared *ex ova* by the author, 38 km east of El Salto, 2439m in the Sierra Madre Occidental range of Durango, Mexico on July 13, 1985. The adults emerged on August 28, 1985. These will be deposited in the Natural History Museum of Los Angeles County along with four paratypes (2♂, 2♀) from the same locality. The remaining 14 paratypes (both reared and field collected) were taken between the city of Durango and the village of El Salto on Mexico Hwy. 28 (1964–1986). Two of these paratypes will be distributed to each of the same institutions listed for *C. affinis albipalpus*.

Etymology. This patronym honors Dr. Thomas Algernon Chapman (1842–1921), Scottish physician and lepidopterist. Dr. Chapman named and described the related species, *Callophrys avis* from sage scrub plant communities in SE France, the Iberian Peninsula and North Africa (Chapman, T.A., 1909). Additionally, he published a life history complete with a description of each larval stage, along with photographs and comparisons to closely related *C. rubi* in detail atypical for his time (Chapman, T.A., 1910).

Diagnosis. Unlike the closest ally, *C. a. apama*, the ventral hindwings of both sexes of *C. a. chapmani* exhibit a distinct mesial row of dark brown scales between veins M3 and 2A near the tips. The mesial brown scaling along the maculations forms a single continuous band one mm. in width. The green scaling of the ventral hindwing is typically olive green in males and dark green in females. The labial palp scaling is tricolored (black and brown, with white tips).

Range and habits. *C. a. chapmani* is multivoltine and only occurs in the Sierra Madre Occidental range above 2200m in the states of Sonora and Durango in Mexico. It frequents disturbed areas that include sun-exposed fields and arroyos along roadsides. Both sexes prefer to perch on and obtain nectar from their larval hostplants, *Ceanothus huichagorare* and *Eriogonum atrorubens*.

ECOLOGY

Adult *C. affinis* are univoltine in the northern part of their range, appearing between late March and June in Colorado and Wyoming and into July for higher elevation populations (Ferris and Brown, 1981). Bionomics of *C. affinis* from the Pacific Northwest are presented by Christensen (1981). Colorado prairie populations are double-brooded in some years, emerging in May with a second brood appearing in late July and/or August (A.D. Warren, pers. comm.). In western Nebraska, flight occurs only in June and early July. In northern Arizona, relatively large populations were observed above 2287m elevation between late May and early July. These may be bivoltine since adults are also on the wing in August and Septembers. Unlike most populations of *C. affinis* where bivoltinism is unproven, the Sacramento Mountains adults were collected between early June and late August, suggesting bivoltinism in most years. In the Sierra Madre Occidental of Durango, Mexico, specimens obtained between April and September reveal a multivoltine existence.

Unlike related California *Callophrys* that exhibit a preference for open areas (Ferris 1971b) and hilltopping/territorial behavior (Gorelick, 1971), *C. affinis apama* adults preferred to visit flowering vegetation along open roads and canyon bottoms and stayed relatively close to stands of their larval hostplant. This tendency was also mentioned by Ferris (1971b) pertaining to Wyoming populations. Behavioral similarities to *C. affinis affinis* such as hilltopping have been reported in several Colorado and New Mexico localities (Stanford 1977, S.J. Cary pers. com.). No hilltopping behavior was observed in the *C. a. affinis/homoperplexa* blends of Albany and Laramie counties in Wyoming or in the populations studied in Banner and Cheyenne counties in Nebraska. Male *C. affinis* specimens from several localities in the vicinity of Aspen, Colorado (Pitkin County), exhibited variation in VHW maculations. These males exhibited hilltopping behavior (R.E. Stanford pers. com.). The sparse, non-contiguous VHW maculation pattern of these Pitkin County specimens is reminiscent of such patterns observed in many *homoperplexa* specimens from other Colorado localities. These maculation patterns indicate the existence of a probable blend zone between *C. a. affinis* and *C. a. homoperplexa* in this area. In that no significant ecological or behavioral isolation is evident, these taxa are undoubtedly conspecific as per the discussion by Kohn & Orians (1962).

Adults of *C. a. apama* encountered in montane localities west of the Continental Divide in Arizona, New Mexico, and Utah frequently visited the flowering shrub, *Ceanothus fendleri* A. Gray (Rhamnaceae). This plant typically blooms between May and July and is used both as a larval hostplant and as a nectar source. Utah populations also used *C. fendleri* along with *Eriogonum racemosum* Nuttall (Polygonaceae), even when these occur together in the same locality. In addition, *C. affinis affinis* in UT uses many species of *Eriogonum*: *E. alatum*, *E. heracleoides* Nuttall., *E. umbellatum* Torrey, and *E. racemosum* (Jack L. Harry pers. com.) (Table 2)

Mexican populations typically occur in association with *Eriogonum atrorubens* Engelmann and *Ceanothus huichagorare* Loesner, a species closely allied to *C. fendleri*. On these plants, nectaring was observed in the morning and late in the day, with oviposition usually occurring during the early afternoon hours on both plants

In most localities in the Front Range of the Rocky Mountains and east of the Continental Divide in the U.S., *Ceanothus fendleri* was the preferred hostplant whenever present. In its absence, species of *Eriogonum* were adopted: *E. flavum* Nuttall (Wyoming), *E. umbellatum* (Colorado), and *E. alatum* (New Mexico).

While *C. affinis apama* appear to be on the wing virtually everywhere one finds abundant *Ceanothus fendleri* above 2287m, this association in regards to potential *Eriogonum* hosts was not observed. In Mexico, *Eriogonum atrorubens* occurs in oak-juniper grasslands of Chihuahua and Zacatecas, and in the Sierra Madre Oriental of southern Coahuila (Reveal 1967), areas providing no records or evidence of any *Callophrys*. In this regard, Gilbert and Singer (1975) pointed out that many butterfly species are much more restricted in their distributions than are their potential hostplants.

Males employed shrubs such as *Cercocarpus* species (New Mexico, Colorado, Wyoming), *Rhus aromatica* Ait. (Nebraska, Colorado, New Mexico), *Quercus gambellii* Martin and Drew, and *Q. undulata* Torrey (Colorado, New Mexico) as perching sites used to initiate courtship flights. Such behavior was observed between 9 AM and 4 PM. They may also perch on tall grass, as reported by Scott (1975).

Courtship and mating displays were frequently observed in sun-exposed terrain either on low vegetation, larval hostplants, or on male perching sites between 9 AM and 12 PM. *C. affinis apama* oviposition behavior was similar to that seen in other *Callophrys* (Gorelick, 1971). Females preferred to remain in close association with the larval hostplant throughout their flight period, employing it also as a nectar source between 9 AM and 12 PM. After some abdominal probing, females placed a single egg on each floral tip

TABLE 2: Host plant associations for *Callophyrs affinis* subspecies

Locality*	*Ceanothus fendleri*	*Eriogonum alatum*	*Eriogonum racemosum*	*Eriogonum umbellatum*	*Eriogonum heracleoides*	*Eriogonum flavum*	*Eriogonum atrorubens*	*Ceanothus huichagorare*
Arizona								
1. Strayhorse Cmpgd.,White Mountains, Greenlee Co.	*C. affinis apama*							
2. Schultz Pass, Coconino Co.	*C. affinis apama*							
New Mexico								
3. Zuni Mountains, Valencia Co.	*C. affinis apama*							
4. Jemez Mountains, Los Alamos Co.	*C. a. apama x homoperplexa*							
5. Bandelier National Monument, Sandoval Co.		*C. a. apama x homoperplexa*						
6. Sacramento Mountains, Lincoln Co.		*C. a. albipalpus*						
Utah								
7. Singletree Cmpgd. Wayne Co.		*C. affinis apama*		*C. affinis apama*				
8. 7.4 mi. south of Torrey, Wayne Co.	*C. affinis apama*		*C. affinis apama*					
9. 3.2 mi. north of Long Valley jct., Kane Co.			*C. affinis apama*					
10. Hwy 24, Piute Co.			*C. a. affinis*					
11. 28 mi. SE Moab		*C. affinis apama*						
12. Rich Co.				*C. a. affinis*				
13. 4 mi. NE of Accord Lakes, Sevier Co.		*C. a. affinis*						
14. Wilkerson Pass, Park Co.		*C. a. affinis*						
15. 2.6 mi. SW of Lynn, Box Elder Co.					*C. a. affinis*			
WYOMING								
16. Woodruff, Lincoln Co.				*C. a. affinis*				
17. nr. Evanston, Uintah Co.				*C. a. affinis*				
18. east of Laramie. Albany Co.						*C. a affinis x homoperplexa*		

TABLE 2: continued

Locality*	*Ceanothus fendleri*	*Eriogonum alatum*	*Eriogonum racemosum*	*Eriogonum umbellatum*	*Eriogonum heracleoides*	*Eriogonum flavum*	*Eriogonum atrorubens*	*Ceanothus huichagorare*
Nebraska								
19. Sidney rest area Interstate Hwy 80, Cheyenne Co.						*C. a affinis x homoperplexa*		
20. Bull Canyon, Banner Co.						*C. a affinis x homoperplexa*		
Mexico								
21. Sierra Madre Occidental, Durango							*C. a. chapmani*	*C. a. chapmani*

*Locality details:
1. Strayhorse Cmpgd., Hwy 666, 8000', White Mountains, Greenlee Co. [GAG]
2. 5 mi. N. of Flagstaff Schultz Pass, 7800', Coconino Co. [GAG]
3. Zuni Mountains, 8000', Valencia Co. [GAG]
4. Jemez Mountains, nr. Los Alamos, Burnt Mesa, Hwy 4, 7000', Los Alamos Co. [GAG]
5. Bandelier National Monument, 7000' Sandoval Co. [SJC]
6. Sacramento Mountains, 5 mi. north of Ruidoso, 7000', Lincoln Co.
7. Singletree Cmpgd., Hwy 12 11 mi. south of Torrey, 8300', Wayne Co. [JLH]
8. 7.4 mi. south of Torrey, North Slope Rd, 8000', Wayne Co. [JLH]
9. 3.2 mi. north of Long Valley jct., Hwy 89, 7200' Kane Co. [JLH]
10. Hwy 24, 1 mi. south of jct., UT Hwy 24/25, 8300', Piute Co. [JLH]
11. 4.5 mi. SSW Buckeye Reservoir, 7700', 28 mi. SE Moab [JLH]
12. 1.4 mi. north of SW corner of Lincoln Co., WY, 6600', Rich Co. [JLH]
13. 4 mi. NE of Accord Lakes, 8400', Sevier Co. [JLH]
14. 2 mi. E. of Wilkerson Pass, 9100', U.S. Hwy 24, Park Co. [JLH]
15. 2.6 mi. SW of Lynn, 6900', Box Elder Co. [JLH]
16. 8.2 mi. NE of Woodruff, 6800', Lincoln Co. [JLH]
17. 10 mi. N. of Evanston, 6700', Uintah Co. [JLH]
18. east of Laramie, 4450' Albany Co. (young stages unobserved; adults occur in association with *Eriogonum flavum*)
19. Sidney rest area Interstate Hwy 80, 4200', Cheyenne Co. (young stages unobserved; adults occur in association with *Eriogonum flavum*)
20. Bull Canyon, 17 mi. SW of Harrisburg, 4500' Banner Co. (young stages unobserved; adults occur in association with *Eriogonum flavum*)
21. Sierra Madre Occidental, 13 mi. E. of El Salto, 8000', state of Durango [GAG]

between 10 AM and 12 PM.

First generation females oviposited at the tip of the shoot, preferring the floral calyx (Figs. 15–16). First instars fed on new leaves at the tip, or on unopened sepals and petals when available. Later instars moved to the relatively immature leaves a few centimeters from the tip of the stem where they fed after consuming the flower bud. Mature larvae consumed the young leaves. Females in later broods oviposited on sepals or terminal leaves and emerging larvae fed on the flowers, moving from flower to flower on the stem. Mature larvae generally assumed the color of these flowers (Figs. 17–21).

While eclosions were noted in most field-collected eggs during the study, each of eight eggs collected on the flowers of *C. fendleri* growing below San Francisco Peaks (8 km north of Flagstaff, Arizona) was sucked dry by a hemipteran (J. Emmel pers. com.). Field-collected larvae below San Francisco Peaks, and Rose Peak along U.S. Hwy 191 in eastern Arizona were subjected to occasional parasitism by *Apanteles* sp., a braconid wasp. Along a 1-kilometer length of road at both localities, it was not uncommon to find up to 60 first and second instar larvae in a single day. These larvae exhibited mortality from disease and parasitism of up to 45%. In captivity, mature larvae crawled from the leaves and flowers onto the substrate and attached themselves to the surface or underside of the dead leaves where they pupated.

In canyons along New Mexico state highways 37 and 48 amongst stands of *Pinus ponderosa* Douglas ex Lawson, *Quercus undulata*, *Artemisia dracunculoides* Pursh., and *Eriogonum jamesii* Benth., where *Ceanothus fendleri* was not found, attempts to collect eggs and larvae of *C. affinis* on *Eriogonum jamesii* were unsuccessful despite its use by both females and males as a nectar source.

In the Sierra Madre Occidental, west of Durango above 2439m, oviposition and mating behavior was found to be the same as observed in *C. a. apama*. A

FIGS. 15-21: Immature stages of *Callophrys affinis*. **15–16**. Egg of *C. affinis chapmani* on sepal of *Eriogonum atrorubens* flower, Durango, Mexico. **17**. Mature larva of *C affinis apama* on *Ceanothus fendleri*, Greenlee Co., AZ. **18**. Mature larva of *C. affinis affinis* on *Eriogonum umbellatum*, Lincoln Co., WY. **19**. Mature larva of *C. affinis albipalpus* on lab host, *Eriogonum grande rubescens*, Lincoln Co., NM. **20**. Mature larva of *C. affinis chapmani* on *Eriogonum atrorubens*, Durango, Mexico. **21**. Mature larva of *C. affinis chapmani* on *Eriogonum atrorubens*, Durango, Mexico

search of a grassy meadow adjacent to farmlands along the highway 21 km east of El Salto (vicinity of Llano Grande) yielded 143 *Callophrys* eggs (116 living, 11 dead, 16 eclosed) collected in four days (July) on abundant stands of *Eriogonum atrorubens*. In addition, 77 first instar larvae were collected, with up to 6 larvae on the same plant. Parasitism, infertility, and larval mortality reduced this number to eight specimens successfully reared to adulthood. Approximately 25 first instar larvae were preserved for later study. Along the roadside 45 km east of El Salto, an area characterized by *Pinus engelmanni* Carr., *P. durangensis* Martinez,

Arbutus sp., *Quercus sp.*, and *Arctostaphylos sp.* between 2439–2500m, a total of four variable instar, green-colored larvae were taken on the same day from *Ceanothus huichagorare*. No red-colored larvae were found on the abundant *E. atrorubens* growing nearby yet two variably red and green larval morphs were collected on *E. atrorubens* bloom stalks growing along the roadside 38 km east of El Salto.

Field-collected adults were rare. No more than three adults of either population were typically seen on any given July day during the study. Interestingly enough, all modern records of *C. affinis* from the Sacramento Mountains are from areas burned by wildfires in the 1970s.

The known larval hosts for *C. affinis* in New Mexico (*C. fendleri*, *E. alatum*) are early successional plants. Outside of occasional wildfires and other disturbances, a decline of hostplants thus appears to be due to ecological succession (Pratt 2001). This suggests that the occurrence of *C. affinis* is determined primarily by the ecological structure of its habitat or its successional stage rather than the larval host, and it may therefore use any suitable hostplant(s) that are present at a given site. In addition, erosion brought on by excessive summer rainfall and the potential loss of *Eriogonum atrorubens* due to grazing and local human consumption add to selective pressures operating on the population of *C. affinis* along Hwy 28 in the Sierra Madre Occidental of the state of Durango in Mexico.

CONCLUSIONS

Macular band variation, phenotypic intergrades, synchrony and similar hostplant choices and behaviors warrant the inclusion of *C. apama* as a subspecies of *C. affinis*. Additionally, both behavioral and geographic isolating factors appear to have arisen in the southernmost distribution of *C. affinis*. This scenario conforms well to that described by Cox *et al* (1977), Holland (1988) and Shields (1996) in regards to geographic isolation in southwestern North American butterflies.

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APPENDIX: MATERIAL STUDIED

Callophrys affinis affinis (W.H. Edwards)

no locality, W.H. Edwards collection, designated ***lectotype***, F.M. Brown (1967), 1♂

no locality, W.H. Edwards collection, designated ***lectotype*** , F.M. Brown (1967), 1♀

no locality, W.H. Edwards collection, designated ***paratype***, F.M. Brown. (1967), 1♂

NEVADA:

Elko Co: Spruce Mtn., Pequop summit, Steptoe Valley., T31N R64E Sec. 33, VI-8 (no year or collector given)

Lander Co: Kingston Canyon, VI-18-1970, 1♂, C.D. Ferris, coll., Austin summit, VI-13-2002, 2m, P.A. Opler, coll.

Lincoln Co: Highland Peak, Highland Range, VI-17-1990, 1♂, 1♀, G.T. Austin, coll.

Nye Co: Antone Creek, Toquima Mtns.; VI-13 & VI-15-1933, 2♀, F.W. Morand, coll.;Jett Cyn., V-25/26-1974, 1♂, 1♀, J. DeBenedictis & W.E. Knoshaug, colls.

White Pine Co: Mt. Wheeler, VI-2 to 6-1929, 2m, F.W. Morand, coll.; Wilson Creek Range, base of Mt. Wheeler, 8700', VI -7 to 8-1985, 1♂, 1♀, G.A. Gorelick & G.T. Austin, colls., Indian Creek, Schell Creek Range, V-10-1984, 1♂, G.T. Austiin, coll.; Snake Creek, 8000', Snake Range, VI-27-1972, 1♂, 1♀, Scott L. Ellis, coll.

UTAH:

Box Elder Co: 2.6 mi. SW Lynn, 6900', coll. ex larvae on *Eriogonum heracleoides* (emerged IV-21-1988), 2♂, J.L. Harry, coll.

Garfield Co: Panguitch-Cedar Break Rd., Markagunt Plateau, VI-20-1972, 2♂, 1♀, Scott L. Ellis, coll.

Juab Co: Eureka, 7500' elev., no date, 4♂, R.C. Williams collection; VI-18-1910, 1♂, 1♀, T,. Spalding, coll.

Park Co: 2 mi. E. of Wilkerson Pass, 9100', U.S. Hwy 24, coll. ex larvae on *Eriogonum alatum*, VII-7-1988 (emerged: VIII-18-1988), 1♂, 1♀, J.L. Harry, coll.

Piute Co: UT Hwy 24, 1 mi. So. of jct., UT Hwy 24/25, 8300', coll. ex larvae on *Eriogonum. racemosum* (emerged X-19-1986),1♂, J.L. Harry, coll.; 0.7 mi up Hwy 25, Fish Lake Road, VI-21-1971, 1♀, J.A. Scott, coll.

Rich Co: 1.4 mi. north of SW corner of Lincoln Co., WY (0.1mi.W. state line), 6600', coll. ex larva on E. umbellatum, VI-1983 (emerged VIII-9-1984), 1♂; coll. ex larvae on *Eriogonum umbellatum*, VI-1985 (emerged II-1986), 4♂, J.L. Harry, coll.; 4.5 mi. NE Woodruff, east side of Crawford Mtns., 6800',4♀, coll. ex larvae on *E. umbellatum* (emerged II-13-1986), J.L. Harry, coll.

Sanpete Co: 18 mi. w. of Levan, VI-22-1979, 1♂, W.H.Whaley, coll.

Sevier Co: Fish Lake, VI-24-1927, 1♂, 1♀, Ashby Boyle collection; Old Woman Plateau, VII-2-1986, 1♂, C.A. Miles, coll.; 0.1 mi. N. Hogan Pass, 8800', V-5-1987, 2♂, J.L. Harry, coll.; 4 mi. NE Accord Lakes, Duncan Draw, 8400', coll. ex larvae on *Eriogonum*.alatum (emerged V-1988), 2♂, 4♀, J.L. Harry, coll.

Summit Co: Snyderville, VII-27-1980, 1♀, Ken Tidwell, coll.; North fork, Provo River, Uintah Mtns., 7500', VI-29-1965, 1♂, 2♀, John Justice, coll.; 8000', VII-5-1964, 2♀, Ken Tidwell, coll.; VI-15-1963, 1♂;VII-5-1964, 1♀, J. Don Eff, coll.

Uintah Co: Blue Mountain Plateau, Dinosaur National Monument, VI-1968, 2♂, Scott L. Ellis, coll.

Utah Co: Provo Peak, VII-30-1982, 1♂, C.A. Miles, coll., Silver Lake, VII-15-1899?, 3♂, 2♀, Henry Skinner, coll., VII-17-1949, 1♂, 6♀, A.J. Snyder, coll.

County unknown*: City Creek Canyon, VII-12 to 15-1899, 2♂, Henry Skinner, coll.

***cited as the type locality erroneously by Clench (1944); corrected type locality (Fort Bridger, WY) published by F.M. Brown (1970).**

WYOMING:

Carbon Co: Bottle Creek Campground, southwest of encampment, 8400', VI-25-1972, 1♀; VI-17-1981, 1♂, 1♀; VI-21-1982, 1♀; VII-2-1982, 1♂, C.D. Ferris, coll.

Fremont Co: Sinks Canyon Rd. at Slate Creek, VII-1-1979, 1♂, J. Brock, coll.

Natrona Co: Casper Mountain, V-30-1988, 1♂, Karolis Bagdonas, coll.

Teton Co: Teton Mtns., VII-8 to VII-17-1937, 4♂, 3♀, R.W. Wind, coll. [Nevada State Museum]; Jenny Lake, Teton Mtns., VI-14-1931, 1♀, no coll.; 7♂, 14♀, no date, Wallace-Bauer coll'n; VI-15 to 17-1956, 4♂, 2♀, J. Don Eff, coll.; VII-12-1937, 1♂, 1♀, R.G. Wind, coll.; Teton National Park along Snake River, VI-1/15-1979, 3♂, 2♀, T. McGann and U. of Wyoming (Zoology Dept.)

Albany Co: Pole Mountain, 8500', VII-21-1977, 1♀ , C.D. Ferris, coll.; VII-1- 1996,1♂, G.A. Gorelick, coll.

Lincoln Co: Cokeville, VI-16-1979, 1♂, W.H.Whaley, coll.; 8.2 mi. NE Woodruff, Wildhorse Spring, 6800', coll. ex larvae on *E. umbellatum* (emerged III-12-1986), 5♂, J.L. Harry, coll.; 4.5 mi. E. of Rex Peak, 0.4 mi. SE rd jct., 6900', coll. ex larvae on *E. racemosum*, VI-1985, (emg'd III-24-1985), 1♀, J.L. Harry, coll.; coll. ex larvae on *E. racemosum*, VI-1986, (emerged III-11-1986), 3♂, 4♀, J. L. Harry, coll.

Uintah Co: Evanston, VI-4-1885, 1♂, ex Skinner coll'n; 10 mi. No. of Evanston, 0.5 mi. E. of county road, 6700', coll. ex larvae on *E. umbellatum* (emerged III-12-1986), 3♂, J.L. Harry, coll.

Sublette Co: Trail's End Campground., Elkhart Park, 9350', VII-22-1991, 2♀, Larry D. Beutler, coll.

Sweetwater Co: Pine Buttes, VII-1942, 1♂, 1♀, L. Bauer, coll.; 25 mi. south of Bitter Creek, VII-1942, 1♂, L. Bauer, coll.

IDAHO:

Franklin Co: Birch Creek, 5700', VI-6-1990, 1♀, C.D. Ferris, coll.

Oneida Co: 3rd Creek Trailhead, 3 mi. east of SR 36, 6400', VI-23-2002, 2♂, R.E. Stanford, coll.

MONTANA:

Beaverhead Co: Polaris, VI-2-1943, 1♀, H.A. Howland, coll.; Lemhi Pass, 7340-7400', VII-15-1978, 1♀, J.F.G. Clarke, coll.; VII-21-1995, 1♂, J. Verhulst, coll.

Big Horn Co: Bighorn Canyon, 4610', V-28-1995, 1♂, C. Harp, coll.

Carbon Co: East Rosebud Canyon, 1750m, VII-5-1966, 1♂, C. Durden, coll.; VI-7-1992, 1♂, B. Vogel, coll.; East Rosebud Lake, 1850m, VI-27-1966, 1♂, C. Durden, coll.

Fergus Co: Little Snowy Mountains, VII-13-1976, 1♀, S. Kohler, coll.

Gallatin Co: Hebgen Lake, VI-21-1962, 1♂, J.A. Scott, coll.

Granite Co: Black Pine Road, VI-26-1990, 1♂, S. Kohler, coll.

Hill Co: Beaver Creek, Bear Paw Mountains, VI-20/28-1982, 10♂, 2♀, N. G. Kondla, coll.

Judith Basin Co: 15 mi. SW of Utica, 4800', VI-28-1998, 1♂, R. Stanford, coll.

Madison Co: Camp Creek, east of Melrose, 5485', VI-7-2001, 1♂, S Kohler, coll.; off Camp Creek Road, east of Melrose, VI-18-2001, 1♀, S. Kohler, coll.

Missoula Co: Ninemile Prairie, VI-9/18-1979, 9♂, 1♀, S. Kohler, coll.; Ninemile Prairie, up ridge to north near Hwy. 200, 3900', VI-8-2001, 1♂, S. Kohler, coll.; Shoofly Meadows, VII-4-2003, 1♂, D. Thompson, coll.

Powell Co: S. Helmville , VI-5-1989, 2♂, S. Kohler, coll.

Silver Bow Co: Rocky ridge trailhead, 2.5 mi. W. of Feely Divide Creek, VI-19-2003, 1♂, S. Kohler, coll.

Sweet Grass Co: East side, Crazy Mountains, VI-27-1966, 2♂, J. Scott, coll.; VIII-17-1966, 1♀, J. Scott, coll.; near Big Timber Creek, 4400', VI-28-1966, 1♂, J.A. Scott, coll.; Swamp Creek Road, Crazy Mountaiins, VII-12-1978, 3♂, 2♀, S. Kohler, coll.

Wheatland Co: breaks west of U.S. Hwy. 191, 4950', 13 mi. south of Harlowton, VI-28-1998, 1♂, R. E. Stanford, coll.

COLORADO: °

Garfield Co: near.Rifle, 2♂, 2♀ (no date or collector given); Roan Plateau, 9200', VI-18-1996, 2♂, C.P. Slater, coll.

Grand Co: Beaver Creek, VI-8-1977, 1♂, J. Donald Eff, coll.; Cottonwood Pt., 9800-10,000', 4 mi. south of Hot Sulphur Sprs., VI-3-1992, 4♂,; VI-30-1993, 5♂, 2♀; VII-1-1993, 2♂, 1♀, all A.D. Warren, coll.; County Road 50, 4 mi. east of jct., U.S. Hwy 40, 8 mi. west of Hot Sulphur Springs, VI-29-1991, 1♀,; VII-14-1991, 3♂, A.D. Warren, coll.

Pitkin Co: nr. .Aspen Airport, 8100', VI-16-1973, 1♂; VI-13-1979, 3♂, R.E. Stanford, coll.; Aspen, V-25-1992, 1♂, R.E. Stanford, coll; 0-3 mi. west of. Aspen, VI-12 to 15-1969, 3♂, 1♀ ; VI-13-15-1979, 4♂, R.E. Stanford, coll. [GM-CSU]

Routt Co: Steamboat Springs, 7200', VI-20-1973, 2♂, R.E. Stanford, coll. [GM-CSU]; Little Snake River, 8000', VI-20-1973, 2♂, R.E. Stanford, coll. [GM-CSU]

Summit Co: 1 mi. W. of Keystone, VI-30-1990, 1♀, A.D. Warren, coll.

° Additionally, both male and female adult specimens identified as C.a. affinis are housed in the collection of A.D. Warren [ADW] and were taken from localities in Rio Blanco and Moffat counties.

C. affinis washingtonia Clench

CANADA:

BRITISH COLUMBIA:

Oyama Lake, IV-22-1983, 1♂ ; Vernon, V-5-1983, 4♂, 1♀ ; Goose Lake, V-7-1984, 2♂ , all C.S. Guppy, coll.; Kalamalka Lake, Cosen Bay, nr. Vernon, V-22-1976, 6♂, J. Shepard, coll., Stubb Creek, Hwy 3, 8mi. E. Grand Forks, V-5-1973 1♂, J. Shepard, coll.; Douglas Lake Rd., 30 mi. E. Merritt, V-22-1976, 1♂, J. Shepard, coll.

WASHINTON:

Columbia Co: Blue Mtns., 4800' elev., VI-17-1961, E.J. Newcomer, coll.; along Tucannon River, Blue Mountains, VI-8-1963, 1♀, R.E. Woodley, coll.; south of Gilbirth Spring, T9N R40E sec. 35NE Y4, 4550', BMTR.15, VII-3-1964, 1♂, J. & S. Shepard, coll.

Douglas Co: Pine Creek, 700m, V-18-2000, 3♂, J. & S. Shepard, coll.

Kittitas Co: Manastash Ridge, view point, Hwy. I-82, 2800', V-1-1983, 5♂, 2♀, J. Hinchliff, coll.; Manastash Ridge, 2672', V-18-1984, 1♂, J. & S. Shepard, coll.

Lincoln Co: Hawk Creek, 2300', V-17-1985, 2♂, J. & S. Shepard, coll.; head of Hawk Creek, V-28-1984, 1♂, J. & S. Shepard, coll.; Hawk Creek Cmpgd., no. of Creston, V-19-1979, 2♂, 1♀, J. Shepard, coll.

Okanogan Co: Brewster, V-9-1939, 1♂, J.C. Hopfinger, coll. ***(paratype)***; V-14-1956, 1♀, J.C. Hopfinger, coll. [CMNH]; Barker Mtn., 3800', VI-3-2000, 1♂, J. & S. Shepard, coll.; Strawberry Mtn. Lookout, 4200', VI-21-1961, 1♂, Jon Shepard, coll.

Stevens Co: Pascal Cemetery, nr. Fort Spokane, V-28-1984, 2♂, J. & S. Shepard, coll.

Whitman Co: Steptoe Butte, VI-15-1964, 1♂, 1♀, Jon Shepard, coll.

OREGON:

Baker Co: FR 11 to Bald Mtn., VI-19-01, 3♀, Vern Covlin, coll.; Cave Creek Rd., 4000', Burnt River, w. of Durkee, V-27-1973, 1♂ (very worn), J. Hopfinger,

coll.

Crook Co: Ochoco Mtns., Hwy. 126, ca. 1 mi. NE Nat. For. boundary, VI-10-2003, 2♂, A.D Warren, coll.

Gilliam Co: Lonerock, 2000', VI-7-1961, 2♀, D.L. Bauer, coll.

Grant Co: Aldrich Mtn., Malhaur Nat. For., VI-2-1992, 6991', 5♂, 1♀, J. Hinchliff, coll.; V-31-2001, 4♂, 1♀, A.W. Warren, coll..

Harney Co: Pueblo Mtns., 6500', Arizona Creek, VI-23-1979, 1♂ (worn), Mark Smith, coll.; summit of King Mtn., ca. 6400', VI-14-99, 9♂, 4♀, Vern Covlin, coll.

Malheur Co: Trout Creek Mtns., 7000', 10 mi. WNW McDermott, VI-8-1980, 1♂, 1♀, Mark Smith, coll.; 5-6 mi. N. of Beulah Reservoir, Bendire Mtn. Rd., 4700', V-17-2001 27♂, 3♀, A.D. Warren, E. Runquist, D. McCorkle, collectors

Malheur/Baker Co. line: south of Rd. 16, 2-3 mi. SW Hwy. 26, VI-19-02, 4♂, 1♀, A.D. Warrren, coll.

Umatilla Co: summit of Tower Mtn., ca. 6700', VII-5-99; VI-7-00; VI-14-01, 18♂, 8♀, Vern Covlin, coll.

Wallowa Co: ca. 10 mi. N. of Wallowa on rd. to Troy, VI-23-02, 1♀, A.D. Warren, coll.

IDAHO:

Adams Co: near mouth of Wildhorse River, V-12-1959, 1♀, S.G. Jewett, coll.

Boise Co: 5 mi. west of. Idaho City, Cold Spring Creek, VI-8-1976, 1♀, J.F.G. Clarke, coll.

Camas Co: Willow Creek Cyn., V-27-00, 1♂, A.D. Warrren, coll.

***Callophrys affinis affinis/ homoperplexa* blend**

WYOMING:

Albany Co: east of Laramie, T15N R73W S1, 4450', VII-17-1971, 2♂; VI-30-1972, 1♂; VII-1-1972, 1♀; VII-6-1972, 1♂; VII-8-1972, 1♀; VII-10-1972, 2♀; VII-18-1982, 1♀, VI-18 to VII-1-1996, 12♂, 4♀, C.D. Ferris, coll., VI-26/30-1996, 6♂, G.A. Gorelick, coll.

Laramie Co: 20 mi. W. Cheyenne, Hwy 210, VI-22-1985, 1♂, P.A. Opler, coll.; 24 mi. W. Cheyenne, Hwy 210, VI-15-1985, 1♂, P.A. Opler, coll.; Curt Gowdy St. Pk., 24 mi. W. Cheyenne, Hwy 210, VII-6-1997, 5♂, G.A. Gorelick, coll; 8 mi. S. Cheyenne, VI-18-1985, 1♂, 2♀; VII-22-1985, 1♀, P.A. Opler, coll.

Carbon Co: near Battle Mountain, 7500', VI-20-1973, 1♂, R.E. Stanford, coll.

NEBRASKA:

Morrill Co: 6 mi. S. Redington, VI-27-1974, 1♂, W.T. Morgan, coll.

Cheyenne Co: Hwy I80, Sidney rest stop, 4200', VI-29-1996, 20♂, 4♀; VII-10-1997, 1♂, 1♀, G.A. Gorelick, coll.; VI- 1 to VI-29-1996, 8♂, Jim Reiser, coll.

Banner Co: Bull Canyon, 17 mi. SW Harrisburg, 4500', V-23-1994, 4♂, Jim Reiser, coll.; VI-30-1996, 4♂, 2♀, G.A. Gorelick, coll.

COLORADO.

Jackson Co: Sand Dunes (North Sand Hills SRMA), northeast of Walden, VI-18-1978, 1♂, Peter Eades, coll. (probable blend)

Larimer Co: County road 80C, 7.8 mi. E. Jct., county road 89, VII-6-1996, 1♂, A.D. Warren, coll. (very worn specimen - probable blend)

Weld Co: 7 mi. NW Carr, VI-13-1985, 1♂, P.A. Opler, coll.; 8 mi. NW Carr, VI-18-1985, 11♂, 4♀, P.A. Opler, coll.; 9 mi. NE Grover, 5455', VI-8-1991, 1♀, R.E. Stanford, coll.; Pawnee Buttes, Pawnee National Grasslands, 13 mi. south of Wyoming Border (north of Colorado state Hwy. 14), VI-21-1978, 1♂, Peter Eades, coll.

Callophrys affinis apama (W.H. Edwards)

"ARIZ", W.H. Edwards collection, designated ***lectotype*** by F.M. Brown, 1967, 1♂

"ARIZ", W.H. Edwards collection, designated ***paratype*** by H.R. Clench, 1973, 1♀

ARIZONA:

Apache Co: Greer, VI-12-1936, 1♂, G.H. & J.L. Sperry, coll.; Greer, White Mtns., VII-11-1995, 1♂, Ken Davenport, coll.; Wheatfields Creek, 8000', Chuska Mtns., VII-8-1978, 1♂, R.W. Holland, coll., Lukachukai Creek Campground, 7000', Chuska Mtns., VI-14-1971, 1♂, R.W. Holland, coll.;. McNary, VI-20-1981, 1♀, G.A. Gorelick, coll.; 1mi. E. McNary, VI-21-1981, 9♂, 3♀, G.A. Gorelick, coll.; 2 mi. S. McNary, VI-21-1981, 1♀, G.A. Gorelick, coll.

Gila Co: Tonto Creek Campground, nr. Kohls Ranch, VI-26-1956, 1♀, no coll.; "Gila Co.", VI-1902, 2♂, O.C. Poling, coll.; Sierra Ancha Mtns., VII-7-1933, 3♂, 3♀, Harold M. Bower, coll; VII-4 & VII-10-1934, 2♂, D.K. Duncan, coll.; Globe, VI-4-1934, 1♀, no coll.; VII-11-1933, 2♂, no coll.

Yavapai Co: School House Gulch, Prescott, VII-9-1993, 4♂, Ken Davenport, coll.; Prescott, VII-7-1917,1♂, J. Gunder coll'n; VII-9-1993, 3♂, Ken Davenport, coll.; E. of Prescott, VII-11-1952, 1♀, Lloyd Martin, coll.; no locality, VII- 1928, 1♂, O. Buchholz coll'n.; Wolf Creek, S. of Prescott, VII-20-1959, 6♂, 3♀, R.F. Sternitzky, coll.

Greenlee Co: Strayhorse Campground, White Mountains, VII-28-30-1937, 25♂, 4♀; VII-1-3-1937, 29♂, 11♀, all Don Meadows, coll.; VII-7-1958, 1♀, J.W. Tilden, coll.; 8 mi. S. Strayhorse Cmpgd., 8000', Hwy 666, VI-25-1981, 15♂, 3♀, G.A. Gorelick, coll.; Rose Peak, VII-7-1958, 2♂, 1♀, J.W. Tilden, coll.; 4 mi. S. Rose Peak, 7600', Hwy 666, VI-24-1981, 5♂ 2♀, G.A. Gorelick, coll.; White Mountains, VI-16-1947, 1♂, 1♀, E.P. Mellon II, coll., VI-28-1937, 1♀, M.E. Smith, coll., VI-26-1936, 1♀; VI-20 to 26-1936, 5♂, 1♀; VII-30-1937, 1♀, all L.P. Grey, coll.; VI-22-1936, 2♂; VI-28-1937, 1♂; VII-1-1937, 3♂, 1♀, all T.M. Dunkle, coll.; VII-26-1937, 4m, 1♀; VII-1-1937, 3♂, 1♀, T. Dunkle, coll.; VI-22-1942, 3♂, 4♀, H.A. Freeman, E.R. Hulbirt, colls.; VII-3& 4-1951, 3♂, 1♀; VI-16-1948, 1♂, E.R. Hulbirt, coll.; White Mountains, VI-8-1929, 1♂, L.I. Hewes, coll.; VII-18-1961, 2♂, Keith Brown, coll.; Hannagan Mdws., White Mtns., VI-20-1930, 3♂, J.C. Hopfinger, coll.; VI-20-1937, 2♂, 2♀, J. Baker, coll.; Blue Mtns., VI-30-1933, 1♂, E.R. Hulbirt, coll.

Graham Co: Mt. Graham, 1882, 2♂, Herbert K. Morrison, coll. (Skinner collection) (***paratype***); Graham Mtns., VII-4-1932, 1♂, R.G. Wind, coll.

Coconino Co: Lockett Lake Road, 7400', VI-5-1989, 1♂, Ken Davenport, coll.; Flagstaff, VII-27-1916, 2♂, J.A. Comstock coll'n.; Schultz Pass, 7800', San Francisco Peaks, V-27-1960, 1♂, Lee D. Miller, coll.; 5 mi. NW Flagstaff, VI-4-1967, 1♀; V-19-1968, 5♂, 1♀; VI-11-1969, 1♂, R. Funk, coll.; Schultz Pass Rd., 4 mi. N. Flagstaff, V-29-1985, 5♂, 4♀, G.T. Austin, coll.; VII-21-1982, coll. ex larvae on *Ceanothus fendleri* (emerged IV-5-1983), 4♂, 2♀; VI-30-1986, coll. ex larvae (emerged III to V-1987), 5♂ 1♀, Dave Daniels, coll.; Alpine Garden Club tract, 5 mi. NW Flagstaff, VI-14-1970, 8♂, 3♀, R.Wielgus, coll.

Cochise Co: vic. Fort Grant, SW of Mt. Graham, 1♂, W.H. Edwards collection (***lectotype***), Huachuca Mtns., VI-23 to 30, no year, 12♂, Barnes coll'n.; VI-6-1910, 4♂; VI-6-1916, 2♂ J.A. Comstock coll'n; VI-22-1910, 2♂, 2♀, E.I. Huntington coll'n; IX-8-1915, 1♀; V-24 to 30-1919, 1♂ ,W.G. Wright coll'n; V-16-1923, 1♂, V-24-1930, 1♂, R.C. Williams coll'n.; Carr Peak, Huachuca Mtns., VI-19-1940, 7♂; VI-23-?- , 2♂, all A.C. Twomey, coll., Chiricahua Mtns., VI-20-30-1908, 6♂, 1♀, Victor L. Clemence, coll.; VI-30-1916, 1♂, V.W. Owen, coll.; VII-10-1958, 2♂, 1♀, J.P. & G.C. Hubbard, coll.

Navajo Co: Santa Rita Mtns., 5000-8000', July, 1♂, F.H. Snow, coll.; VI-20-1903, 1♀, Stephens, coll.; Pinal Mtns., VII-5 & 14-1900, 2♂; V-30-1925, 1♂, no coll.; Navajo Mtn., VI-14-1936, 1♂, no coll., VI-19-1935, 2♀, R.G. Wind, coll.; VII-12 & 13-1933, 4♂, 1♀, H.N. Hultgren, coll., VI-21-1935, 1♂, R.G. Wind, coll.; Williams Creek, North fork White River nr. McNary, V-29-1932, 1♂; VI-7-1932, 2♂, 1♀, no coll.; White Mtns.

Pima Co: Baboquivari Mtns., VII-15 to 30-1903, 2♂, 1♀, O.C. Poling, coll.; VIII-1 to 15, 1924, 15♂, 3♀, J. Gunder, coll.; Catalina Mtns., 7500', VI-13-1937, 4♂, 8♀, O. Buchholz coll'n.; 8500', VI-21-1936, 3♂, 1♀, C.F. dos Passos coll'n.; Mud Springs, Santa Catalina Mtns., 6500', VII-17 to 20 -1916, 1♂, 2♀, no coll.; Catalina Mtns., 8500', VI-22 to 26-1936, 2♂, 2♀, L.P. Grey, coll.

UTAH:

Garfield Co: Blue Spruce Camp, 18 mi. north of Escalante, 8000', VII-5-1963, 1♂, F. Rindge, coll. [AMNH]

Iron Co: Burnt Peak Road, summit, 2412m, VI-21-1971, 1♂, 2♀, J.A. Scott, coll.

San Juan Co: Monticello, VI-25-1930, 1♀, Ashby D. Boyle coll'n; 4.5 mi. SSW Buckeye Reservoir, 7700',coll. ex larvae on *E. alatum* (emerged VI-9 to 12-1989), 9♂, 3♀, J.L. Harry, coll.; Navajo Mtn., 6000', VI-16 to 20-1936, 21♀, Allyn Museum collection.

Kane Co: U.S. Hwy 89, 3.2 mi. N. Long Valley Jct., 7200', coll. ex larvae on *E. racemosum* (emerged V-21-1987), 6♂, 2♀, J.L. Harry, coll.

Wayne Co: Singletree Campground, 8300', 11 mi. So. Torrey, collected ex larvae on *C. fendleri* and *E. racemosum* (emerged IV-25-1987), 5♂, J.L. Harry, coll.; 7.4 mi. so. Torrey, 8800', N. Slope Rd., coll. ex larvae on *C. fendleri* and *E. racemosum* (emerged IV-20-1987), 1♂, 1♀, J.L. Harry, coll.

Grand Co: 4.4 mi. no. Mt. Waas, 18 mi. E. Moab, 8500', VI-26-1987, 1♂, J.L. Harry, coll.

NEW MEXICO:

Catron Co: 2-3 mi. E. of Mogollon, 7200-7600', VII-11-1961, 1♀, AMNH collection.

McKinley Co: Grasshopper Canyon, 6800', 10 mi. S. Ft. Wingate, VI-26-1981, 4♂, 2♀, G.A. Gorelick, coll.; Grasshopper Spring, 7500', Zuni Mtns., V-7-1977, 2♀; V-23-1977, 3♂; V-16-1976, 3♂, all R.W. Holland, coll.; Tohatchi Peak, 8300', Chuska Mtns., VI-18-1978, 2♂, R.W. Holland, coll.; 1 mi. N. Tohatchi

Outlook, 8400', Chuska Mtns., IV-29-1972, 1♂; VI-4-1978, 1♂ ; VI-18-1978, 1♀ , VI-18-1978, 1♀, all R.W. Holland, coll.; Ft. Wingate, V-25 to VII-1-1909, 12♂, 8♀, AMNH collection. Prop Cyn., 8000', Zuni Mtns., V-14 & V- 29-1976, 3♂ ; V-30-1977, 2♂ ; VIII-15-1976, 1♂ , R.W. Holland, coll.

Valencia Co: Pole Cyn., 8000-8500', Zuni Mtns., V-6-1977, 1♂; V-30-1977, 2♂ ; VI-12 to 24-1977, 3♂, 1♀; VII-29-1977, 1♂ , all R.W. Holland, coll.; Ojo Redondo, Zuni Mtns., V-16-1970, 1♀ , R.Bailowitz., coll.

Grant Co: McMillan Campground, 13 mi. N. Silver City, 6000-7000', VII-16 to VII-19-1964, 25♂, 18♀ ;Cherry Creek Campground, 6900', 13 mi. N. Silver City, VII-18-1964, 3♂, all F., P., & M. Rindge, colls.; Cherry Creek Cyn. & McMillen Cyn., 6700-7300', Pinos Altos Mtns., June-July 1976, 28♂, 29♀, C.D. Ferris, coll.; Pinos Altos Mtns., Pinos Altos, VII-4 to 10 -1958, 3♂, 1♀ , J.P. Hubbard, coll.; Pinos Altos Mtns., Cherry Creek, VII-6-1958, 3 ♂ ; VII-19-1959, 1♂ , J.H., coll.; VII-10-1958,1♂, J.P. & G.C. Hubbard, colls.; Cherry Creek, 7100' Gila Nat'l Forest, VII-1-1977, 1♂ , C.D. Ferris, coll., vic. McMillan Cyn., 7400', Gila Nat'l Forest, VII-1-1977, 2♀ , C.D. Ferris, coll.; Signal Peak Rd., Gila Nat. For., VI-29-1978, 1♂, C.D. Ferris, coll.; 12-14 mi. N. Silver City, 7000', VII-6-1985, 8♀ , C.D. Ferris, coll.; VII-3-1986, 4♀ ,7♂, G.A. Gorelick, coll.

°Otero Co: Cloudcroft, VI-19-1902, 1♀, no coll.; High Rolls, V-22-?, 1♂, both in Carnegie Museum collection [CMNH] (*°Received from the Engel collection, these very early captures bore no collector labels and are probably mislabeled specimens)*

MEXICO:

Chihuahua: Mun. Casas Grandes, head of Rio Piedras Verdes, 7200', 30 15'N, 108 15'W, 1899, 1♀, Townsend, coll. [CMNH]; Madera, 7200', VII-6-1947, 2♀ , W. Gertsch & M. Cazier, colls. [AMNH]; VIII-1968, 2♂, T. Escalante, coll., Arroyo Mesteno, Sierra del Nido, 7600', VII-21-1959, 1♀ , W.C. Russell, coll.; 10 mi. E. Namiquipa, VII-3-1947, 8♂ , M. Cazier & W. Gertsch, colls.[AMNH]; near Babicora, 5.7 mi. E. jct., road to Madera, VII-29-1984, 1♀ , D.Daniels, coll.

Callophrys affinis apama/
***C. a. homoperplexa* blend**

NEW MEXICO:

Los Alamos Co: Burnt Mesa, Hwy 4 west of Los Alamos, Bandelier National Monument, 1♂, VI- 20 -1997; coll. ex larvae on *C. fendleri*, VI-22-1997 (emerged VII to IX-1997), 6♂, 2♀, G.A. Gorelick, coll.

Sandoval Co: Jemez Springs, 7000', V-25 to VI-13-1913, 9♂, 13♀ ; V-21-1921, 1♀ ; VI-2-1921, 3♀ , all J. Woodgate, coll., Bandelier National Monument, 7000', VII-17-1999, 2♂, 2♀, S.J. Cary, coll.

***Callophrys affinis homoperplexa* Barnes & Benjamin**

NEW MEXICO:

Colfax Co: Dale Mtn., 8400', Johnson Mesa, VI-21-1997, 1♂, S.J. Cary, coll.; Tolby Campground, Hwy 64, 7000', June 2, 1996, 1♂, 1♀, G.A. Gorelick, coll.

Santa Fe Co: Hyde State Park, 8 mi.NE. Santa Fe, 8700', Sangre de Cristo Mtns., VII-29 to 31-1964, 1♀ , F., P., & M. Rindge, colls.; Chupidero Cyn., 8450', Sangre de Cristo Mtns., VII-23-1934, 1♂ , M. Hebard, coll.

Rio Arriba Co: San Antonio Mtn., 9000', VI-21-1978, 3♂, J.A. Scott, coll.

San Miguel Co: near Hot Springs, 7000', Las Vegas, VII-1882, 1♂, 2♀, F.H. Snow, coll.

Union Co: Capulin Mountain National Monument, VI-28-1968, 1♀, no coll.

COLORADO:

Larimer Co: Horsetooth Mtn. Park., 5 mi. SW. Ft. Collins, V-6-1977, 1♂ , J. Buchholz, coll.; VI-23-1985, 2♂ ; V-5-1985, 1♂ , R.E. Stanford, coll.; V-30 to VI-8-1987, 5♂ , P.A. Opler, coll.; VI-29-1997, 2♀, P.A. Opler, coll., VI-29-1997, 2♂ , G.A. Gorelick, coll.; Lory State Park, 5 mi. W. Ft. Collins, VI-8-1985, 2♂ , P.A. Opler, coll.; VI-29-1997, 2♂, Andrew D. Warren, coll.; "A" Mountain on Horsetooth Res. Rd., VI-25-1995, 1♀, A.D. Warren, coll.; 4 mi. W. of Hwy. I-25 on Woodman Rd., VI-2-1992, 1♂, A.D. Warren, coll.

Jefferson Co: Apex Trail at Heritage Square, V-13-1990, 1♂; V-11-1991, 1♂; VI-6-1990, 4♂, A.D. Warren, coll.; Indian Hills, nr. Denver, VI-21-1936, 1♂, W.D. Field, coll.; Mother Cabrini Shrine, Hwy. 40 W. of Denver, VI-10-1961, 2♂ , VI-14-1966, 1♀, R.J. Jae, coll.; VII-5-1965, 1♀ , John A. Justice, coll.; V-26-1990, 2♂, A.D. Warren, coll., Chimney Gulch, V-24 to30-1907, 3♂ ; VI-8-1915, 2♂ , E. Oslar, coll. (from Barnes collection, incl. 1 ***paratype***); VI-6-1937, 1♂ ; V-13-1938, 1♂ , Bob Potts, coll.; Chimney Gulch, 1/4 mi south, V-6-1966, 1♂ , J.A. Scott, coll.; V-25-1927, 1♂ , E.I. Huntington coll'n; VI-6-1937; Rooney Ranch, VI-17-1956, 1♀, R.J. Jae, coll.; Lookout Mtn., nr. Golden, 6500-7200', VII-8-1967, 5♂, 1♀ ; VI-11 to 18-1968, 7♂, 2♀ , all Mike Fisher, coll.; Castle Rock, near Golden, V-21-1966, 1♂ , J.A. Scott, coll.; °Golden, V-24 to 30 (no year), 2♂ ; VI-8 to 15 (no year), 2♂ ; V-16 to 23 (no year) , 1♂ , V-24-1930 , 1♂, all Barnes and Benjamin (***paratypes***); Golden, VI-1910, 2♂, F. Skinner, coll.; V-28-1939, 2♀, C.C. Albright, C.D. Schryver, colls.; VI-11-1939, 1♂, C.C. Albright, coll.; V-2-1943, 1♂, C.D. Schryver, coll.; Clear Creek Canyon, V-8 to 15-1907, 1♂ , Ernest J. Oslar, coll.; Clear Creek, 6000-7000', VI-20-1922, 1♂ , G.P. Engelhardt, coll.; VII-3-1984, 1♂ , P.A. Opler, coll.; Red Rocks Park, 6000', V-11 & 25-1956, 2♂ , R. J. Jae, coll.; V-24-1964, 1♂, 1♀ , VI-4-1966, 2♂, J.A. Scott, coll; Red Rocks Park, VI-10-1971, 1♂ , R.J. Jae, coll.; Red Rocks Park, 2 mi. NW Morrison, VI-5-1968, 1♂, 1♀, Mike Fisher, coll.; Ralston Butte, V-23 & 24-1994, 23♂, 2♀ ; V-29-1988, 4♂ ; VI-10-1994, 2♂ ; VII-10-1985, 2♀ , all J.A. Scott, coll.; Tinytown, V-26-1984, 2♂; V-15 to VI-25 (1984-94), 17♂, 7♀ , all J.A. Scott, coll.; Tinytown (trail to Mt. Lindo), V-31-1993, 1♂, 1♀; VI-7-1992, 1♀; V-27-1991, 1♀; V-29-1989, 1♂; VI-9-1998, 1♂, all A.D. Warren, coll.; Lookout Mtn., V-29-1988, 2♂ ; VI-15-1995, 5♂ , J.A. Scott, coll.; Indian Peak, V-14-1994, 2♂ , J.A. Scott, coll.; El Dorado Mtn., VI-11- 1994, 1♂ , J.A. Scott, coll.; Zion, 2100m, V-28-1991, 1♂ , C.P. Slater, coll.; Mt. Zion, V-30-1981, 1♂; V-14-1994, 2♂;V-26-1984, 2♀, J.A. Scott, coll.; VI-1-1990, 1♂, 1♀; V-28-1989, 2♂; V-30-1991, 1♂; V-28-1998, 2♂, A.D. Warren, coll.; Guy Hill, VI-18-1992, 1♀ , J.A. Scott, coll.; Falcon County Park, V-30-1984, 1♂ ; VI-15-1989, 2♂; VI-6-1994, 2♀, J.A. Scott, coll.; Mt. Falcon, V-27-1994, 2♀ , J.A. Scott, coll.; Tucker Gulch, VI-12-1982, 1♂ , C.P. Slater, coll.; VI-15-1995, 1♂ , J.A. Scott, coll.; Apex Gulch, VI-5-1990, 2♂ ; VIII-20-1990, 1♂ ; VI-20-1995, 4♂ ; V-19-1994, 1♂ V-29-1991, 2♂ , all J.A. Scott, coll.; Coal Creek, VII-17-1991, 1♂, J.A. Scott, coll.; Green Mtn., V-10 and VI-3-1986, 2♂, J.A. Scott, coll.; Crawford Hill, VI-5-1980, 5♂, 1♀ , J.A. Scott, coll.; N. Crawford Gulch/Canyon, V-30-1981, 1♂; V-24-1988, 1♂ , J.A. Scott, coll.; Golden Gate Cyn., VI-12-1956, 1♂ , Lincoln F. Brower, coll.;

° Type locality of *C. a. homoperplexa*. Paratypes exist also from Boulder and Denver

Boulder Co: Eldora, VI-15-1941, 1♀, P.S. Remington, coll.; Boulder, VI-20-1949, 3♀ , J.C. Hopfinger, coll.; "July" , 1♂ , (*paratype*), no coll.; Boulder Canyon, VI-18 to 20-1933, 1♀, 1♂, P.S. & C.I. Remington, colls.; Mtns. No. of Boulder Cyn., VI-2-1965, 2♀ , John Justice, coll.; Baird Park, Gregory Cyn., V-23-1965, 1♂ , J.A. Scott, coll.; nr. Baird Park, Gregory Cyn., VI-7-1964, 1♀ , VI-14-1965, 1♂ , John Justice, coll.; V-4-1965, 2♂, V-12 to 19-1965, 6♂ , J.A. Scott, coll.; Gregory Cyn., 5900', V-29-1954, 1♂; V-20-1966, 1♂, J. Don Eff, coll., V-23-1962, 1♂; VI-3-1962, 1♀; V-19-1966, 1♂, J.A. Scott, coll.; V-1 to 6-1966, 8♂, 1♀ , S.A. Johnson, coll.; V-20-1970, 1♂ , R.J. Jae, coll.; V-4 to 23-1965, 1♂ , J.A. Scott, coll.; IV-28 to V-30-1966, 21♂, 2♀ , J.A. Scott coll.; Cardinal Hill, VII- 1-1957, 1♂, J. Don Eff, coll.; Sunshine Cyn., 7200', VI-1-1947, 3♂ , V-28-1953, 1♂, all J. Don Eff, coll.; V-30-1962, 2♀ , J.A. Scott, coll.; 1 mi. NW Nederland, VII-2-1989, 1♂ , J.A. Scott, coll.; nr. summit, Flagstaff Mtn., VII-15-1975, 1♂ , J. Vernon, coll.; Flagstaff Mtn., V-23-1948, 2♂; VI-19 to 21-1953, 2♂ , all J. Don Eff, coll.; V-30-1961, 3♂ , J.A. Scott, coll.; V-29-1951, 2♂ , O. Buchholz coll'n ; Four Mile Cyn., VI-17 to 19-1953, 4♀, 3♂; V-16 to 19-1958, 1♀, 2♂; VI-25-1965, 1♀; V-15-1966, 2♂, 1♀, all J. Don Eff, coll.;V-9-1959, 2♂ , J. Don Eff, coll.; Four Mile Creek Cyn., nr. Crismon, V-16 to 24-1958, 6♂, 1♀; VI-5-1959, 2♂; V-2 to 17-1962, 4♂, 2♀, all J. Don Eff, coll.; Packer's Gulch, nr. Crismon, V-15-1966, 1♂, J. Don Eff, coll.; Lefthand Cyn., V-4-1932, 1♂ ; V-30-1951, 1♂, V-24-1953, 5♂; V-29-1954, 2♂, all J. Don Eff, coll.; VI-28-1952, 1♂, O. Buchholz collection; V-23-1962, 1♂; VI-9-1968, 1♂; VI-8-1994, 1♂, J.A. Scott, coll.; Magnolia Road, VI-13-1972, 1♂ , J. Don Eff, coll.; 2 mi. SW Boulder, 6500', V-18-1963, 1♂, U. Lanham, coll.; Sugarloaf, V-30-1955, 2♂, J. Don Eff, coll.; V-20-1958, 2♀, E.R. Hulbirt, coll.; Iron Mtn., Sugarloaf Rd., V-13-1962, 1♂, J. Don Eff, coll.

Denver Co: Ruby Hill, 5390', V-25-1994, 1♀, R.E. Stanford, coll [GM-CSU]

Gilpin Co: No. Clear Creek, 7200', VII-2 to7 (1977-8), 4♂, 1♀, J.A. Scott, coll.; VII-3-1982, 1♂, R.E. Stanford, coll.; East Portal, Moffat Tunnel, VI-19-1977, 1♂ , J.A.Scott, coll.; Aspen Springs, 8900', VI-8-1985, 1♂, R.E. Stanford, coll., Blackman Meadows Trail, 8400-8700', Golden Gate State Park., V-24-1975, 1♂, R.E. Stanford, coll.

Gunnison Co: Almont, VI-20 to 30-1925, 2♀ , J.D. Gunder, coll.; One Mile Camp, 8 mi. NE Almont, 8200', VII-8-1957, 2♂, 1♀ , F. & P. Rindge, colls.; 5 mi. W. Gunnison, 7000', VI-17-1966, 1♂, 1♀ ; Iola, 7600', VI-19-1967, 1♀ ; Curecanti Creek, 8000', VI-2-1962, 2♂, all Scott L. Ellis, coll.; Blue Mesa Reservoir, jct. Hwys 50 &149, VI-4-1996, 3♂, G.A. Gorelick, coll.

Logan Co: County Road 9, 6.5 mi. N. of Ft. Morgan, chalk bluffs, V-28-2000, 1♂, 1♀, R E. Stanford, coll.

Morgan Co: S/N scarps, Wildcat Creek, SR 52, 7-11 mi. N. of Ft. Morgan, V-28-2000, 4♂, R.E. Stanford, coll.

Adams Co: 1 mi. W. fairgrounds, 5100', V-25-1994, 1♂, R.E. Stanford, coll.

Custer Co: Davenport Camp, 36 mi. So. Florence, 8500', VI-30-1967, 3♂, 1♀, F., P., & M. Rindge, colls.; Silver Cliff, VI-29-1968, 1♂ , J.A. Scott, coll.;

Washout Creek, VII-4-1967, 1♂, J.A. Scott, coll.; Smith Creek Campground., VI-13-1971, 1♀, J.A. Scott, coll.; _ mi. E. Smith Creek Campground., Hwy 82, VII-28-1970, 1♂, J.A. Scott, coll.; VI-3-1996, 1♂, G.A. Gorelick, coll.; Bull Domingo Mine, VI-18-1973, 1♂, J.A. Scott, coll.; Ben West Hill, VI-12-1970, 1♂, J.A. Scott, coll.; 3.2 mi. W. of Wetmore, Lewis Creek Trail, VI-11-1991, 1♀, A.D. Warren. coll.

Fremont Co: 1 mi. So. Cotopaxi, VII-1-1969, 1♂, J.A. Scott, coll.

Park Co: nr. Antero Jct., 9300-9500', VI-23-1973, 1♂, R.E. Stanford, coll.

Arapahoe Co: Piney Creek, 6000', VI-2-1974, 1♂; VI-10-1979, 2♂, R.E. Stanford, coll.; Piney Creek, Smoky Hill Rd., 6700', VII-4-1965, 1♂, J.A. Scott, coll.; V-20-1993, 5♂; V-28-1993, 3♂; VI-5-1992, 1♂; VI-6-1992, 2♂; V-29-1994, 3♂, A.D. Warren. coll.

Pueblo Co: 2 mi. up Greenhorn Trail, Greenhorn Campground, VI-22-1967, 1♂, J.A. Scott, coll.; Greenhorn Trail, w. of Rye, VI-4-1971, 2♂, J.A. Scott, coll.; Beulah, VII-7-1899, 1♂, W.D. Kearfott, coll.; VI-12-1970, 4♂, J.A. Scott, coll.; 4 mi. NW Beulah, VI-29-1970, 1♀, J.A. Scott, coll.;

Los Animas Co: near Weston, VII-13 to 19-1975, 2♂, 1♀, J. Vernon, coll.

Douglas Co: Indian Creek Campground., VII-6-1995, 1♂, J.A. Scott, coll.; Mitchell Gulch @ Founders Village, 6400', VII-31-2000, 3♂; Surrey Ridge, VII-17-1989, 1♂; Hidden Pointe area, ca. 8 mi. NNW Castle Rock, VI-13-1998, 1♂; VII-4-1998, 1♀; VI-11-1998, 1♂; VI-6-1998, 1♀; VI-18-1998, 2♂; VI-7-1998, 1♀; VII-16-1998, 1♂; VI-24-1999, 3♂, 2♀; Newlin Gulch, ca. 8 mi. NNE Castle Rock, VI-28-1999, 2♂, 1♀,; VII-17-1999, 4♂; canyon N. of Palmer Lake, VII-29-2000, 1♂; Daniels Park, VII-12-1998, 1♂, 1♀; V-31-1998, 1♂; McMurdo Gulch, 3 mi. NE of Castle Rock, VI-17-1999, 2♂; Hunt Mountain, ca. 6 mi. S. of Castle Rock, VII-24-1999, 1♂; VII-11-1999, 2♂; VI-26-1999, 3♂, 1♀; Wolfensburger Road, ca. 2 mi. W. of Castle Rock, VI-19-1999, 3♀; mouth of Jarre Canyon, VI-4-1998, 1♂, all A.D. Warren. coll.

Elbert Co: Running Creek Field Sta., 6950', T9S, R65W Sec 26, SE 1/4, VI-25-1976, 1♀, S. Condie, coll.; Pohl Ranch, 6850', T6S, R65W, Sec 26, SW 1/4, 1♂, no coll.; near Elbert, 7000-7400', VI-26-1976, 1♂, R.E. Stanford, coll.; south side of County Line Rd., 6.2 mi. E. of Gun Club Rd., VI-10-1993, 3♂, A.D. Warren. coll.

Teller Co: 4 mi. SW. of Florissant, VI-26-1989, 1♂, 1♀, A.D. Warren, coll.; Florissant Fossil Beds, 8550', R70W, T13S, Sec 30, Maytag, VI-22-1976, 1♂, S. Condie, coll.

Ouray Co: 4 mi. N. Ouray, 7400', VI-5-1966, 1♂, F. M. Brown, coll.

El Paso Co: Mt. Hermon Mon. Area, 7500', VII-8-1956, 4♂, no coll.; Star Ranch, VI-26-1931, 1♂, F.M. Brown, coll.; VI-27-1965, 1♂, no coll.; 4 mi. W. of Hwy. I-25 on Woodman Rd., VI-2-1992, 1♂, A.D. Warren, coll.

Chaffee Co: nr. Mt. Princeton Hot Sprs., Hwy 162, 7500', VI-20-1966, 1♂, 1♀, Scott L. Ellis, coll.; 1 mi. WSW of Buena Vista, VI-13-1992, 2♂, A.D. Warren, coll.

Dolores Co: West Fork Camp, 20 mi. NW Dolores, 7800', VI-30-1957, 3♂, F. & P. Rindge, colls.

Clear Creek Co: Fall River Rd., 2 mi. W. Idaho Sprs., 7500', VI-4-1967, 1♂; VI-3 to 8-1968, 2♂, Mike Fisher, coll.; Clear Creek, 7000-8000', V-27-1979, 1♂, R.E. Stanford. coll.

Montrose Co: Alpine Trail Rd., VI-22-1973, 1♂, no coll.; north .rim, Black Canyon National. Monument, 7809', VI-30-1967, 1♂, 2♀, Scott L. Ellis, coll.

Lincoln Co: N. microwave tower, 6.5 mi. W. CO Hwy 71, 5850', VI-30-1993, 1♀, R.E. Stanford, coll.; CO Hwy 71, 5400', 21.6 rd.mi. N. Limon, Li/Wa Co. line, VI-30-1993, 1♂, R.E. Stanford, coll.

Archuleta Co: NE of Pagosa Sprs., June 30, 1965, 1♂, sight record, J.A. Scott

Saguache Co: County Road 31 above Vulcan, west slope portion of county, VI-16-2001, 2♂, Michael S. Fisher, coll.

***Callophrys affinis albipalpus* ssp. nov.**

NEW MEXICO:

Lincoln Co: Cedar Creek Camp, 5 mi. N. of Ruidoso, 7000', Sacramento Mtns., VI-30-1961, 2♂, F., P., & J. Rindge, colls.; New Mexico State University's Montgomery Biological Research Laboratory, 5 mi. n. of Ruidoso, 7000', Sacramento Mtns., VII-26 to 28-1978, 2♀, VII-21 & 22-1980, 2♀, all Greg Forbes, coll. (R.W. Holland collection.); VII-4-1981, 2♂, 4♀, G.A. Gorelick, coll.; VI-28-1982, 1♂, ex ovum (Emgd: IV-27-1983); VII-1982, 7♂, 7♀, ex ova reared on lab host, *Eriogonum grande rubescens* (Emgd: VIII-1982)

***Callophrys affinis chapmani* ssp. nov.**

MEXICO:

Sonora: Mun. Nacori Chico, 7300',11.6 mi. N.of Mesa Tres Rios and 44.9 mi. so. of Huachinera, 108 49'W, VII-2-1979, 1♀, R.W. Holland, coll., 13.7 mi. N. of Mesa Tres Rios and 42.8 mi. S. of Huachinera, 7600', 108 49'W, VII-2-1979, 1♂, R.W. Holland, coll.

Durango: El Salto, 27.7 mi. E., 8000', VII-18-1964, 1♀, J.A. Powell, coll.; VII-11-1981, 1♀, R.W. Holland, coll., VII-15-1981, 1♂,1♀, G.A. Gorelick, coll; VIII-5-1981, 1♀, G.A. Gorelick, coll., VII-10/11-1983, 2♂, 4♀, G.A. Gorelick. coll., VII-15-1983, 2♀, G.A. Gorelick, coll.; 13 mi. E. El Salto, Hwy. 28, 8000', VII-10-1983, 1♀, G.A. Gorelick, coll.; Mun. Llano Grande, 16-17 mi. E. El Salto, Hwy. 28, VII-13-1985, 2♂, 3♀, coll. ex ova on *Eriogonum atrorubens* (Emgd: VIII-28-1985) G.A. Gorelick, coll; 16.3 mi. E. El Salto, Hwy. 28, IV-14-1986, 1♀, Greg Ballmer, coll. ex larva on *Eriogonum atrorubens*.

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CLOUD FOREST BUTTERFLY FAUNA OF THE PANTEPUI – POOR OR POORLY KNOWN? DESCRIPTION OF NEW SPECIES AND RECORDS OF NEW GENERA OF PRONOPHILINA: *ERETRIS AGATA* AND *OXEOSCHISTUS ROMEO* (NYMPHALIDAE: SATYRINAE)

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ABSTRACT. Two new species of Pronophilina (Nymphalidae, Satyrinae) - *Eretris agata* and *Oxeoschistus romeo* - are described from the Guyana shield, also known as the Pantepui, a region of table mountains situated in southeastern Venezuela, northwestern Guyana and adjoining Brazil. They are only the third and fourth genera of the diverse neotropical montane subtribe Pronophilina (Nymphalidae, Satyrinae) reported for this vast biogeographical region. Their affinities are evaluated indicating close relationship with the Pronophilina of the Venezuelan Cordillera de La Costa. The current state of knowledge of the Pronophilina in the Pantepui is discussed. Low figures of diversity are interpreted as a result of isolation from the center of origins and diversity in the central Andes, and partly as a consequence of heavy undersampling.

Additional key words: Andes, affinities, bamboo, endemic species, Guyana shield, island biogeography, *Protopedaliodes*, species richness.

INTRODUCTION

Pantepui is a term originally proposed by Mayr and Phelps (1955) to designate the region of table mountains situated in southern Venezuela and adjacent areas of Brazil and Guyana. Even though throughout the years there were many contradictions and various definitions of Pantepui (Huber, 1987; Brown, 1979), all the authors concurred that this vast area is worth identifying as a separate biogeographical entity identified by a number of biotic (i.e. endemic taxa) and abiotic features.

Nearly a century ago, Strand (1912) described from the Pantepui the first species of butterfly belonging to the predominantly Andean subtribe Pronophilina (Miller, 1968; Adams, 1985; Pyrcz & Wojtusiak, 2002)—*Pedaliodes roraimae* (see fig. 5). His discovery passed completely unnoticed (Viloria & Pyrcz, 1995) and only recently, during the last decade, was there an increase of interest in the butterfly fauna of the Pantepui in general (Neild, 1996) and the Pronophilina in particular, resulting in the description of several new taxa. Four of them, *Pedaliodes demarmelsi* Viloria (1995), *P. chaconi* Viloria (1998), *P. terramaris* Viloria & Pyrcz (1999) and *P. yutajeana* Viloria & Pyrcz (1999) are closely related to each other and to *P. roraimae*. *Protopedaliodes kukenani*, described by Viloria & Pyrcz (1994) from the top of Kukenan and Roraima, represents a well differentiated endemic genus. Viloria & Pyrcz (1999) described a further two species belonging to this genus: one from Roraima — *Pr. ridouti*, and one from the Auyán Tepui — *Pr. profauna*. All of the species described hitherto from the Pantepui belong to the *Pedaliodes* complex (Viloria, unpublished Ph.D. thesis). The two new species described herein belong to other genera and sections of the subtribe Pronophilina previously not reported in South America outside the Andes and their peripheral ranges (Sierra Nevada de Santa Marta, Cordillera de La Costa) – *Eretris* Thieme (1905) and *Oxeoschistus* Butler (1867). Their discovery is very significant as it emphasizes how little the Pronophilina fauna of the Pantepui is known, how much research is still to be done, and also raises interesting zoogeographical issues.

Subtribe Pronophilina

The genera *Eretris* and *Oxeoschistus* belong, according to Miller (1968), to the neotropical subtribe Pronophilina (considered by Harvey (1991)and Lamas *et al.* (2004) as a sub-tribe within the tribe Satyrini), an entirely neotropical section of the worldwide subfamily Satyrinae (Nymphalidae). The Pronophilina can be divided into three groups based on ecological and morphological criteria: Chileno-Patagonian (considered by Lamas & Viloria 2004 as belonging to the predominantly Australian tribe Hypocystini), Caribbean (only the genus *Calisto* Lathy) and tropical montane. The latter dominant section comprises approximately 460 species (Lamas *et al.*, 2004) distributed in the cloud forests and paramos of Central and South America. In continental Central America 18 species are restricted to the highest mountains of Panama and Costa Rica, and 10 to Guatemala and the neighboring states of Mexico. In South America, the vast majority, more than 95%,

occur in the Andes and its peripheral ranges: the Sierra Nevada de Santa Marta and the Cordillera de La Costa. Seven species are found in the highlands of southern Brazil. The second region outside the Andean Cordilleras where tropical montane pronophilines occur is the Pantepui.

The species belonging to the subtribe Pronophilina occur in well-defined and sometimes very narrow bands of altitude. Their altitudinal zonation has been attracting the attention of naturalists since the early twentieth century (Fassl, 1911, 1915 and 1918; Krüger, 1924 and 1925), and recently was more extensively discussed by Adams & Bernard (1977, 1979 and 1981), Adams (1985 and 1986) and Pyrcz & Wojtusiak (1999, 2002). Endemism is also a notable feature of the Pronophilina. In each north Andean range, between 10% and 30% of taxa are endemic at the specific level (Adams, 1985). The endemism ratio is higher in most isolated units, such as the Sierra Nevada de Santa Marta, the Cordillera de Mérida and also the Pantepui. Adams (1985) concludes that the average altitude range of the endemic species in all three Colombian Cordilleras is set higher, close to the upper forest limit, than that of the non-endemic species. However, Pyrcz & Wojtusiak (1999) show, based on sampling in western Colombia, that this is not always the case. The highest diversity of the subtribe is reported close to the upper forest limit, varying from range to range, but generally falling at 2600–3000m (Adams, 1985; Pyrcz & Wojtusiak, 1999; 2002). Several species occur in the paramo grassland above the timberline as high as 4500m. Very few Pronophilina were reported below 1000m.

Adult Pronophilina, like other satyrines, are mostly sedentary (Adams, 1986; Pyrcz & Wojtusiak, 2002) and even inside the cloud forest they are generally restricted to particular habitats (Adams, *op. cit.*). Most species show restricted vagility and even though this aspect of their behavior was not studied rigorously, field observations indicate that adults move little vertically or horizontally and keep close to their host plants or roosting places (DeVries, 1987). The biology of the Pronophilina remains largely unexplored but it appears that their larvae feed mostly on montane bamboo, in the Andes chiefly belonging to the genus *Chusquea* (Poaceae) (Schultze, 1929; Adams & Bernard, 1981; DeVries, 1987; Pyrcz & Greeney, in prep.). However, Pelz (1997) reared an Ecuadorian species, *Parapedaliodes parepa* (Hewitson), on a substitute secondary grass, *Poa festuca* (Poaceae), whereas Pyrcz *et al.* (1999) report that several species also use *Guadua* bamboo as their host plants. There are indications that the Pronophilina, or at least some of them, are oligophagous. In Ecuador, Pyrcz (unpubl.) reared the first to fourth instars of *Junea doraete* (Hewitson) on several different species of *Chusquea*. Bamboos are most abundant in clearings, roadsides, at the forest edge and along paths. Adults of all species of Pronophilina are attracted to decomposing organic matter, particularly to feces, carrion and rotten fruits. Therefore, the use of baited traps provides a very good method of sampling

Consulted collections: **BMNH**: The Natural History Museum, London, United Kingdom. **MBLUZ**: Museo de Biología de la Universidad del Zulia, Maracaibo, Venezuela. **MCC**: Mauro and Clara Costa, Caracas, Venezuela. **MIZA**: Museo de Entomología, Universidad Central, Maracay, Venezuela. **MZUJ**: Muzeum Zoologiczne Uniwersytetu Jagiellońskiego, Kraków, Poland. **SIW**: Smithsonian Institution, Washington, USA. **TWP**: Tomasz Wilhelm Pyrcz, Warsaw, Poland.

Acronyms used: **FW**: forewing. **HW**: hindwing. **D**: dorsal surface. **V**: ventral surface.

Eretris agata Pyrcz, new species

(Figs. 1, 2, 6, 14)

Diagnosis: Compared to allied species: *E. encycla* (figs. 7, 11–13, 15), *E. oculata* (fig. 16) and *E. calisto* (fig. 17)(all C. & R. Felder), the male of *E. agata* has no red markings along the VHW postmedian band's basal edge. The upperside is darker —blackish—not dark chocolate brown (which is noticeable in freshly emerged individuals). It is larger than nominotypical *E. encycla* from the Cordillera de la Costa, being approximately the size of the Cordillera de Mérida population. But *E. agata* has bigger ocelli than both and a different HW shape, somewhat ovaloid rather than squarish.

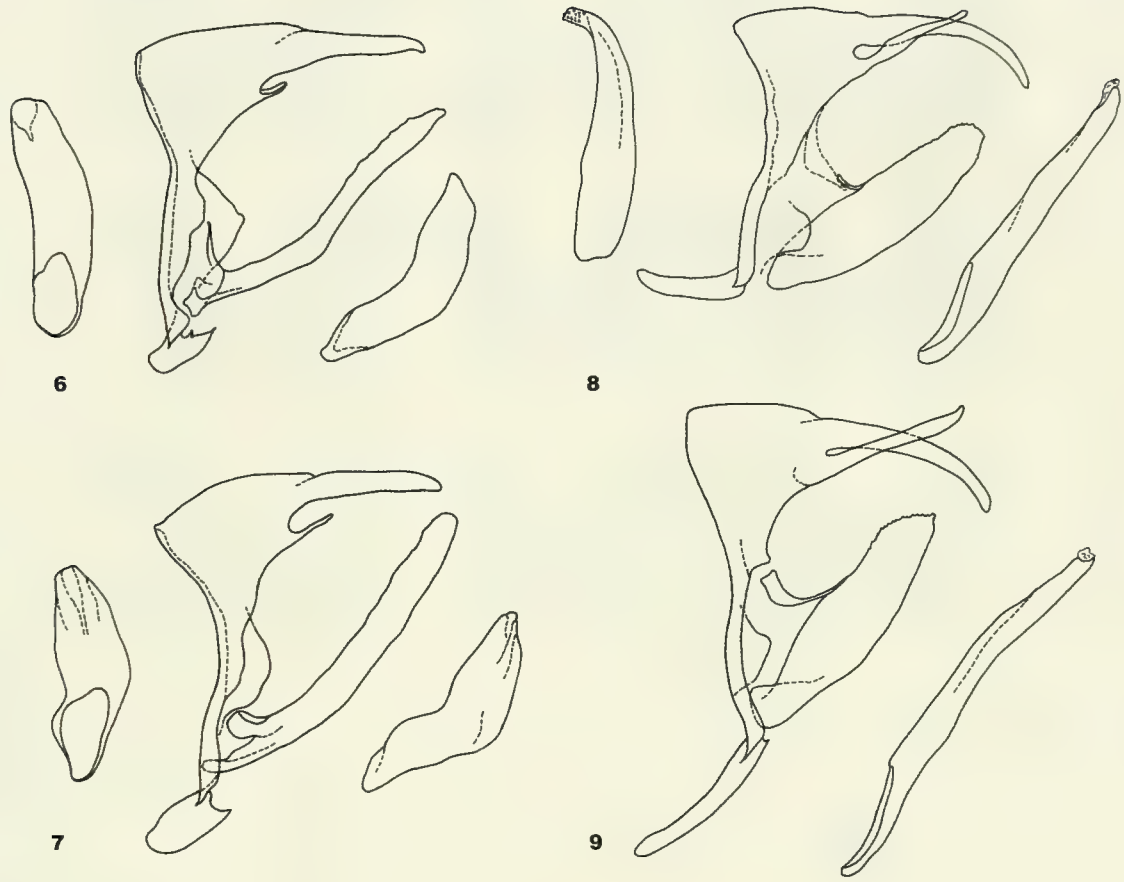
Description: ***Male*** (Fig. 1): **Head**: Eyes chocolate brown, lustrous, covered with dense and long setae; labial palpi covered with dark brown hair; antennae 8–9mm, orange brown, basal half covered ventrally with white scales, club only slightly thickened compared to shaft, two terminal segments black. **Thorax**: dorsally blackish brown, legs beige, tibiae covered ventrally with gray hair. **Abdomen**: dorsally and laterally blackish brown, ventrally gray. **Wings**: FW length: 22–24mm, mean: 23.2mm; n=5; apex blunt, distal margin straight. HW outer margin slightly undulated, inner margin incised below tornus. DFW ground color glossy blackish brown in freshly emerged individuals, gradually fading and becoming lighter as the wings are exposed to sunshine; distal one third with a distinctively lighter shade from costa to tornus; a nearly straight darker submarginal line running parallel to distal margin; fringes dark brown. DHW ground color same as on the FW; a very slightly lighter shade submarginally at apex, occasionally extending along submarginal area, especially in older individuals; a thin parallel undulated blackish brown submarginal line, darker than the ground color; an even thinner marginal line parallel to outer margin; fringes dark brown. VFW ground color glossy brown, lighter than on the upperside; four oblique dark brown lines, a median one, slightly arched across discal cell, a postmedian one from costa towards anal margin, fading away before touching it, nearly straight except for two curves between vein Cu1 and anal margin; a submarginal one, thinner than two basals, parallel to distal margin, slightly irregular from costa to vein M2, then nearly straight; a marginal line, very thin, parallel to the distal margin. VHW ground color from base to postmedian line dark brown, slightly suffused with tiny golden scales along inner margin and postdiscal area, which is noticeable only in freshly emerged individuals; a shallowly curved dark brown median line, darker than the ground color; a thicker chocolate brown postmedian line from costa to inner margin near tornus, roughly parallel to distal margin, slightly irregular and undulated but

FIGS. 1–5, Some Pronophlina from the Pantepui. **1**. *Eretris agata* , **n. sp.**, male dorsum/venter; **2**. *Eretris agata,* **n. sp.**, female dorsum/venter; **3**. *Oxeoschitus romeo,* **n. sp.**, male dorsum/venter; **4**. *Oxeoschistus romeo,* **n. sp.**, female dorsum/venter; **5**. *Pedaliodes roraimae* male dorsum/venter

without any deeper curves; a series of six submarginal rounded ocelli ringed with light orange and with small white triangular pupils, one in each cell from Rs–M1 to Cu2–1A, the biggest in Cu1–Cu2, the second biggest in Rss–M1, the remaining approximately the same size, half the size of the biggest, not touching the lines basad or distad of them, except the one in Cu2–1A, which crosses the submarginal line; a chocolate brown submarginal line, parallel to distal margin, thinner than the postmedian one; a thin dark brown marginal line parallel to outer margin.

Genitalia (Fig. 6): Uncus stout, ended with a short hook; gnathos short, less than one-fourth the length of uncus, slat-like; valvae long and thin with a characteristic shallow curve in the middle; aedeagus tubular, simple; saccus shallow.

Female (Fig. 2): **Head**, **thorax** and **abdomen** as in male. **Wings**: Wing shape as in male. FW length 23.5mm. DFW ground color dull dark brown, slightly lighter than in the male; color light brown distally from a postmedian oblique darker line running from costa to inner margin near tornus; a dark brown submarginal line, parallel to distal margin; a thin dark brown marginal line parallel to distal margin. DHW ground colour dark brown, same as in basal two-thirds of the FW; a brick-red postmedian line with a dark brown distal edge roughly parallel to distal margin from mid costa towards inner margin fading away at vein Cu2; a double dark brown and light brick-red submarginal scalloped line parallel to outer margin, fading away between vein Cu1 and tornus; a thin yellow marginal band edged basally with dark brown; a prominent oval submarginal ocellus in cell Cu1–Cu2, ringed with yellow and with a white pupil. VFW ground color medium brown, light brown distally from the postmedian line;



FIGS. 6–9. Male genitalia of Pronophilini. **6**. *Eretris agata*, **n. sp**. (aedeagus extracted in lateral and dorsal view). **7**. *Eretris encycla encycla* (aedeagus extracted in lateral and dorsal view). **8**. *Oxoeschistus romeo*, **n. sp.** (aedeagus extracted in lateral view, valva extracted in dorsal view). **9**. *Oxoeschistus puerta* ssp. (aedeagus extracted in lateral view).

the pattern of dark brown lines as on the upperside but edged with crimson red, the median and submarginal ones distally, the postmedian one basally; a thin yellow marginal band, edged basally with dark brown; a small rounded subapical ocellus in cell M1–M2, ringed with yellow and with a minute white pupil. VHW ground color medium brown; the pattern of dark brown lines as in the male, except that median and submarginal ones are edged distally with a thin crimson red line, whereas the postmedian is edged basally with a band of the same colour which overshadows most of the brown; submarginal ocelli of the same size and color as in the male; a thin yellow marginal basally dusted with dark brown.

Type material: Holotype ♂: Venezuela, Estado Bolívar, Sierra de Lema, road El Dorado - Santa Elena de Uairén km 132, 1983, 1350–1400m, M.C. Costa *leg*., MIZA Maracay; Paratypes: 9 ♂ and 1 ♀: same locality as the holotype, 22–23.II.2004, M.C. Costa & T. Pyrcz *leg*. (2 ♂ in MCC, 1 ♂ in BMNH, 1 ♂ in MIZA, 5 ♂ and 1 ♀ in TWP).

Etymology: This species is dedicated to Agata, a daughter of its discoverers Mauro and Clara Costa, Italo-Venezuelan lepidopterists from Caracas.

Behavior: *Eretris agata* was discovered along the El Dorado – Santa Elena de Uairén asphalt road between kilometer 130 and 135 (figs. 19–23). All the individuals were collected along the cloud forest edge when moving from inside the forest to the roadside, apparently looking for sunning spots. Several stands of an unidentified bamboo, its most likely host plant, were found some 20–30 meters inside the forest and more individuals were observed there. They were keeping to sunny gaps, occasionally patrolling and perching on large leaves at 3–5 meters above the ground. In the same habitat another species of Pronophilina was observed, *Pedaliodes roraimae* showing similar behavior but venturing more often into open areas, as well as another cloud forest Euptychiini satyrine, *Forsterinaria* sp.

Remarks: The genus *Eretris* (Thieme) comprises approximately fifteen species distributed in South and Mesoamerica (Lamas, *et al*., 2004). Three species are

found in Guatemala/Mexico and Panama/Costa Rica, and the remainder in the Andes. There has been no cladistic analysis of *Eretris*, but the genus is morphologically highly homogenous and presents several plausible synapomorphies. It can be recognized from other Pronophilina by several characters emphasized in the original generic description (Thieme, 1905), such as short antennae reaching roughly one third the length of costa and the lack of a FW upperside male androconial patch. The most outstanding feature of the color pattern are fully developed submarginal ocelli on the VHW and a rarely present vestigial M1–M2 ocellus on the VFW. The wing venation with the HW cross-vein m1–m2 bent inside discal cell is typical of the Pronophilina (Miller, 1968; Viloria, Ph.D.). Male genitalia of *Eretris* are very particular and can be recognized by a short, flattened, singularly sculptured aedeagus, short subunci and thin slat-like non-sculptured valvae.

The systematics of *Eretris* is very demanding because the differences between most species are very subtle. Additionally there is considerable infraspecific (Adams, 1986) and individual variation. The most obvious and significant taxonomic characters in the color pattern are all on the VHW: the shape and color of postmedian, submarginal and marginal lines, the size and number of submarginal ocelli and the color between the submedial line and the anal margin.

Oxeoschistus romeo Pyrcz & Fratello, new species

(Figs. 3, 4, 8)

Diagnosis: This species is immediately recognized from other congeners by the highly irregular shape of the FW orange band characterized by deep basal and distal intrusions compared to regular, nearly linear, edges of other related species, especially *O. simplex* Butler and *O. puerta* (Westwood) (fig. 9).

Description: ***Male*** (Fig. 3): **Head**: eyes blackish brown, setose; palpi white covered with black hair; antennae two fifths the length of costa, dark brown, club formed gradually, slightly thicker than shaft. **Wings**: FW length 31mm; apex blunt; distal margin slightly convex; HW outer margin scalloped. FW and HW fringes medium brown. DFW basal and postbasal area medium brown; median area crimson red progressively darkening distally; a wide, brick orange band extending from postmedian to submarginal area with an irregular basal edge and deep incursions of dark brown along costal margin in the subapical area, along vein M3 and in cell Cu2–1A, and a dentate distal edge; dark brown rounded submarginal spots M1–M2, M3–Cu1 and the largest of all in Cu1–Cu2; submarginal area dark brown becoming gradually lighter towards distal margin. DHW basal and median area medium brown; a wide brick orange band extending from postmedian to submarginal area with a nearly straight inner edge except for a shallow postdiscal incision and a dentate distal edge; a series of dark brown rounded spots situated in the middle of the band smaller than on the FW in Rs–M1, M1–M2, M3–Cu1, Cu1–Cu2 and two in Cu2–1A, all of them surrounded by a crimson red halo; submarginal area dark brown reaching distal margin from costa to vein M2; an orange marginal band from vein M2 to tornus where merging with the postmedian orange band. VFW color pattern similar as on the upperside; median orange band slightly lighter, whitish along basal edge towards costa, subapical area along costa and inside cell R5–M1 suffused with chestnut; subapical black spot in M1–M2 with a white pupil; subapical pale yellow spot in cell R5–M1; apical and submarginal areas suffused with beige scales. VHW ground color rufous brown; median line nearly straight, from costa to vein 1A basally edged with white; a band extending from postmedian to submarginal area shaped as on the upperside, white along basal and distal end, rufous orange in the middle, and a series of six black dots with white pupils situated in the middle of the band from Rs–M1 to Cu2–1A, two in the latter, except in cell M2–M3 where instead a lighter pale yellow patch.

Genitalia (Fig. 8): Uncus twice the length of tegumen, hooked; gnathos two-thirds the length of uncus, curved upwards; saccus deep, slat-like; valvae approximately the same width in basal and distal part with slightly serrate distal extremity and curved inwards; aedeagus slightly longer than valvae, smooth and straight.

Female (Fig. 4): **Head**, **thorax** and **abdomen** similar to the male. **Wings**: FW length 33 mm; DFW and DHW similar to the male; orange band a shade lighter, pale orange. VFW similar to the male; orange band a shade lighter, pale orange; VHW similar to the male but lighter, suffused with white scales along distal edge of the submarginal line.

Type material: Holotype ♂: Guyana, N. slope Mt. Roraima, 2nd Camp, 1300m, 5°16N, 60° 44W, 12.III.–16.IV.2001, Romeo Williams, Wiltshire Hinds *leg.*, SIW. Paratype ♀: same data.

Etymology: This beautiful montane satyrine is gratefully named after Romeo Williams, a Guyanese national. A friend of the junior author, Romeo has been an indispensable team member for the recent lepidoptera expeditions to a number of Guyana's remote montane regions. Beyond these expeditions, Romeo's bush skills, work ethic and dedication have added immeasurably to numerous other biological field endeavors in Guyana's hinterlands.

Remarks: The genus *Oxeoschistus* Butler comprises thirteen species, including one highly polytypic species — *Oxeoschistus simplex* Westwood with five recognized subspecies. The genus *Dioriste* Thieme is considered herein as a subjective junior synonym of *Oxeoschistus* following Lamas *et al.* (in press). Accordingly, seven species of *Oxeoschistus* are found in the Andes and six in Central America. One species, *O. puerta*, is represented by separate subspecies in Costa Rica, Panama, Colombia and northern Venezuela. The genus is therefore particularly well represented in Central America, as compared to other genera of Pronophilina (except for the genus *Drucina* Butler, endemic to Central America), and the fact that there are as many species outside and within the Andes is unique for the subtribe. A few genera are represented in Central America by one or two species, rarely more (*Pedaliodes* Butler, *Pseudomaniola* Röber), and many have no representative at all, including *Corades* Doubleday, *Junea* Hemming, *Daedalma* Hewitson and *Mygona* Thieme among others.

Adult *Oxeoschistus* are recognized by large size for the standards of the subtribe, with an average FW

FIGS. 10–18. *Erestris* taxa related to *E. agata*. **10**. *Eretris encycla* ssp. (Las Golondrinas, N-W Ecuador) **11**. *Eretris encycla* ssp. (Mérida, S-W Venezuela) **12**. *Eretris encycla* ssp. (Tandapi, W Ecuador) **13**. *Eretris encycla encycla* (Colonia Tovar, N Venezuela) **14**. *Eretris agata* **n. sp.** (Sierra de Lema, Venezuela) **15**. *Eretris encycla* ssp. (Santa Lucía, S-W Ecuador) **16**. *Eretris oculata* (Jorge Chavez, N Peru) **17**. *Eretris calisto* (Zamora, S Ecuador) **18**. *Eretris* sp. (San Andres, S Ecuador)

length 3–3.5cm, blunt FW apex and undulate HW margins. Most species have conspicuous orange or yellow upperside markings usually shaped as a median band. VHW is characterized by usually fully developed large postmedian ocelli present in all cells (except M2–M3) in most species. Antennae are slender, approximately 2/5 of the FW length. Eyes are setose as in other Pronophilina (Viloria, Ph.D.). Male genitalia can be recognized by a long uncus, and particularly long subunci, in some species approaching the length of the uncus, elongate valvae without any secondary process and a serrate dorsal surface, deep saccus and long, straight aedeagus. Although, there was no cladistic analysis of the subtribe, these morphological characters indicate *Pseudomaniola* Röber or *Pronophila* Doubleday as possible sister genera (Pyrcz, in prep.).

Affinities

Currently, there are 10 species of Pronophilina known to occur in the Pantepui. Three of them belong to an endemic genus *Protopedaliodes* (presenting several specialized morphological structures), whose affinities within the speciose *Pedaliodes* complex are unclear (Viloria, Ph.D.). Five species belonging to *Pedaliodes*—*P. roraimae*, *P. demarmelsi*, *P. chaconi*, *P. terramaris* and *P. yutajeana*— are closely related allopatric taxa. They could eventually be considered, due to the slight morphological differences, as subspecies of *P. roraimae*. Viloria & Pyrcz (1995) discuss the affinities of *P. roraimae* and indicate that its closest ally is *P. pisonia* (Hewitson). Salient morphological similarities can be observed in the wing shape and colour pattern and more importantly in the shape of the male androconial patch and male genitalic structure (Viloria *et al.*, 2001). *P. pisonia* occurs in the Venezuelan Cordillera de La Costa and the parallel Cordillera del Interior in low elevation cloud forests, at 1200–1700m.

E. agata presents a series of wing color pattern similarities to: *E. oculata* (C. & R. Felder) distributed along the eastern slopes of the Andes between Colombia and northern Peru, *E. calisto* (C. & R. Felder) found in central and eastern Colombia, eastern Ecuador and northern Peru and *E. encycla* (C. & R. Felder) occurring in the Venezuelan Cordillera de La Costa and Mérida, and in western Colombia and Ecuador (figs. 10–18). The VHW ocelli of *E. agata* are intermediate in size as compared to other congeners: smaller than in *E. oculata*, about the same size as in some populations of *E. encycla* (an undescribed subspecies) from the Western Cordillera in Colombia and Ecuador, and larger than in *E. encycla*. The shape

of the VHW postmedian band is most similar to *E. oculata*, less sinuate than *E. calisto* and *E. encycla*, both similar in this respect. *E. agata* has no orange or yellowish scales in the VHW anal area or basad to the postmedian line, similar to *E. encycla* (although some individuals of the nominate subspecies do have some yellow scaling) and *E. oculata*, and contrary to *E. calisto*, which always presents some yellow or orange pattern. The exclusive character of *E. agata* is that all three VHW lines are all brown, whereas in all other compared species they are crimson red. Additionally, the typical incision of the anal margin of the HW is shallower in *E. agata* than in other species, and the HW is ovaloid rather than squarish, in this respect it resembles an undescribed species of the "*calisto*" stock from southern Ecuador and northern Peru (Pyrcz, in prep.). Male genitalia of *E. agata* show some similarities to *E. oculata*, especially characteristic valvae with a shallow curve in the middle and a tubular, simple aedeagus. In *E. encycla* the aedeagus is somewhat inflated in the middle and shorter. However other sclerites, tegumen, uncus, vinculum and transtilla, are nearly identical to *E. encycla* and *E. calisto*. These two species have rather long gnathi, roughly one third to half the length of uncus. The gnathi of *E. agata* are slightly shorter. On the other hand, the gnathi of *E. oculata* are rudimentary short tips, and in this respect are unique compared to other congeners.

Oxeoschistus romeo, as already pointed out in the new species diagnosis, basically presents all typical generic characters of the color pattern. However its DFW median orange band pattern is unique because it is modified as compared to allied species. Instead of a regular band with roughly parallel outer and inner edges, it presents an extremely irregular, erratic shape with several deep intrusions. Diagnostic features can be pointed out in the VHW pattern, especially the fact that the white-edged postmedian band is unbroken, smooth and runs roughly parallel to the outer margin. This character is found in *O. simplex* distributed throughout Colombia, *O. puerta* found in the Venezuelan Cordillera de La Costa, Mérida, Perija and northern Central and Eastern Cordillera in Colombia, and *O. duplex*. The latter is found in central (Junín, Pasco) and southern (Cuzco, Puno) Peru and Bolivia (Yungas). The male genitalia of *O. romeo* provide a series of very useful diagnostic characters. They clearly indicate *O. puerta* and *O. simplex* as the closest allies. In all these species, the gnathi are thinner than the uncus, about two-thirds its length and hooked upwards, the saccus is very long, and the aedeagus is nearly straight. The valvae of *O. simplex* are singularly serrate in the distal–dorsal one-third and occasionally present small processes. The valvae of *O. puerta* and *O. romeo* are shorter and more compact, dorsal teeth are not as prominent and do not have any secondary process (figs. 8–9).

The above considerations indicate, the genus *Protopedaliodes* taken apart, close faunal affinities between the Pronophilina of the Pantepui and the Pronophilina occurring in the Venezuelan Cordillera de La Costa: *P. pisonia*, *E. encycla* and *O. puerta*. It is therefore sound to consider that this range was the primary source of cloud forest Pronophilina for the Pantepui. The colonization of the Pantepui might have taken place through ecological corridors across the Orinoco plains during cold glacial phases in the Pleistocene, when temperatures were 5°–9° cooler than at the present (Bush, 2002, 2004). These ecological conditions might have favored the growth of premontane forest vegetation (including *Chusquea*) at much lower elevation than currently (Cowling *et al.*, 2001); thus allowing the dispersal of pronophilines, especially the species inhabiting lower elevations (below 1500m). This scenario is plausible considering that at the southern limit of the latitudinal range occupied by the subtribe, where climate is cooler with low winter temperatures, several species of Pronophilina live in the lowlands. For example, in southern Brazil and northern Argentina *Praepedaliodes phanias* (Hewitson) occurs commonly at 200m and feeds on local *Aulonemia* sp. bamboo (Pyrcz, unpubl). In south-central Bolivia, near Santa Cruz de la Sierra, a local population of *Physcopedaliodes physcoa* (Hewitson) occurs in a relictual forest at 400m. Interestingly enough, the same species is found in central Peru (Chanchamayo) at higher elevations—1200–1600m (Pyrcz, unpubl.).

Diversity

Eretris agata and *Oxeoschistus romeo* represent the ninth and tenth species and only the third and fourth known genera of the subtribe Pronophilina in the Pantepui. A faunal comparison (*Appendix*) showing data from ten Andean localities gathered along altitudinal transects (only sympatric or parapatric species occurring along the same slope are considered) yields the immediate conclusion that the Pronophilina fauna of the Pantepui is extremely species poor as compared to the Andes.

The most straightforward factors responsible for this disproportion would be the lower ecological diversity and the smaller area of montane habitats in the Pantepui as compared to the Andes. Whereas in the Andes suitable habitats for the Pronophilina are found within the wide elevational belt roughly between 1000–4000m corresponding with cloud forests and paramo, in the Pantepui they are restricted by the

highest elevations of the table mountains, which is generally below 2500m, except for a few higher tepuis slightly exceeding this elevation (La Neblina, Roraima, Kukenán). In the Andes, cloud forests form a nearly continuous belt extending over 2500km along the eastern slopes from Bolivia to Venezuela, and over 1000km along the western slopes from northern Peru to northern Colombia. In the Pantepui, on the other hand, cloud forests are scattered and restricted to the slopes of isolated table mountains (Huber, 1995).

However, there are also significant differences in the observed species richness between various localities within the Andes. The index falls steadily from central towards northern Andes, from more than 100 species in southern Ecuador (Zamora) and northern Peru (Molinopampa) to 70–80 in central Colombia, and 55 in western Venezuela (El Tamá), roughly 50% of the figure in Zamora. These areas do not differ in ecological diversity and suitable habitat area (Vuilleumier & Monasterio, 1986), therefore, other factors are to be involved.

The decrease in species richness is more radical in the peripheral ranges of the northern part of the continent, the Venezuelan Cordilleras de Mérida, Perijá and La Costa, and the Colombian Santa Marta range. Sharp diversity break-downs correspond with several topographical and ecological barriers. A very important one is the so-called Táchira depression, a deep valley separating the Colombian Cordillera Oriental from the Cordillera de Mérida (Vuilleumier & Ewert, 1978; Pyrcz & Viloria, in press). Other barriers include: the Valle del César separating Perijá from the Sierra Nevada de Santa Marta (Adams, 1985) and the Lara plateau separating the Cordillera de Mérida from the Cordillera de la Costa (and the parallel, low Cordillera del Interior). The fauna of the Cordillera de la Costa (awaiting monographic treatment, Pyrcz *et al.*, in prep.) accounts for 24 species of Pronophilina, less than half of that of El Tamá, and merely one fourth of the species-rich southern Ecuador. This yields the conclusion that these barriers act as a 'filter' for the dispersal of pronophilines from the center of diversity in the main Andes (corresponding with the putative center of radiation of the subtribe, situated in the central Andes between Ecuador and Bolivia, Pyrcz, in prep.) into peripheral ranges.

The tepuis are separated from the already impoverished Cordillera de La Costa by vast lowlands, the Orinoco plains (300–400km) and from the Eastern Cordillera by the upper Llanos (>500km). If a simple area/distance from source calculation is carried out according to the classical island geography model (MacArthur & Wilson, 2001), a dramatic decrease in the Pantepui is to be expected.

Low diversity figures for the Pantepui may also be partly a consequence of the severe undersampling of this region. Admittedly, the sampling for pronophiline butterflies in the Pantepui has so far been negligible. The few specimens collected throughout the years are an outcome of random or even casual collecting, either by scientists other than entomologists (usually geologists, botanists or ornithologists who most frequently visited the region), or tourists. The reasons for this poor knowledge of the Pronophilina fauna in the Pantepui are multiple. First of all, Venezuelan authors (DeMarmels *et al.*, 2003) point out that the region is very remote and difficult and costly to reach. It certainly is true in the case of the summits of the most remote tepuis such as La Neblina, Tapirapecó, Duida or Marahuaca. These tepuis can be accessed easily only by helicopter. Otherwise, a long arduous expedition is necessary usually entailing canoeing for several days and many days of jungle trekking. Both ways are very costly, which is a very strong barrier for any biological research. However, the a few tepuis situated in the eastern part of the Guayana highlands, especially Roraima, Kukenan, Auyan and a handful of other smaller table mountains, are relatively easy and inexpensive to reach. As a matter of fact, one of the new species described herein was collected in the area called La Escalera, along the asphalted main road leading from Km. 88 to Santa Elena de Uairén, which is crossed daily by dozens of vehicles!

La Escalera can be considered as the only relatively well sampled area within the entire Pantepui. In the local cloud forest at 1300–1400m only two species of Pronophilina were documented—*Pedaliodes roraimae* and *Eretris agata*, and a third—*Oxeoschistus romeo*—is likely to occur. The question arises: is the reported diversity low in relative terms as compared to the Andes? Not necessarily, considered that we are discussing diversity at 1300–1600m. As already stated, the highest diversity of the subtribe in the Andes falls at elevations between 2500 and 3000m (Adams, 1985; Pyrcz & Wojtusiak, 1999, 2002). Below 1600m diversity is at its lowest. For comparison, in the Andean Western Cordillera in Colombia—Tambito (Pyrcz & Wojtusiak, 1999) and Ecuador—Las Golondrinas (Pyrcz & Wojtusiak, in prep.), where total species richness along sampled elevational gradients (1600–2500/2600m) exceeds 60, only three species were reported below 1600m. Interestingly enough, they are representatives of three genera reported from La Escalera: *Pedaliodes phrasiclea* Grose-Smith, *Eretris depresissima* Pyrcz and *Oxeoschistus simplex* (Butler), which underlines a structural similarity to the Pantepui fauna at a similar

FIGS. 19-23. Type locality of *Eretris agata*, **new species**. **19**. *Chusquea*? sp. bamboo in a forest clearing. **20**. Bamboo node detail. **21**. *Chusquea*? sp. bamboo, likely host plant of *E. agata*. **22**. Young *Miconia* sp. (Melastomataceae). **23**. Swampy forest with bamboo clumps

altitude.

There are sight reports of further species and genera of Pronophilina in the Pantepui by experienced lepidopterists. Mauro Costa (pers. comm.) observed for a while an individual butterfly, which he identified as *Lasiophila* or *Mygona*, as he was able to notice its diagnostic pattern of the HW underside. This observation took place on the above-mentioned road at Km 130 (1400m). Andrés Orellana (pers. comm.) observed for some time a butterfly on the summit of Roraima, brown with some golden sheen, which he believes could have been a *Lymanopoda* Westwood (a species rich Andean genus of the subtribe Pronophilina).

The junior author has participated in two large-scale expeditions to major Guyana tepuis in the Pakaraima Mts: Mt. Wokomong (ca. 1675m) in November 1993 and Mt. Ayanganna (ca. 2050m) in April 1999. During the Mt. Wokomong expedition, approximately one week was spent at an elevation between ca. 1425m–1575m with plenty of bright sunshine. Even though a medium-sized bamboo was very common along the summit ridge (ca. 1575m), no pronophilines were captured or definitively seen. On the Mt. Ayanganna expedition there was the same result, with a little over a week spent at elevations (ca. 1375m–1675m) where at least some pronophilines were expected. Again there was plenty of brilliant sunshine, but on Mt. Ayanganna, bamboo did not seem common on the small part of this huge mountain massif that we explored. It was disappointing that we spent no time collecting on the summit plateau (ca. 2050m). On a previous botanical expedition, botanist Terry Henkel reported seeing dark medium-sized butterflies common on the summit plateau when the sun was shining. Were these pronophilines, and if so, could they differ from species on the not too distant Mt. Roraima?

All this emphasizes an urgent need for well-organized sampling and thorough research of the cloud forest butterfly fauna of this extremely interesting region of South America. There is little interest among local entomologists in promoting and carrying out research, and especially field work, in this part of Venezuela. Unfortunately, when it comes to foreigners, the restrictions imposed by Venezuelan laws (these laws having as their primary goal the protection of the environment and native Amerindian culture) in recent years, have practically created such bureaucratic obstacles that permits are nearly impossible to obtain rendering any investigation very difficult (see Viloria & Pyrcz, 1999 comments on this issue).

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Appendix: Pronophilini species richness in 11 localities along altitudinal transects

Genera	San Lorenzo	Colonia Tovar	Manaure	La Culata	Betania	Choa Chi	Puracé	Runtún	Zamora	Molino-pampa	Roraima
Arhuaco	1	0	0	0	0	0	0	0	0	0	0
Cheimas	0	0	0	1	0	0	0	0	0	0	0
Corades	4	3	4	6	7	7	7	8	10	8	0
Daedalma	0	0	0	0	1	2	2	3	3	3	0
Drucina	0	0	0	0	0	0	0	0	0	0	0
Junea	0	0	0	0	1	2	2	2	2	2	0
Apexacuta	0	0	0	0	0	0	1	1	1	2	0
Lasiophila	1	1	1	1	2	3	3	3	4	4	1?
Mygona	0	1	1	1	1	2	2	2	2	2	0
Oxeoschistus	0	1	1	1	1	2	2	2	2	3	1
Pseudomaniola	1	1	1	1	2	1	1	1	4	4	0
Pronophila	2	2	3	2	3	3	3	4	6	5	0
Thiemeia	0	1	0	0	0	0	0	1	1	1	0
Pedaliodes°	7	8	12	15	19	29	34	32	42	42	1
Paramo	1	0	0	0	0	0	0	0	0	0	0
Dangond	0	0	1	0	0	0	0	0	0	0	0
Redononda	0	0	0	1	0	0	0	0	0	0	0
Protopedaliodes	0	0	0	0	0	0	0	0	0	0	2
Eretris	1	1	3	2	3	6	5	5	5	5	1
Lymanopoda	2	2	6	5	6	10	9	10	10	10	1?
Manerebia	1	1	2	2	4	4	3	4	7	6	0
Steroma	1	1	1	1	1	1	1	1	2	3	0
Steremnia	0	0	0	0	1	2	3	3	5	5	0
Diaphanos	0	0	0	1	0	0	0	0	0	0	0
Idioneurula	0	0	0	0	1	1	0	0	0	0	0
Ianusiussa	0	0	0	0	1	0	1	1	0	0	0
Tamania	0	0	0	0	1	0	0	0	0	0	0
Total species	**22**	**24**	**35**	**37**	**55**	**75**	**79**	**83**	**107**	**105**	**5 (7)**
Total genera	**11**	**12**	**12**	**14**	**17**	**15**	**16**	**17**	**16**	**16**	**4 (6)**

° *Pedaliodes sensu lato*

Localities co-ordinates and faunal data source:

- San Lorenzo: Colombia, Sierra Nevada de Santa Marta, north slopes, 11°08'N 74°03'W (Adams & Bernard, 1977)
- Manaure: Colombia, Serranía de Perijá, west slopes, 10°23N 72°58'W (Adams & Bernard, 1979; Viloria, Msc. thesis, unpubl.)
- La Culata: Venezuela, Cordillera de Mérida, Sierra de la Culata, southeast slopes, 8°41'N 71°08'W (Adams & Bernard, 1981; Pyrcz & Wojtusiak, 2002)
- Colonia Tovar: Venezuela, Cordillera de La Costa, north slopes, 10°26'N 67°15'W (Raymond, 1982; Pyrcz, in prep.)
- Betania: Venezuela, Cordillera Oriental, Sierra del Tamá, north slopes, 7°27'N 72°26'W (Pyrcz & Viloria, in press)
- Choachi: Colombia, Cordillera Oriental, Cundinamarca, east slopes, 4°33'N 73°57'W (Adams, 1986; Pyrcz, 1999)
- Puracé: Colombia, Cordillera Central, Cauca, east slopes, 2°22'N 76°16'W (Adams, 1986; Pyrcz, 1999)
- Runtún: Ecuador, Cordillera Oriental, Tungurahua, north slopes, 1°25'S 78°25'W (Pyrcz et al. 1999; Pyrcz & Viloria, 1999, Pyrcz, 2000, unpubl.)
- Zamora: Ecuador, Cordillera Oriental, Nudo de Sabanillas, east slopes, 3°58'S 79°03'W (Pyrcz et al. 1999; Pyrcz & Viloria, 1999, Pyrcz, 2000, in press)
- Molinopampa: Peru, Cordillera Oriental, Chachapoyas, southeast slopes, 6°10'S 77°34'W (Pyrcz, 2004)

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THE HIGHLY SEASONAL HAWKMOTH FAUNA (LEPIDOPTERA: SPHINGIDAE) OF THE *CAATINGA* OF NORTHEAST BRAZIL: A CASE STUDY IN THE STATE OF RIO GRANDE DO NORTE

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ABSTRACT: The *caatinga*, a thorn-shrub succulent savannah, is located in Northeastern Brazil and characterized by a short and irregular rainy season and a severe dry season. Insects are only abundant during the rainy months, displaying a strong seasonal pattern. Here we present data from a yearlong Sphingidae survey undertaken in the reserve *Estação Ecológica do Seridó*, located in the state of Rio Grande do Norte. Hawkmoths were collected once a month during two subsequent new moon nights, between 18.00h and 05.00h, attracted with a 160-watt mercury vapor light. A total of 593 specimens belonging to 20 species and 14 genera were collected. *Neogene dynaeus*, *Callionima grisescens*, and *Hyles euphorbiarum* were the most abundant species, together comprising up to 82.2% of the total number of specimens collected. These frequent species are residents of the *caatinga* of Rio Grande do Norte. The rare Sphingidae in this study, *Pseudosphinx tetrio*, *Isognathus australis*, and *Cocytius antaeus*, are migratory species for the *caatinga*. Ninety percent of specimens and 75% of species were collected during the rainy season. With the arrival of the dry season, when bushes and trees lose their leaves and the herbaceous layer disappears, Sphingidae abundance decreases rapidly. Richness and abundance of species through the year is highly seasonal and correlated with rainfall. *Erinnyis alope alope*, *Eumorpha fasciatus*, *E. vitis vitis*, and *Manduca brasilensis* were recorded for the first time in NE-Brazil.

Additional keywords: *Callionima grisescens*, dry savannah, *Hyles euphorbiarum*, *Neogene dynaeus*, Northeastern Brazil, Sphingidae.

INTRODUCTION

Sphingidae are widely distributed and comprise approximately 1200 species, which occur predominantly in tropical regions (Lemaire & Minet 1999). Sphingidae are generally among the first Lepidoptera to be surveyed in a region. Despite this, studies related to the taxonomy, geographical distribution, relationship with host plants, and adult food sources are scarce for Sphingidae (Kitching & Cadiou 2000).

In Brazil to date, 180 species of Sphingidae have been recorded in regional surveys (Brown 1986), more than half in the Amazon basin: 61 species in the state of Amazonas (Motta 1998) and 90 in the state of Pará (Moss 1920). Seventeen species were recorded in the state of São Paulo (Coelho et al. 1979), 55 in the state of Paraná (Laroca & Mielke 1975), and 65 in the state of Rio Grande do Sul (Biezanko 1982; Corseuil et al 2001).

In Northeastern Brazil the Sphingidae fauna is still poorly studied. The only published data concern a community of Sphingidae and associated plants from an area of *tabuleiro nordestino* (a kind of *cerrado*, isolated from the Central Brazilian *Cerrado*) on the coast of the state of Paraíba (Darrault & Schlindwein 2002); this study recorded 24 species of Sphingidae for the area. A preliminary list for the caatinga region, based on sporadic visits to the field counts 14 species (Duarte & Motta 2001). Both surveys add up to a total of 32 species for NE - Brazil.

The *caatinga*, a 834,666km^2 thorn-shrub succulent savannah (Andrade-Lima 1981), is the predominant vegetation in Northeastern Brazil (Fig. 1). The region is characterized by seasonal rainfall that defines the phenophases of the vegetation. During the dry season, which lasts approximately eight months (May–December), the vegetation loses its leaves. Sporadically there are years with almost no rain and drought can be severe (Andrade-Lima 1981, Sampaio et al. 1991, Machado et al. 1997). Therefore, the seasonal characteristics of the *caatinga*'s climate and vegetation must influence the seasonality of Sphingidae and the development from an immature stage to adult (Janzen 1983, Haber & Frankie 1989, Darrault & Schlindwein 2002). The annual development cycle of the Sphingidae is not known for the *caatinga* region.

Generally, the relationships between larvae of Sphingidae and their host plants are highly specific. In many cases, the larvae accumulate toxic compounds from the plants that protect the larvae against predators. Such host plants include species of Apocynaceae, Euphorbiaceae, Solanaceae, and Rubiaceae (Biezanko

FIG.1. Map of Brazil indicating Northeastern Brazil, the distribution of the *caatinga* and the location of the study site "Estação Ecológica do Seridó (ESEC - Seridó)", state of Rio Grande do Norte. Source: FREIRE, 2003.

1982, Janzen 1983, Moss 1920). The relationships between adult Sphingidae and sphingophilous flowers, however, does not seem to be specific (Darrault & Schlindwein 2002, Haber & Frankie 1989).

Pittaway (1993) affirms that a species may be submitted to seasonal cycles of abundance and scarcity, or its occurrence throughout the year may be constant for an area. According to this author, species abundance may also decline or increase in response to environmental conditions and to the degree of migration.

Here we present data for the composition, species richness and abundance of Sphingidae through the year in the *caatinga* in the nature reserve *Estação Ecológica do Seridó* in the state of Rio Grande do Norte, NE-Brazil.

MATERIALS AND METHODS

Study area

The study was undertaken in the nature reserve *Estação Ecológica do Seridó* (ESEC-Seridó) in the municipality of Serra Negra do Norte, state of Rio Grande do Norte, NE - Brazil (Fig.1). The reserve covers an area of 1,166.38 ha located between 06°35' and 06°40'S and 37°20' and 37°39'W, at an altitude of approximately 170 m. The climate is hot and dry (mean annual temperature of 28°C), with a rainy season that varies from January/February to April/June (mean annual rainfall of 497 mm). The rest of the year is characterized by a severe drought (IBAMA 1989) (Fig. 2). The temperature and rainfall data were obtained from the climate station in the reserve.

The vegetation is an arbustive to arboreous *caatinga*, with an herbaceous stratum that is only well-developed during the rainy period (Prado 2004).

Sampling

Sphingidae were collected between March 2002 and May 2003 (with the exception of May 2002). The moths were attracted by a 160-watt mercury light source positioned against a white wall. The light dispersed over an extensive area. Specimens were collected during two consecutive new moon nights per month from 18.00h to 05.00h on the following day. The moths were killed with an injection of ethyl acetate between the thorax and abdomen. The specimens were then placed in entomological envelopes and prepared in the laboratory.

The identification of the material collected was based on D´Abrera (1986) and Kitching & Cadiou (2000). Specimens were deposited in the entomological collection of the Federal University of Pernambuco (UFPE, Recife), the entomological collection of the Department of Systematics and Ecology of the Federal University of Paraíba (UFPB, João Pessoa), and in the Museum of Natural History of Seridó (located in the ESEC Seridó reserve).

Three abundance criteria were established using Rabinowitz et al. (1986), based on the number of specimens collected per species: rare (1 to 2 specimens), common (3 to 19 specimens), and abundant (20 to 50 specimens).

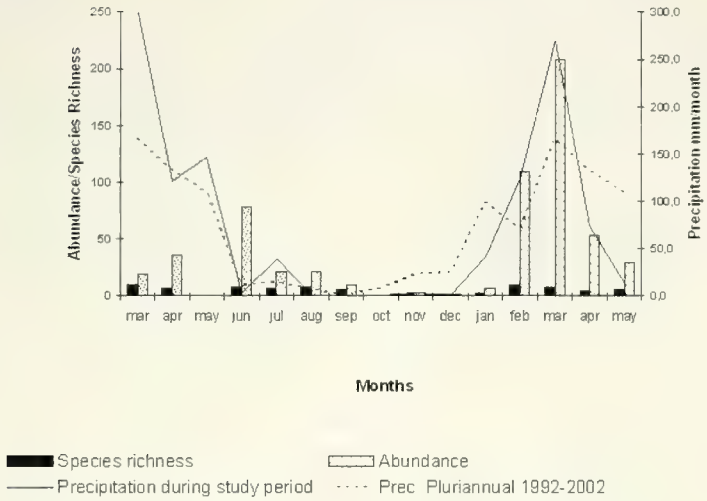

FIG. 2. Annual and pluriannual precipitation and abundance and richness of species of Sphingidae of the Estação Ecológica do Seridó between March 2002 and May 2003 (May 2002 was not sampled).

The following indices were calculated: Shannon-Wiener, Spearman's correlation coefficient and Pearson's correlation coefficient. The indices were calculated using the BioStat version 2.0 (Ayres *et al* 2000) and Krebs version 5.1. (Krebs 1999).

RESULTS

Sphingidae species richness and abundance

In the nature reserve Esec-Seridó, 593 specimens of 20 species were recorded (Table 1). From this total, 90% of specimens and 75% of species were collected during the rainy months (February to June) (Fig.2). From October to December, only three specimens of two species were recorded, *Erinnyis ello ello* and *Xylophanes tersa tersa* (Fig. 2). In October, no hawkmoths appeared at the light traps.

Neogene dynaeus (38%), *Callionima grisescens elegans* (28%), and *Erinnyis ello ello* (8.8%) were the predominant species, accounting for over two-thirds of all Sphingidae collected (Fig. 3). The six most abundant species comprised 91.7% of the total of specimens, while the six least abundant summed to only 1.7% Fig.3).

Neogene dynaeus occurred during the rainy season, from February to June, and *Callionima grisescens elegans* from February to September (Fig.4). The rare species *Cocytius antaeus*, *Isognathus australis*, and *Pseudosphinx tetrio*, were recorded only in the dry months (Table 1).

Spearman's correlation index was 0.6196 for species abundance versus rainfall and 0.5913 for species richness versus rainfall, showing significant correlations. In contrast, correlations for both rainfall and species richness versus temperature, calculated using Pearson's coefficient, were negative. The accumulated species curve was representative, showing no increase during the last months (Fig.5).

DISCUSSION

Species richness, abundance and seasonality

Our results show that species abundance and richness of Sphingidae are highly seasonal in the *caatinga* region. This seasonality is influenced by the distinct

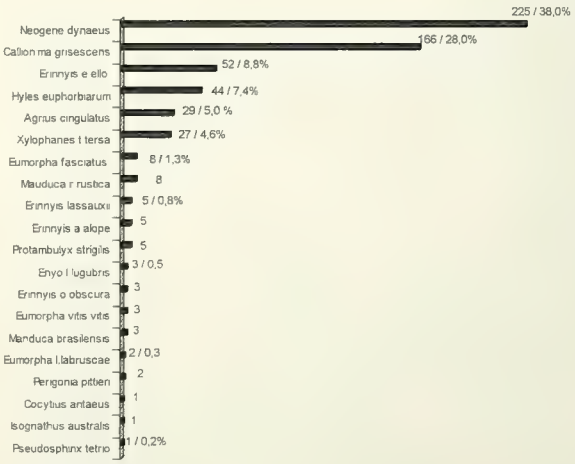

FIG.3. Number of specimens and relative abundance of species of Sphingidae recorded between March 2002 and May 2003 at the Estação Ecológica do Seridó.

TABLE 1. Species of Sphingidae recorded in the Estação Ecológica do Seridó, municipality of Serra Negra do Norte, state of Rio Grande do Norte, Northeast Brazil, between March 2002 and May 2003.

Species	Month	Rare*	Common*	Abundant*
Macroglossinae				
Macroglossini				
Hyles euphorbiarum (Guérin & Percheron, 1835)	Feb - Mar, Aug			X
Xylophanes tersa tersa (Linnaeus, 1771)	Apr, Jun-Sep, Dec			X
Dilophonotini				
Callionima grisescens elegans (Rothschild, 1894)	Feb-Sep			X
Erinnyis lassauxii (Boisduval, 1859)	Mar		X	
Erinnyis obscura obscura (Fabricius, 1775)	Jan, Apr-May		X	
Erinnyis alope alope (Drury,1773)	Feb, May, Jul-Aug		X	
Erinnyis ello ello (Linnaeus, 1758)	Jan-Mar, May-Aug, Dec			X
Enyo lugubris lugubris (Linnaeus, 1771)	Mar-Apr		X	
Isognathus australis Clark, 1917	Sep	X		
Perigonia pittieri Lichy, 1962	Feb	X		
Pseudosphinx tetrio (Linnaeus, 1771)	Sep	X		
Philampelini				
Eumorpha fasciatus (Sulzer,1776)	Feb, Apr		X	
Eumorpha labruscae labruscae (Linnaeus, 1758)	Mar, Aug	X		
Eumorpha vitis vitis (Linnaeus, 1758)	Feb-Mar		X	
Smerinthinae				
Ambulycini				
Protambulyx strigilis (Linnaeus, 1771)	Jun-Jul		X	
Sphinginae				
Acherontiini				
Agrius cingulatus (Fabricius, 1775)	Feb-Ago			X
Sphingini				
Cocytius antaeus (Drury,1773)	Aug	X		
Manduca brasilensis Jordan, 1911	Feb-Mar, Jun		X	
Manduca rustica rustica (Fabricius,1775)	Mar-Apr, Sep		X	
Neogene dynaeus (Hübner,[1827]-[1831])	Feb-Jun			X

*The abundance categories follow Rabinowitz *et al* (1986).

phenophases of the vegetation as well as by the rainy period. Most Sphingidae occurred only during two months (March and April) of the rainy season; 65% of species occurred in these months. Other insect groups are probably also influenced by biotic and abiotic factors in the *caatinga* to the same degree. In the rainy season, leaves of host plants are available to larvae.

The species *Erinnyis ello ello* showed an even distribution of abundance throughout the year. This was probably related to the existence of leaves of the host plants of native and cultivated species of Euphorbiaceae like *Manihot* for the larvae and sphingophilous flowers for the adults. No species occurred continuously throughout the entire year.

The high seasonality of the Sphingidae was expected as, during the leafless dry season, the *caatinga* offers no food for the larvae and no nectar sources for the adults. Almost all perennial plants that flower during the dry season in the *caatinga* are melithophilous, ornithophilous or chiropterophilous (Machado & Lopes 2004).

other states of NE-Brazil. The species may show sporadic occurrence in the contact zone of *caatinga* with neighboring ecosystems. *Hyles euphorbiarum* and *Erinnyis ello ello*, like most of the other species recorded, are widely distributed in the Neotropical region (D'Abrera 1986, Biezanko 1982, Hodges 1971, Kitching & Cadiou 2000).

Nevertheless, rare species like *Pseudosphinx tetrio*, *Isognathus australis*, and *Cocytius antaeus* were found exclusively during the dry period, when there were no host plants for the larvae in the leafless environment. Therefore, we suppose that these Sphingidae migrated from adjacent regions, such as the non-seasonal Atlantic rain forest with its evergreen vegetation. These hawkmoths probably do not reproduce in the *caatinga*. *P. tetrio* and *C. antaeus* are widely distributed. *Isognathus. australis* was considered endemic to NE-Brazil (Schreiber 1978). Our survey shows the occurrence of four species not previously recorded for NE-Brazil (*Erinnyis alope alope*, *Eumorpha fasciatus*, *E. vitis vitis*, and *Manduca brasilensis*), increasing to 36

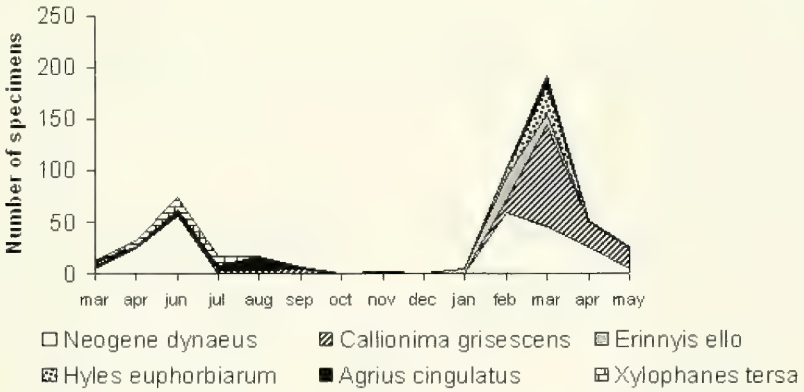

FIG.4. Seasonality of the six most frequent species of Sphingidae at the Estação Ecológica do Seridó between March 2002 and May 2003.

Caatinga- resident and migratory Sphingidae

The abundant Sphingidae in the *caatinga* occur exclusively during the rainy season. Therefore, *Neogene dynaeus* (Fig.7a), *Callionima grisescens elegans* (Fig.7b), *Hyles euphorbiarum*, and *Erinnyis ello ello* are *caatinga*-resident species closing the whole ontogenetic cycle during the short period of rainfall. The host plants for their larvae, as well as sphingophilous flowers for the adults, thus should be plants of the *caatinga* vegetation.

Schreiber (1978) considered *Neogene dynaeus* and *Callionima grisescens elegans* to be endemic to the state of Pernambuco, one of the neighbor states of Rio Grande do Norte. Yet the author did not specify with which vegetation types these species are associated. Based on our data, they are endemic to the *caatinga* region, and they probably also occur in *caatinga* of the

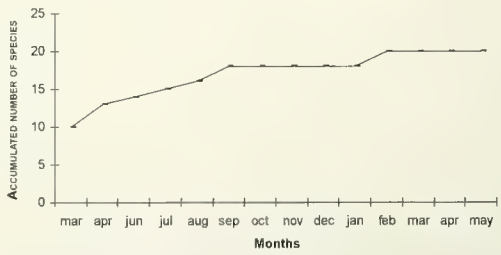

FIG.5. Accumulated number of species of Sphingidae recorded between March 2002 and May 2003 at the Estação Ecológica do Seridó.

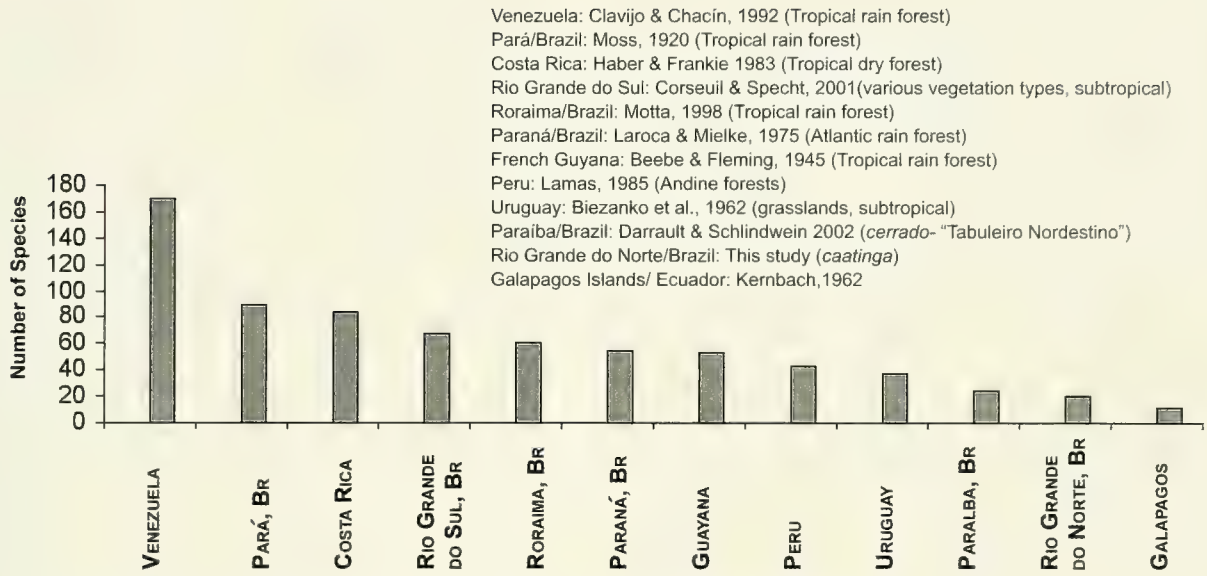

FIG. 6. Number of species of Sphingidae recorded in surveys undertaken in the Neotropical region.

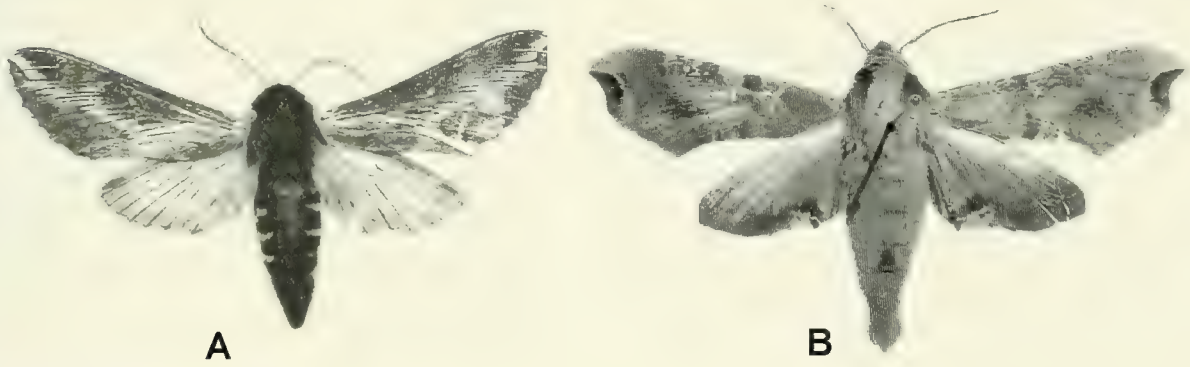

FIG. 7. The most common hawkmoths of the *caatinga*. a) *Neogene dynaeus* b) *Callionima grisescens elegans*

the number of Sphingidae in this region. When compared to Northern, Southern, and Southeastern Brazil and to other countries of the Neotropical region, the species richness recorded here was low (Fig.6). The abundance, on the other hand, was high. The accumulated species curve shows that the number of species in this locality is representative and probably may not or only slightly be increased in a prolonged survey.

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BEHAVIORAL OBSERVATIONS ON THE EARLY STAGES OF *JAMIDES CELENO* (CRAMER) (LYCAENIDAE) AT CAT TIEN NATIONAL PARK, VIETNAM: AN OBLIGATE MYRMECOPHILE?

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ABSTRACT. The life history of *Jamides celeno* has been well documented across its range. The larvae feed on plants from six families and are attended by ants from seven genera. This paper documents a new host plant record and additional attendant ant species from observations made in Cat Tien National Park, Vietnam. We discuss ecological and behavioral traits of the early stages of *J. celeno* and their associated ants, and suggest that the categorization of *J. celeno* as a facultative myrmecophile may be incorrect.

Additional key words: Ant feeding, *Camponotus*, facultative, Formicidae, mutualism, Polyommatinae.

The lycaenid butterfly, *Jamides celeno* (Cramer) is a sexually dimorphic species in the subfamily Polyommatinae. It is widespread in south and east Asia distributed from Sri Lanka, India and Nepal to Taiwan and south China, and throughout the Malaysian Archipelago to New Guinea and the Solomon Islands (Corbet *et al.* 1992). In Vietnam, *J. celeno* is one of the most common species of butterflies, occurring in many habitats ranging from primary evergreen forest and forest gaps to cultivated areas (Monastyrskii & Devyatkin 2002). Larvae of *J. celeno* feed on a variety of plants in the families Fabaceae, Caesalpinaceae, Sterculiaceae, Meliaceae, Zingiberaceae and Marantaceae (Robinson *et al.* 2001), and the early stages have been recorded in association with ant species across seven genera (Corbet *et al.* 1992, Ballmer 2003, Cleary & Grill 2004). Larval association with ants, termed myrmecophily, is a well-known phenomenon in the Lycaenidae (Newcomer 1912, Hinton 1951, Pierce *et al.* 2002). Symbiotic interactions fall into two broad categories: obligate, where the survival of the butterfly species is dependent on the presence of ants; or facultative, where butterfly larvae may or may not have ants in attendance (Fiedler 1991a, Eastwood & Fraser 1999). As a rule, obligate myrmecophiles associate with a single species or a group of closely related species of ants, whereas facultative myrmecophiles typically associate with a variety of ant species, often from different genera or subfamilies (Pierce *et al.* 2002). Accordingly, recent workers have categorized *J. celeno* as a facultative myrmecophile (Fiedler 1996, Ballmer 2003). During a survey of arthropod biodiversity in Nam Cat Tien Park, Vietnam, we observed *J. celeno* adults and early stages on a regular basis. The Nam Cat Tien section of Cat Tien National Park is located in Dong Nai Province 150 km north of Ho Chi Minh City in the monsoonal tropical region of southern Vietnam. It contains the largest remaining lowland tropical forest in southern Vietnam. A semi-evergreen regeneration forest dominated by *Lagerstroemia* spp. (Lithraceae), it has an average annual rainfall of ~2300 mm and average temperatures ranging from 15 °C to 35 °C. The local Chau Ma and S'Tieng people have practiced shifting cultivation in and around the park for generations. Our visit in July 2002 coincided with the wet season, which lasts from April/May to October/November. This paper documents new ecological and behavioral traits of *J. celeno* early stages and their associated ants, and discusses the category of myrmecophily to which *J. celeno* is usually assigned.

OBSERVATIONS

Adult *J. celeno* were often encountered in open areas adjoining tracks and roads through Cat Tien National Park, but many adults were also observed within the forest where their presence usually indicated the proximity of a breeding site. Understory plants were typically less than 3 m in height and larvae were encountered on leaf flushes about 1.8 m above ground (1.82 m ± 0.63 SD, n=11). Larvae formed loose aggregations (2.36 ± 0.92 SD individuals, n=11) and fed exclusively on the soft new growth flush of *Euodia meliaefolia* Benth. (Rutaceae) growing in the understory. Eggs were laid on the new leaves when there was sufficient foliage to sustain a small cohort of larvae. Leaf flush varied from pale green to pale yellow in color before changing to a darker green as the leaves hardened. Larvae were either green or yellow, but

always matched the color of the leaves on which they were resting. Mature larvae became brown before leaving the tree to pupate. Larvae rested under the foliage during the day and began feeding late in the afternoon (ca. 1600 h). Their feeding patterns followed the flush of new growth as it progressed but larvae did not appear to be food-limited. Nevertheless, the butterfly had a window of only about 2-3 weeks on each tree in which the life cycles of multiple broods could be completed before the leaves hardened. Larval duration was approximately six days from egg hatching to pre-pupa, and pupal duration for three individuals was seven (n=2) and eight days.

Of the eleven larval aggregations observed, five ant species in two subfamilies were in attendance: *Camponotus* (*Tanaemyrmex*) sp. (n=3); *Camponotus* (*Myrmosaulos*) *singularis* (F. Smith) (n=2); *Polyrhachis* (*Myrmhopla*) *rufipes* F. Smith (n=1); *Anoplolepis gracilipes* (F. Smith) (n=2) (all Formicinae); and *Crematogaster* sp. (n=2) (Myrmicinae). Ant and butterfly voucher specimens are lodged at the Museum of Comparative Zoology, Harvard University (RE-02-A057, 58, 61, 73, 87, 88, 90, 91, 94, 105, 106, 107, 108, 160). Two larvae were found untended on different plants but the following day one (presumably the same larva) was tended by six *C. singularis* and the other mature larva could not be found on the plant or in the leaf litter. Six to ten ants typically tended larval aggregations, thus providing a significant deterrent to potential enemies of the larva. On one occasion a single *Crematogaster* was found tending a larva together with several *Camponotus singularis*. When the *Crematogaster* came into contact with one of the *Camponotus*, however, it leapt off the leaf. On another occasion several *Crematogaster* were observed tending three *J. celeno* larvae but later the same day the larvae were tended by *Camponotus singularis*. Ants were observed antennating the entire dorsal surface of the larvae and at times the ant's tongue could be seen extending to touch the larval cuticle as well as the dorsal nectary organ (see Bell 1918 for a very detailed description of the morphology of *J. celeno* early stages).

J. celeno larvae pupated at the base of the host-plant or in the leaf litter surrounding the base of the tree. Larvae tended by *Camponotus* (*Tanaemyrmex*) sp. pupated in a protective chamber or byre constructed by the ants from soil and leaf debris at the base of the tree where ants remained in attendance. Other ant species, including *C. singularis*, which did not construct a byre, were not found tending pupae. *A. gracilipes* were found in proximity to, but not tending, three prepupal larvae in the leaf litter.

Individuals of both species of *Camponotus*, but especially *C. singularis*, were observed chewing on leaf edges where *J. celeno* larvae had been feeding. *C. singularis* remained on the leaves and continued chewing the leaf edges, after the lycaenid larvae had left to pupate, eventually leaving a rough sawtooth pattern along the leaf margin. Evidence of ant chewing was also seen on the edges of leaves adjoining those where lycaenid larvae had been feeding. A few small stingless bees were attracted to the lycaenid feeding sites.

DISCUSSION

The presence of ants at leaf margins in proximity to feeding lepidopteran larvae has been recorded previously (Ford 1945, Owen 1971, Fiedler 1991a); the ants apparently taking phloem exuding from leaves damaged by butterfly larval feeding. It is known that adult leafcutter ants in South America derive most of their nutrition from leaf phloem as they cut or chew the leaves before feeding the pulp to their fungal symbionts (Hölldobler & Wilson 1990). We could find no other records of ant chewing on leaves damaged by herbivores or around the leaf edges, and it is not known if ants behave in this manner in the absence of butterfly larvae.

The construction of a byre or gallery to house phytophagous lycaenid larvae, or to 'farm' honeydew-producing insects generally, is a well-known phenomenon among nectar-gathering ants (Hölldobler & Wilson 1990; Anderson & McShea 2001). Several lycaenid species in the Australian genus *Ogyris*, namely *O. genoveva* (Hewitson), *O. zosine* (Hewitson), *O. idmo* (Hewitson), and *O. otanes* (C. Felder & R. Felder), have an obligate relationship with *Camponotus* ants (Eastwood & Fraser 1999). In these associations, butterfly larvae feed nocturnally on mistletoe high up in the trees but hide during the day in galleries constructed by the ants at the base of the trees (Eastwood 1997). Accordingly, it was surprising to find that *Camponotus* ants in Vietnam constructed a similar structure for *J. celeno*, suggesting that the behavior is a plesiomorphic trait in *Camponotus* that evolved before the evolution of mutualistic associations with *Ogyris* or *Jamides*. A similar behavior has been recorded with Mexican *C.* (*abdominalis*) *atriceps* F. Smith, tending the riodinid *Anatole rossi* Clench (Ross 1966), and South American *Camponotus* tending Polyommatine lycaenids (Benyamini 1995). It seems that the butterfly larvae on all three continents are independently exploiting a trait in *Camponotus* ants, which are pre-adapted to construct byres around free-living insect mutualists. It is also interesting that *J. celeno* larvae behaved differently in choosing pupation sites when attended by different ant species. The *Camponotus* (*Tanaemyrmex*) sp. may have shepherded penultimate lycaenid instars into the byre.

However, relationships between lycaenid larvae and ants are known to differ depending on the attendant ant species (Axén 2000; Fraser *et al.* 2001).

As is the case with other *Jamides* species (Fiedler 1996), *J. celeno* did not display preference for a particular ant species, but the regularity with which we found larvae and ants together suggests that ant attendance is important for the survival of this species in the study area. Furthermore, in Thailand, Ballmer (2003) recorded 48 *J. celeno* larvae feeding within *Pueraria phaseoloides* (Roxb.) Benth. (Fabaceae) flowers and all were tended by ants, although the ants were from six genera. Cleary and Grill (2004) recorded 1079 *J. celeno* larvae in Borneo predominantly attended by *A. gracilipes*, and found there were significantly more caterpillars on plants with ants present than on plants without ants. This present study recorded five ant species from four genera, and additional attendant-ant species are noted in the literature. Although many attendant-ant species are recorded, the regularity of attendant-ant records and the high proportion of attendance levels suggest that tending ants may play a significant role in the survival of *J. celeno* overall. *J. celeno* larvae have also been found without ants (Parsons 1999, Cleary & Grill 2004); however, many other obligate lycaenid species have likewise been found untended (e.g. Eastwood & Fraser 1999). Furthermore, a recent survey of the obligate myrmecophile *Jalmenus evagoras* (Donovan), which was thought to associate preferentially with a single species of ant, showed this butterfly associated with seven species (from the same genus) across its range (RE unpublished data). Accordingly, it is plausible that for some obligate myrmecophiles, attendant-ant species specificity may be less important.

The categorization of lycaenid-ant relationships was based historically on ant attendance in non-tropical Lepidoptera (e.g. Malicky 1969, 1970; Henning 1983; Fiedler 1991a,b). Lycaenids are regarded as facultative if they associate with a variety of ant species, and obligate if they consistently associate with only one or a few closely related ant species. Ants that attend obligate myrmecophiles are typically aggressive, are spatially or temporally dominant and form long-lived colonies (Atsatt 1981; Pierce 1987; Fiedler 1991a, 2001; Eastwood & Fraser 1999). Thus, they are a predictable resource that provides optimal protection for lycaenid larvae. In the rainforest, however, an extremely diverse and heterogeneous ant fauna could necessitate association with many ant species if lycaenid larvae were to survive attacks from predators and parasites. In particular, the protection conferred by mutualistic ants could be an important and effective defence against predacious ants, which are ubiquitous and known to attack lepidopterous larvae in south east Asian lowland rainforests (Floren *et al.* 2002). While lycaenid survival rates may be variable, depending on the species of tending ant (Eastwood 1997; Fraser *et al.* 2001), ant association should significantly improve the survival rate overall. In particular, it seems likely that pupae tended by *Camponotus* (*Tanaemyrmex*) sp., would have a higher survival rate since the ants protect them in an underground chamber. So, although the relationship that *J. celeno* has with ants is less specific than generally observed for obligate myrmecophiles, lack of specificity in tending ants may be a function of the heterogeneity of the ant community and not necessarily because *J. celeno* has a facultative relationship with ants. In fact, we suggest that the dependence that *J. celeno* has on attendant ants falls somewhere in the upper bounds of the continuum between facultative and obligate. Thus, the categorization of lycaenid-ant relationships, in this instance, into obligate or facultative myrmecophiles based on the number of ant partner species may be overly simplistic or misleading (e.g. Fiedler 1991a, 1996, 2001, Eastwood & Fraser 1999, Ballmer 2003).

J. celeno was recorded feeding on a single host plant at Cat Tien Park, but the record is most likely a temporal phenological preference or local host plant preference since many host plants have been recorded for this butterfly, and local preferences, especially on new growth, are recorded elsewhere (Cleary & Grill 2004). Multiple host plant use, often across several families of plants, is a characteristic of lycaenids having obligate relationships with ants (Pierce & Elgar 1985). The larvae of *J. celeno* are also difficult to detect because of their ability to adopt the color of their substrate and their tendency to hide under foliage during the day; so, in addition to the protection afforded by ants, *J. celeno* employs multiple strategies for survival. These observations highlight how much we still do not know about the intimacy of lycaenid-ant relationships and how much we can still learn about their joint survival strategies and the evolutionary forces shaping their relationships.

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POPULATION BIOLOGY OF TWO SPECIES OF *HELICONIUS* (NYMPHALIDAE: HELICONIINAE) IN A SEMI-DECIDUOUS FOREST IN SOUTHEASTERN BRAZIL

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ABSTRACT. Populations of two species of butterflies, *Heliconius erato* and *Heliconius ethilla*, were studied during 17 months in SE Brazil. For *H. erato*, the number of individuals present per day varied from one to 10. Time of residence was 24.9 ±18.97 days, with the maximum 59 days. Males were recorded traveling distances up to 200 m. A study of wing color patterns of *H. erato* showed results similar to those of previous studies, including the variation in the number of red raylets. For *H. ethilla*, the number of individuals present per day varied from one to 15. Time of residence was 32.6 ± 23.93 days, with the maximum registered of 106 days. Males can travel distances up to 650 m. For both species, the population peaks occurred in March and May of both years. The sex ratio of individuals captured was male biased for most of the months. Age structure was not stable, though intermediate-age individuals dominated in every month. The difference between male and female mean forewing lengths was not significant. These population features agree with patterns previously observed in southern Brazil populations, though with much lower population numbers.

Additional key words: mark-recapture, Heliconiini, red raylets

Although butterflies in the genus *Heliconius* are among the most studied tropical species, with many publications covering diverse aspects of their biology, such as systematics, ecology, genetics and evolution (Turner 1971, Ehrlich & Gilbert 1973, Cook *et al.* 1976, Araujo 1980, Mallet & Jackson 1980, Brown 1981, Ehrlich 1984, Mallet *et al.* 1987, Quintero 1988, Mallet & Gilbert 1995, Ramos & Freitas 1999, Jiggins *et al.* 2001, Gilbert 2003), data from population biology of most species are still unavailable or incomplete (Ramos & Freitas 1999). The work by Ehrlich & Gilbert (1973) brought important information on the biology of *Heliconius ethilla* and is, so far, the only published population report of this species. In contrast, *Heliconius erato* has been studied in many different places in the Neotropics (Turner 1971, Benson, 1972, Araujo 1980, Saalfeld & Araujo 1981, Romanowsky *et al.* 1985, Ramos & Freitas 1999), including studies of genetics and variation on wing color patterns (Saalfeld & Araujo 1981, Pansera & Araujo 1983, Sheppard *et al.* 1985, Oliveira & Araujo 1992, Ramos & Freitas 1999). Most of the published population studies cover only three different regions in the Neotropics (Trinidad, Rio Grande do Sul and coastal São Paulo state) and none in most seasonal semi-deciduous forests or cerrados. In a recent paper, Ramos & Freitas (1999) suggested that *H. erato* is an ecologically plastic species, in use of resources (larval and adults), behavior and population parameters. In this context, the descriptions of different populations of *H. erato* are important to support a broader view about the natural history of this species.

The objective of the present study is to describe and compare population parameters of *H. erato phyllis* (Fabricius) and *H. ethilla narcaea* (Godart) in a small forest fragment of semi-deciduous forest in Southeastern Brazil, reporting also the cyclical annual variation in four color pattern elements in *H. erato*.

STUDY SITES AND METHIDS

The study was carried out in the 250-ha semi-deciduous forest Reserva da Mata da Santa Genebra (22° 49'S, 47° 07'W), a municipal forest reserve in Campinas, São Paulo State, SE Brazil. The annual rainfall is near 1400mm and the average annual temperature is 20.6° C (data from the Campinas Agronomical Institute). The climate of the region is characterized by a dry, cold season (May to August) and a wet, warm season (September to April) (more details and a climatic diagram can be found in Vanini *et al.* 2000). Detailed descriptions and maps of the study area are available in Morellato & Leitão-Filho (1995).

Butterflies were marked, released and recaptured (MRR) along a trail (1150m long divided into 50m sectors) during 17 months, from December 24, 2001 to May 29, 2003 (1–3 times a week), for a total of 91 days (about 3 hours/day). Butterflies were net-captured, individually numbered on the underside of both forewings with a black permanent felt-tipped pen, and released. Individual characteristics of each individual

(age, forewing length, point of capture, sex, food sources and color patterns) were recorded for later analysis (as in Ramos & Freitas 1999). Wing wear, based on six categories (freshly emerged, new, intermediate, old, very old, tattered) was used as an additional measure of age of individual butterflies (following Ehrlich & Davidson 1960, Brussard & Ehrlich 1970, Ehrlich & Gilbert 1973). These six categories were grouped into three (new, intermediate and old) for analysis (as in Freitas 1993, 1996). Age structure was calculated for males only, through the monthly means of daily proportions of each category. Individual vagility was measured as the maximum linear distance from capture to recapture points.

For *Heliconius erato*, four color-pattern variations were recorded: number and shape of the red raylets on the ventral hindwing; presence and color of the cubital spot on the dorsal forewing (more details and pictures in Ramos & Freitas 1999); number of "light yellow squares" on the apical ventral hindwing; and the color of the prolegs (entirely yellow or with tarsal portion red).

The MRR data were analyzed by the Jolly-Seber method for estimating population parameters (software developed by R. B. Francini, UNISANTOS) for obtaining the "estimated numbers". Only males were considered for this analysis due to the low number of females captured. Daily results were recorded as "number of individuals captured per day" (NICD), including recaptures, and "number of individuals present per day" (NIPD). To estimate NIPD, recaptured individuals were considered to be present on all days between the first and last capture.

For *H. erato*, population parameters and residence time were calculated from January to May 2002 and the color patterns data analyzed from December 2001 to December 2002, due to low numbers of captured individuals on other periods. For *H. ethilla* analysis were made form December 2001 to May 2003. The sex ratio was calculated through the monthly means of daily proportions in NIPD.

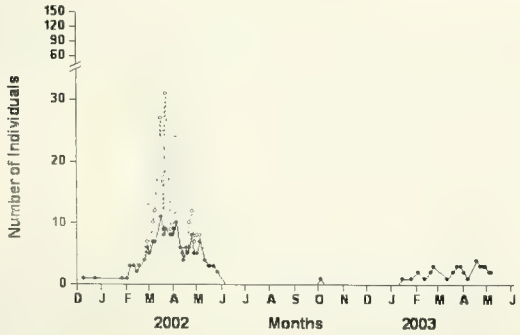

FIG. 1 - Number of males *H. erato* from December 2001 to May 2003 in Santa Genebra, Campinas, SP. Solid circles = NIPD, open circles = estimated number based on Jolly-Seber (bars = 1 standard error).

RESULTS

Heliconius erato phyllis

Population biology. From December 2001 to May 2003, the NICD for males varied from one to five (mean = 1.6; SD = 0.91; n = 52 days). The calculated NIPD varied from zero to 12 (mean = 3.4; SD = 2.03; n = 52 days). Estimated numbers based on Jolly-Seber (Fig. 1) suggests that population numbers are not very much higher than numbers obtained by the NIPD. The population peaks occurred in March and May of both years, although in 2003 the increase in butterfly numbers was about half of that in the same period of 2002. In other months of both years the butterfly numbers remained low and stable (Fig. 1).

Sex ratio. During this study, 47 males and 12 females were captured, giving a male biased sex ratio (χ^2 = 19.59; $p < 0.001$; DF = 1). Males dominated in every month considered (Fig. 2). Males were recaptured from one to six times and females from one to four times; 23 males and three females were recaptured at least once.

Age structure. Even though the proportion of "intermediate" individuals remained greater in every month except for May 2002, the proportions of "new" and "old" individuals were unstable during the months considered. Figure 3 shows the proportion of the three age classes from January to May 2002.

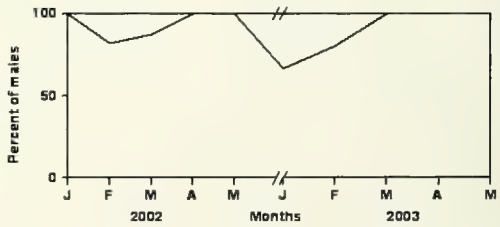

FIG. 2. Sex ratio of *H. erato* from January 2002 to May 2003 in Santa Genebra, Campinas, SP.

Residence time. The residence time varied from three to 59 days (mean = 24.9 days; SD = 18.97). Life expectancy (following Cook *et al.* 1967) was 11.21 days.

Vagility. Only males were analyzed due to the low number of females. The greatest distance recorded along the trail flown by an individual was 200 meters (mean = 65.2 m; SD = 61.12 m; n = 23). Most of the individuals were recaptured at least once in a different

TABLE 1 - Frequency distributions and sample size (N), of the three color patterns recorded in *H. erato* butterflies of both sexes captured in the Santa Genebra from December 2001 to December 2002 (2003 not included due to the low number of captures). For number of red raylets and number of light yellow squares, data are presented as mean ± standard deviation.

Month/year	proleg color		red raylets	Light yellow squares	N
	yellow	red tip			
Dec/01–Jan/02	2	2	5 ± 0	4.25 ± 0.5	4
Feb/02	6	1	4.14 ± 1.07	3.5 ± 0.55	7
Mar/02	8	2	4.3 ± 1.16	3.4 ± 1.35	10
Apr/02	9	3	3.58 ± 1.16	3.17 ± 1.59	12
May/02	6	1	3.71 ± 1.5	3.29 ± 0.49	7
Oct/02–Dec/02	2	0	3.5 ± 2.12	4 ± 1.41	2

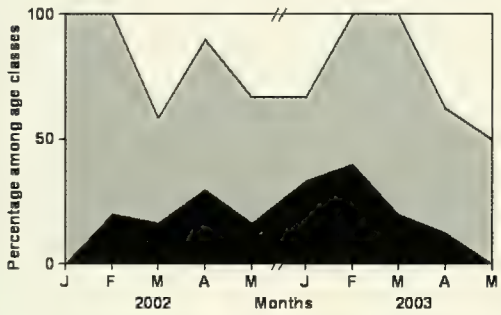

FIG. 3 - Age structure of males *H. erato* from January 2002 to May 2003 in Santa Genebra, Campinas, SP. Black = new individuals, gray = intermediate, white = old.

site from that of first capture (18 out of 23 recaptured individuals).

Wing size. The forewing length of males varied from 30 mm to 39 mm (mean = 35.2 mm; SD = 2.69 mm; n = 47) and of females from 32 mm to 40 mm (mean = 36.1 mm; SD = 2.57 mm; n = 12). This difference was not significant (t = 1,03; DF = 17,7; p = 0,314).

Resource utilization. For 39 visits recorded, 69% were on *Lantana camara L.* (Verbenaceae), 18% on *Chromolaena odorata* (*L.*) R. King & H. Robinson (Asteraceae) and 13% on flowers of other genera, including *Lippia* sp. (Verbenaceae) and *Manettia* sp. (Rubiaceae). In both years, *L. camara* flowers decreased after May, and the visits to other nectar sources increased.

Color patterns. The number of red raylets varied from 1 to 6 in both sexes (mean = 3.88; SD = 1.20; n = 58). Monthly analysis for this trait was done only for 2002, and some months were grouped due to the small number of marked individuals. The average number decreases in colder months (Table 1). The total number of individuals with dot shaped red raylets (41) was greater than the number of individuals with line shaped red raylets (17) (χ^2 = 9.12; p < 0.005; DF = 1) and fits in 3:1 distribution (χ^2 =0.09; p = 0.75; DF=1).

Four categories of cubital spot on the dorsal forewing were recorded with uneven distribution. The predominant category was "yellow" (22 individuals), followed by "absent" (15), "red" (5) and "fusing with the subapical red bar" (5).

The number of "light yellow squares" varied from 0 to 5 in males (mean = 3.0; SD = 1.33; n = 45) and 4 or 5 in females (mean = 4.2; SD = 0.38; n = 12). Monthly analysis for this trait was done only from December 2001 to December 2002, and some months were grouped due to the small number of marked individuals. The average number decreases in colder months (Table 1).

Two color patterns of the prothoracic legs were recorded. The number of individuals with "yellow" legs (33) was greater than the number of individuals with "yellow with red tips" (9) (χ^2 = 13.09; p < 0.001; DF = 1) and also fits in a 3:1 distribution (χ^2 = 0; p=0.99; DF = 1). Monthly analysis for this trait was done only for 2002, and some months were grouped due to the small number of marked individuals (Table 1).

Heliconius ethilla narcaea

Population biology. The NICD for males varied from one to six (mean = 2.0; SD = 1.18; n = 90 days). The NIPD varied from one to 15 (mean = 6.4; SD = 4.43; n = 90 days). As in *H. erato*, estimated numbers based on Jolly-Seber (Fig. 1) are not very much higher than actual numbers obtained by the NIPD. The population peaks (based on NIPD) occurred in March and May of both years, and in the remaining months the population numbers remained low and stable (Fig. 4).

Sex ratio. During this study, 123 males and 35 females were captured giving a male biased sex ratio (χ^2 = 47.9; p < 0.001; DF = 1). Males dominated in every month considered, except for December 2002 (Fig. 5).

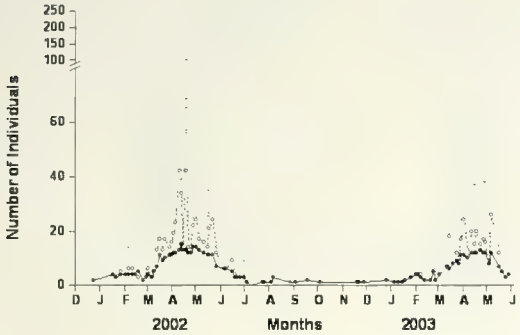

FIG. 4. Number of males *H. ethilla* from December 2001 to June 2003 in Santa Genebra, Campinas, SP. Solid circles = NIPD, open circles = estimated number based on Jolly Seber (bars = 1 standard error).

Males were recaptured from one to 13 times and females from one to three times; 53 males and 11 females were recaptured at least once.

Age structure. The proportion of "intermediate" individuals was greatest in most of the months considered. The proportions of "new" and "old" individuals varied during the months considered. Figure 6 shows the proportion of the three age classes from January 2002 to May 2003.

Residence time. The time of residence varied from two to 106 days (mean = 32.6 days; SD = 23.93). Life expectancy (following Cook *et al.* 1967) was 44.61 days.

Vagility. Only males were analyzed due to the low number of females. The greatest recorded distance along the trail flown by an individual was 650 meters (mean = 83.96 m; SD = 94.45 m; n = 53). Most of the individuals were recaptured at least once in a different site from that of first capture (44 out of 53 recaptured individuals).

Wing size. The forewing length of males varied from 35 mm to 46 mm (mean = 41.5; SD = 2.14; n = 121) and of females from 38 mm to 45 mm (mean = 41.5; SD = 1.77; n = 35). This difference was not significant (t = 0.039; DF = 65.4; p = 0.969).

Resource utilization. For 128 visits recorded, 52% were on *L. camara*, 26% on *C. odorata* and 23% on flowers of other genera, including *Lippia* sp. (Verbenaceae), *Manettia* sp. (Rubiaceae) and *Passiflora suberosa L.* (Passifloraceae). As described for *H. erato*, visitation to other nectar sources increased after May when flower production decreased for *L. camara*.

DISCUSSION

Population biology. The populations showed three distinct phases: growth in January, February and March,

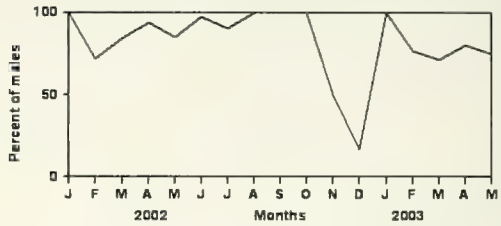

FIG. 5. Sex ratio of *H. ethilla* from January 2002 to May 2003 in Santa Genebra, Campinas, SP.

peak in April and decline in May and June. The instability in numbers differs from the patterns found in other tropical *Heliconius* studies (Turner 1971, Ehrlich & Gilbert 1973; Ramos & Freitas 1999) that reported stable populations throughout the year, and was to some extent similar to those studied in southern Brazil (Araujo, 1980; Romanowsky et al., 1985), with marked seasonal variation in the number of individuals. However, in southern Brazil, population decline seems to be correlated with a decrease in ambient temperature (Saalfeld & Araujo, 1981; Romanowsky et al., 1985), whereas at Santa Genebra the decline is probably due to decrease in rainfall. The number of individuals in the studied populations was relatively low (up to 60 individuals based on Jolly-Seber estimates in both species) compared with studies in south Brazil, where captures could be as high as 60 individuals in a single day (Romanowsky et al., 1985). In the periods of population peak, the number of captured individuals in both species was equivalent to those reported in other studies in tropical sites (Turner 1971, Ehrlich & Gilbert 1973; Ramos & Freitas 1999).

Rainfall is considered as an important factor limiting population numbers for *Heliconius*, since it is closely

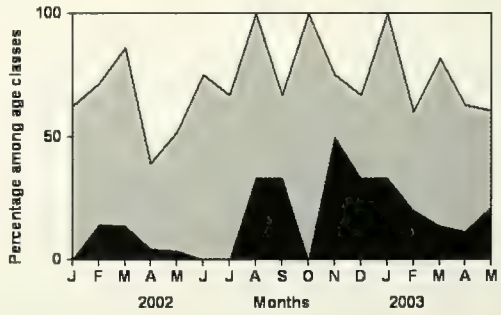

FIG. 6 - Age structure of males *H. ethilla* from January 2002 to May 2003 in Santa Genebra, Campinas, SP. Black = new individuals, gray = intermediate, white = old.

linked with adult resource availability (see Ehrlich & Gilbert, 1973 and Gilbert, 1984). The seasonal variation in rainfall probably explains the population fluctuation patterns reported in the present paper, which is quite different from stable populations reported in tropical or coastal areas where rainfall is constant throughout the year. The accentuated decline and low population numbers in the Santa Genebra populations can also be a consequence of migration of individuals to surrounding subpopulations in more suitable environments (as proposed in Saalfeld & Araujo 1981) outside our sampling area.

High values of residence time agree with other studies of *Heliconius* (Turner 1971, Benson 1972, Ehrlich & Gilbert 1973, Araujo 1980, Quintero 1988, Ramos & Freitas 1999). These numbers may be related to restricted dispersion of adults and to several visits to resources patches. For both species studied here, sex ratio was male biased, agreeing with field results from several butterfly studies (Ehrlich & Gilbert 1973, Mallet & Jackson 1980, Ehrlich 1984, Ehrlich *et al.* 1984, Freitas 1993, Ramos & Freitas 1999). Differential behavior in the sexes may cause this deviation.

The data on resource utilization by both species suggests that they are using all available flowers in the study site. Flowers of *L. camara* were the most visited by both *Heliconius* in Santa Genebra. Previous studies showed that *Lantana* is a major pollen source for some species of *Heliconius* in several tropical sites (Boggs *et al.* 1981, Ramos & Freitas 1999). We suggest that intense use of *Lantana* and other flowers with small pollen grains could be related with more generalist edge species of *Heliconius*.

Comparing both species in the study site, *H. ethilla* is more abundant and persistent than *H. erato*, but both species show the same seasonal fluctuation pattern of population. Both species are suggested as plastic species (Ramos & Freitas, 1999 and this paper), but there are more data available for *H. erato* than for *H. ethilla* at the moment. Additional studies of *H. ethilla*, including host plant use, larval performance and population dynamics in different habitats are needed.

Color patterns in *Heliconius erato*. The decline in the mean number of red raylets in colder months agrees with Pansera & Araujo (1983), Oliveira & Araujo (1992) and Ramos & Freitas (1999). The mean number of "light yellow squares" also seems to decline in colder moths, and the population becomes virtually absent during winter and spring. For this reason it is difficult to perform any analysis to help to clarify the direction and origin of the variation of this and other traits.

The three-to-one proportion between the two colors of prothoracic legs may be a hint about the heritability of this trait. However, due to the low number of *H. erato* captured, it is difficult to infer much about the biology of the color traits considered in this study.

Further studies could investigate the influence of seasonal climate pattern on the availability of resources for long-life butterflies such as *Heliconius*, and how these factors restrain population numbers. Also, the understanding of temporal and spatial fluctuation patterns of color patterns can elucidate ecological processes related to natural selection and genetic variability.

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REPRODUCTIVE BULK IN CAPITAL-BREEDING LEPIDOPTERA

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ABSTRACT. Reproductive bulk is the weight of the individual egg load, also the mathematical product of individual fecundity × mean egg weight. Somatic bulk is its complement. Interrelations among nonindependent maternal weight, reproductive bulk, somatic bulk, fecundity, egg weight and related variables were explored with eight sets of data; three original, and five previously published, all representing four capital-breeder species in three families. In traditional fecundity–maternal weight regressions, response and explanatory variables are not statistically independent because maternal weight includes reproductive bulk. Comparative regressions where nonindependent maternal weight was the explanatory variable yielded median coefficients of determination of 0.62 for fecundity and 0.76, or 0.14, for reproductive bulk among the data sets. When maternal weight was rendered independent by subtracting reproductive bulk, the median coefficient of determination for reproductive bulk plummeted from 0.76 to 0.12, which exposes the extent to which nonindependence inflates regression test statistics. Reproductive bulk nevertheless increased with both independent and nonindependent maternal weight. Nonindependence does not necessarily invalidate the practical use of traditional fecundity–maternal weight regression models. Reproductive bulk is potentially useful as a response variable in regression models of reproductive potential where trade-offs between fecundity and egg weight occur, and where independent maternal weight is otherwise desired as an explanatory variable.

Additional key words: fecundity, egg weight, reproductive potential, reproductive effort, *Malacosoma disstria, Dendrolimus pini, Chilo partellus, Choristoneura fumiferana*

'Capital-breeding' refers to Lepidoptera that depend for reproduction entirely or chiefly on metabolic resources assembled during the larval rather than the adult stage (Boggs 1992, Miller 1996, Tammaru and Haukioja 1996). The great majority of Lepidoptera are capital breeders, as are the great majority of outbreak Lepidoptera (Miller 1996, 2005; Tammaru and Haukioja 1996). Capital breeders that assemble resources entirely during larval growth are termed 'perfect', and those that assemble most resources during larval growth but some during posteclosion adult feeding are termed 'imperfect' (Miller 2005).

Because reproductive potential in capital breeders is solely or heavily dependent on larvae, initial maternal weight has long been considered an indicator of fecundity (Honek 1993, Miller 2005). Indeed, retrospective analysis of capital-breeder fecundity–maternal weight regressions confirms a consistent relation between fecundity and maternal weight (Miller 2005). Moreover, extrinsic factors such as temperature and diet quality during larval development influence fecundity indirectly through their influence on maternal weight. Although lineal maternal size variables, including forewing length and pupal diameter, are also predictive, weight has traditionally predominated.

Trade-offs between fecundity and egg weight for a given maternal weight also can alter fecundity–maternal weight regressions. Trade-offs may vary temporally, spatially, and among subgroups of a cohort. Trade-offs are probably adaptive, and two notable examples are the geographic trade-off clines in *Choristoneura fumiferana* (Clem.) (Tortricidae) and *Malacosoma disstria* (Hbn.) (Lasiocampidae) (Harvey 1983, Parry *et al.* 2001). Trade-offs highlight the potential utility of reproductive bulk as a response variable in regression models of reproductive potential (Miller 2005).

Reproductive bulk, R, is the weight of the individual egg load, or some meaningful fraction of it such as laid eggs or realized fecundity (Miller 2005). R also is the mathematical product of fecundity, F, × mean egg weight, E. Somatic bulk, or nonR, is maternal weight less R, or W - R. The expressions nonR and W - R are interchangeable. Reproductive effort, RE, is the proportion of maternal weight consisting of egg load, or R/(W + R). These definitions are approximations in that they do not account for energy used in maintenance and in the development of reproductive structures (Roff 1992).

Traditional fecundity-maternal weight regressions for capital breeders are usually formulated as

$$F = bW + a \qquad \text{(Eq. 1)}$$

where W is weight of first-day pupae or of adults at eclosion, b is the slope parameter, and a is the intercept or scaling parameter (Honek 1993, Miller 2005). Reproductive bulk–maternal weight regressions may be analogously formulated as

$$R = bW + a \qquad \text{(Eq. 2)}$$

W in Eqs. 1 and 2 almost always includes R such that W = nonR + R. Thus R is represented on both sides of these equations, thereby creating statistical nonindependence between response and explanatory variables (Roff 1992, Honek 1993, Miller 2005). Nonindependence masks data variability, inflates regression test statistics, and exaggerates the strength of relations. If measures of R are available, statistical

independence can be attained with the formulation

$$R = b(W - R) + a \qquad \text{(Eq. 3)}$$

Probably because fecundity is so obviously important in reproduction, and has so often been regressed on nonindependent maternal weight, pure R in capital breeders has been little investigated.

The objectives of this report are (i) to illuminate reproductive bulk, R, by examining its interrelations with nonindependent maternal weight, W + R, or nonR + R, independent maternal weight or somatic bulk, nonR or W - R, reproductive effort, RE, fecundity, F, mean egg weight, E, and (ii) to assess the impact of nonindependence between explanatory and response variables on the reliability of regression models for estimating reproductive potential.

MATERIALS AND METHODS

I sought capital-breeder data sets where R, nonR, F, and E were given or could reasonably be derived. Before analysis, all weights were standardized to fresh weights at adult eclosion expressed in milligrams. Dry weight in data sources was converted to fresh weight using the factor 3.3 (Honek 1993), and pupal fresh weight to adult fresh weight using the factor 0.54, the reciprocal of 1.85 for the opposite conversion (Miller 2005). Data sets were accepted if they included more than eight mothers and did not require more than two conversions to obtain fresh weights of any variable. Some sample sizes are slightly less than in sources because individual observations were not always complete enough for use in this study.

I compared test statistics derived from each data set for regressions of F relative to W + R (Eq. 1), R relative to W + R (Eq.2), and R relative to W - R or nonR (Eq. 3). Most statistics were computed with SYSTAT (1992) software. Correlations refer to Pearson r-values, and coefficients of determination to r^2. Mean REs were based on individual mother REs. Lack of statistical significance at the 0.05 level is indicated by 'ns'. More specific methodological information is given as the analysis of each data set is discussed below.

RESULTS

Eight data sets, marginally to eminently suitable, were found for four capital breeders in three families. Three sets are considered original because they were used only partially in previous publications. Three or more comparative regressions are presented for each data set as well as mean RE and the correlation between F and E. Regression test statistics where W + R rather than W - R is the explanatory variable should be interpreted cautiously because of inherent nonindependence.

No. 1. In this and the following two analyses, pupal weights, fecundities and reproductive bulk for *Malacosoma disstria* (Hbn.) (Lasiocampidae), a perfect capital breeder, were transcribed from enlarged photocopies of scatterplots in Fig. 2 of Parry *et al.* (2001). Regression slopes computed from transcribed values were compared with slopes given in the source, and F-tests showed that departures were small and nonsignificant. In each of these three data sets two conversions were necessary: fresh first-day female pupal weight to fresh maternal weight at eclosion, and dry reproductive bulk to fresh reproductive bulk. Louisiana results are presented first.

Regressions (all n = 29):

$F = 0.98(W + R) + 23.4$, $r^2 = 0.81$, $P < 0.01$.
$R = 0.84(W + R) - 18.5$, $r^2 = 0.85$, $P < 0.01$.
$R = 0.05(W - R) + 181.0$, $r^2 = 0.00$, ns.

Mean RE = 0.76. $r_{F,E} = 0.24$, ns.

No. 2. Michigan *M. disstria*.

Regressions (all n = 29):

$F = 0.77(W + R) + 37.4$, $r^2 = 0.77$, $P < 0.01$.
$R = 0.70(W + R) - 16.4$, $r^2 = 0.86$, $P < 0.01$.
$R = 0.76(W - R) + 85.7$, $r^2 = 0.17$, $P = 0.03$.

Mean RE = 0.63. $r_{F,E} = 0.29$, ns.

No. 3. Manitoba *M. disstria*.

Regressions (all n = 24):

$F = 0.76(W + R) - 30.9$, $r^2 = 0.89$, $P < 0.01$.
$R = 0.64(W + R) - 38.8$, $r^2 = 0.90$, $P < 0.01$
$R = 1.04(W - R) - 2.06$, $r^2 = 0.40$, $P < 0.01$.

Mean RE = 0.50. $r_{F,E} = 0.28$, ns.

No. 4. The Minnesota *M. disstria* data analyzed below originated in simultaneous laboratory rearings of three subgroups of larvae from a cohort of eggs collected near International Falls on *Populus tremuloides* Michx. (Salicaceae). The subgroups were reared at constant temperatures of 20°, 25°, and 30°C on foliage of the source foodplant, and the data used here are subsamples. Experimental procedure is detailed further in Miller (2005). Two conversions were necessary: fresh first-day pupal weight to fresh maternal weight at eclosion, and dry egg weight to fresh egg weight.

Regressions (all n = 24):

$F = 0.71(W + R) + 6.4$, $r^2 = 0.63$, $P < 0.01$.
$R = 0.56(W + R) - 23.7$, $r^2 = 0.68$, $P < 0.01$.
$R = 0.27(W - R) + 60.2$, $r^2 = 0.05$, ns.

Mean RE = 0.44. $r_{F,E} = 0.45$, $P < 0.05$.

No. 5. In the following analysis of data for *Dendrolimus pini* (L.) (Lasiocampidae), a perfect

capital breeder, Eckstein (1911) may have provided the earliest published evidence for relations among the variables of capital-breeder reproductive potential. These are the only data here in which individual maternal weight was reported both before oviposition (gravid condition) and after eggs were laid or removed from ovaries (spent condition). Neither transcription nor conversions were necessary, making this the most experimentally satisfactory data. In the third regression below, W - R was computed indirectly as W_{gravid} - (W_{gravid} - W_{spent}), and in the fourth, directly as W_{spent}.

Regressions (n=55–58)

F = 0.10(W + R) + 33.8, r^2 = 0.60, P < 0.01.

R = 0.82(W + R) - 220.1, r^2 = 0.93, P < 0.01.

R = 1.20(W - R) + 491.6, r^2 = 0.16, P = 0.01.

R = 1.22(W_{spent}) + 477.7, r^2 = 0.17, P = 0.01.

Mean RE = 0.67. RE = 0.000093(W + R) + 0.525, r = 0.59, P < 0.01. $r_{F,E}$ = -0.12, ns.

The third and fourth regressions above differ only negligibly.

No. 6. The source data treated below are from Berger (1989) who reared *Chilo partellus* (Swinhoe) (Crambidae), an imperfect capital breeder, on artificial diet. After adults eclosed and were weighed and individually mated, Berger recorded numbers and weights of eggs laid on the first three nights of oviposition during which 80% of eggs typically are deposited. It appears that mothers were provided with water for imbibing. The data were transcribed from enlarged photocopies of Berger's Figs. 3 and 4. No conversions were necessary.

Regressions (all n = 9):

F = 1.80(W + R) + 247.7, r^2 = 0.20, ns.

R = 0.19(W + R) + 6.33, r^2 = 0.55, P < 0.01.

R = 0.18(W - R) + 12.1, r^2 = 0.35, ns.

Mean RE = 0.25. $r_{F,E}$ = -0.10, ns.

No. 7. In the two following analyses, data sets for *Choristoneura fumiferana* (Clem.) (Tortricidae), an imperfect capital breeder, originated with pupae collected near Duluth, Minnesota, from severely infested *Abies balsamea* (L.) Mill. and *Picea glauca* (Moench) Voss. (both Pinaceae). Eclosing adults were divided into two groups, individually paired, and the group discussed first provided with sponges soaked in sweetened water for imbibing. Numbers of eggs laid by mothers of both groups were recorded daily. Eggs were weighed at least twice, the first time on the first or second day of oviposition, and the second and sometimes third on the fourth day of oviposition or later. Forewing length of mothers was measured after they expired. Experimental procedure is detailed further in Miller (1987). Two conversions, the first involving two steps, were necessary in both sets: forewing length, FL, to dry weight, DW, by the species-specific formula DW = 0.0057[$FL^{3.336}$] (r^2 = 0.97, df = 211, P < 0.01), and from dry to fresh weights.

Regressions (all n = 33):

F = 2.47(W + R) + 91.9, r^2 = 0.31, P < 0.01.

R = 0.52(W + R) + 9.7, r^2 = 0.34, P < 0.01.

R = -0.15(W - R) + 45.9, r^2 = 0.09, ns.

Mean RE = 0.68. $r_{F,E}$ = -0.02, ns.

No. 8. These C. *fumiferana* results are from the second group mentioned above, which was provided with unsweetened water for imbibing.

Regressions (all n = 26):

F = 0.83(W + R) + 97.8, r^2 = 0.06, ns.

R = 0.21(W + R) + 12.4, r^2 = 0.08, ns.

R = -0.18(W - R) + 30.6, r^2 = 0.09, ns.

Mean RE = 0.44. $r_{F,E}$ = 0.11, ns.

DISCUSSION

Comparison of regressions where fecundity, F, and reproductive bulk, R, were response variables to nonindependent W, that is to W + R or nonR + R (Eqs. 1 and 2), shows coefficients of determination to be higher for R than for F among the eight data sets. This result reveals less variability in R than in F relative to the explanatory variable. Median coefficients of determination were 0.76 for R and 0.62, or 0.14 less, for F, and their intraspecific differences ranged 0.01–0.35, with a median difference of 0.08. This result was expected because R integrates fecundity, F, and egg weight, E, and, unlike F alone, takes account of trade-offs between F and E.

By contrast, when independent maternal weight, W - R or nonR, was the explanatory variable (Eq. 3), the median coefficient of determination for reproductive bulk among the data sets was only 0.12. This plummeting of the coefficient reflects the extent to which nonindependence artificially elevates test statistics. The fact that coefficients of determination for Eqs. 1 and 2 are inflated is not surprising; what is surprising is the extent of inflation. Even if barely satisfactory data sets 7 and 8 for *Choristoneura fumiferana* are omitted, the median coefficient of determination for reproductive bulk does not change appreciably (nor does that for fecundity). It is also telling that the corresponding coefficient of determination in an eminently satisfactory data set—No. 5 for *Dendrolimus pini*—dropped from 0.93 to 0.16, and thus reflects the overall trend among the eight data sets. Low coefficients of determination where

response and explanatory variables were independent—all ≤ 0.40—expose the true variability in nonindependent data. Clearly, nonindependence in traditional regressions using W + R as the explanatory variable has led to gross overstatements of the strength of maternal weight in models of reproductive potential.

Slopes in regressions of reproductive bulk relative to independent maternal weight or somatic bulk ranged 0.05–1.2 and were positive if not significant in six of the eight data sets. Positive slopes confirm Honek's (1993) reasoning that larger-bodied mothers are necessary—probably sufficient—for greater R as well as greater F. In the two exceptions, Nos. 7 and 8 for *Choristoneura fumiferana*, negative slopes may be anomalous as suggested by some but not all previous work (Miller 2005), and may be due to conversion errors, although variability in the life system of this species should not be ruled out. Other data sets with slopes not statistically different from zero—Nos. 1, 4, and 6—likewise may be due to transcription and conversion error. As indirectly measured variables become smaller, errors of conversion are magnified. The slope values show that reproductive bulk changes disproportionately relative to independent and nonindependent maternal weight, just as found for fecundity (Miller 2005). Disproportionate change between these variables may have implications for rates of population buildup and decline.

As already mentioned, trade-offs between fecundity, F, and mean egg weight, E, may occur temporally or spatially, and are doubtless adaptive. An example of statistically significant increase in E accompanying increasing F is data set No. 4 for *Malacosoma disstria*. An example of decrease is evident in *Bupalus piniaria* (L.) (Geometridae), where egg diameter was a surrogate for E (Klomp 1966) (data omitted here). Klomp noted the counterintuitive situation where even though surrogate egg weight of individual mothers increased serially, it still decreased overall with increasing fecundity. An example of constant E with increasing F is data set No. 5 for *Dendrolimus pini*. A remarkable further example is *Bombyx mori* (Bombycidae) (Fig. 1), illustrated here because it may represent the most extensive data in existence concerning egg weight relative to fecundity in a capital breeder. Unfortunately, the corresponding maternal weights were unavailable.

Reproductive effort, RE, ranged from 0.20s–0.70s among the eight data sets. RE is expected to vary adaptively in different species and environments (Roff 1992). It appeared static in all but one data set—No. 5 for *Dendrolimus pini*—but RE is derived and its test statistics relative to other reproductive variables are also subject to inflation. In *Choristoneura fumiferana* data sets 7 and 8, mothers provided with sweetened water

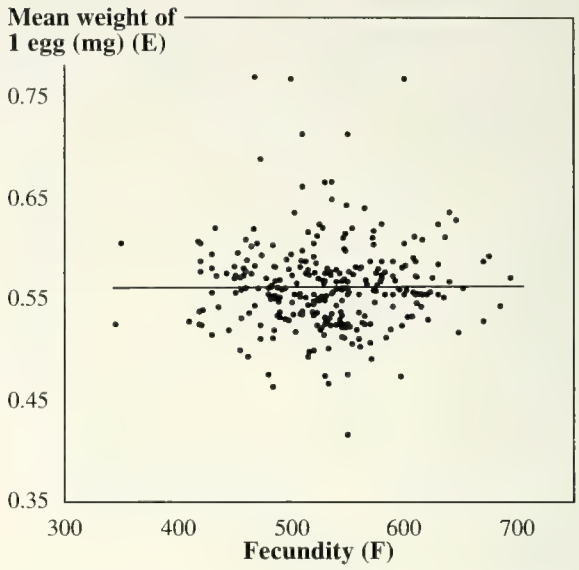

FIGURE 1. Relation of mean egg weight, E, to fecundity, F, in 293 races of *Bombyx mori*. Each point represents one or more females per race. The regression line is described by E = 0.0000109 + 0.56F, $r^2 \approx 0.00$, ns. Data were plotted from tables in Hiratsuka (1999).

had an RE of 0.68 compared with only 0.44 for those provided with unsweetened water; the 0.24 difference further demonstrates the enhancing role of adult nutrition in reproductive performance (Miller 1987, 1989).

Lack of independence between response and traditional explanatory variables does not necessarily invalidate practical use of fecundity-maternal weight regression models for estimating reproductive potential (Roff 1992). Maternal weight, whether independent or not, remains indicative of fecundity and reproductive bulk. In most basic research, however, response and explanatory variables should be statistically independent for reliable results. Further, all weights ideally should be measured directly and in dry form. The use of dry weights would warrant adoption of the stricter terminology of 'reproductive mass' and 'maternal mass'.

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PIGGYBACKING NORTHWARD: MOVEMENT OF *LEPTOTES CASSIUS* (LYCAENIDAE: LYCAENINAE) THOUGHOUT THE SOUTHEAST

Additional key words: butterfly gardening, dispersal, Florida, Georgia, *Plumbago*, South Carolina

The widespread distribution of *Leptotes cassius* Cramer across the many island groups of the West Indies demonstrates its success as a highly effective colonist (Smith et al. 1994). Within the Southeast, *L. cassius* is primarily restricted to south Florida and the Florida Keys where it is generally the most abundant blue of open disturbed sites or semi-open, scrubby habitats. During favorable years with mild winters, it may occasionally expand its range northward through the peninsula into the central and northeastern counties. Records beyond the state's border are rare but isolated vagrants have been reported from Alabama, Mississippi, Arkansas, Louisiana, Georgia and South Carolina (Opler et al. 1995, Opler and Malikul 1998, Scott 1986,). The exact origin of such strays is unknown and may represent isolated dispersal events, hurricane or tropical storm-assisted movements, or temporary seasonal expansion of breeding populations. A fourth explanation, though, may provide an alternate explanation for many of the confirmed records.

In August 1999, while shopping at a small specialty nursery on Hilton Head Island, Beaufort County, South Carolina, I noticed a small blue flying erratically around a patch of colorful flowers. Upon closer inspection, I was surprised to see that it was a male *L. cassius*. Immediately following the discovery, I searched the remainder of the nursery property and adjacent open areas, but did not observe any additional adults. The nursery did, however, have several one to three gallon planters of *Plumbago auriculata* Lam. (Plumbaginaceae) and *P. auriculata* '*alba*' that between them supported 21 larvae ranging from second to fifth intar. I inquired about the origin of the plants and was informed by the nursery staff that they had arrived earlier in the week from a large grower located in south-central Florida.

Between September 1999 to August 2002, subsequent visits were made to the same Hilton Head nursery and to two other similar specialty garden centers located in Bluffton, Beaufort County, South Carolina and Savannah, Chatham County, Georgia. During this period, adults, immatures, or in some cases small breeding colonies of *L. cassius* were found at each nursery in every year except 2002, when adult individuals were found only at the Hilton Head Island location. In each instance, all three nurseries received shipments of *Plumbago* from the same south-central Florida grower. It is not known if purchased plants harboring livestock led to the establishment of additional local temporary breeding colonies.

With the ever-growing popularity of butterfly gardening and native landscaping, it is likely that the frequency of such human-assisted piggybacking of livestock on nursery plant material will continue to increase and thus serve to blur the legitimacy of some county or state records.

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SYNANTHEDON BOLTERI (SESIIDAE) IN MICHIGAN

Additional key words: pheromones, Baskerville-Emin, *Synanthedon sigmoidea*

The clearwing moth, *Synanthedon bolteri* (Hy, Edwards), has a wide-ranging distribution in mostly sub-arctic to arctic areas of North America. This statement is based on scattered records, "... from southern Quebec and Rhode Island west to Colorado and Washington and north to the Northwest Territories and Alaska (Eichlin and Duckworth 1988, p. 86)"

Large numbers of sesiids have been collected since the advent of synthetic sex pheromone use for monitoring clearwing moths (USDA 1979). However, to date, no collectors have reported capturing this species with the use of synthetic sex pheromones, even though these chemicals are commonly used for monitoring clearwing moths across the United States for integrated pest management purposes.

Historically, *S. bolteri* specimens collected in Michigan were rare. Two specimens of *S. bolteri* collected by R.R. Driesbach in southwestern Michigan (Mecosta Co., 31 July, 1941 and Ottawa Co., 17 Aug., 1945) are located in the Michigan State University A. J. Cook Arthropod Research Collection and University of Michigan Museum of Zoology, respectively. In over 30 years of collecting clearwing moths I have encountered only 1 specimen of *S. bolteri* (Figure 1). The male moth was caught on 23 July 1984 in Dickinson County of Michigan's Upper Peninsula in a malaise trap located within a flowering stand of fireweed (*Epilobium angustifolium*). Another clearwing moth, *Albuna pyramidalis* (Walker), was commonly found sitting on fireweed foliage during this same time period.

This situation changed in August 2004, when 30 specimens of *S. bolteri* were collected at two locations over a 5-day period with the use of a Multipher 1® moth trap baited with a grape root borer pheromone lure made by Suterra. This lure composition is 99% E,Z 2,13 -ODDA and 1% Z,Z 3,13 -ODDA. This lure was chosen to capture *Synanthedon sigmoidea* (Beut.), which is reportedly attracted to this lure formulation (Taft et al. 1991). The trap location was selected due to the occurrence of large stands of pussy willow (*Salix discolor*) and several other *Salix* species (Figure 2). Engelhardt (1946) reported that both of these moth species were associated with low growing *Salix* species that have been injured by coleopteran larvae.

Fourteen specimens of *S. bolteri* were captured over a 3-day period (1-3 August 2004) in a willow thicket along the Rock River at the US-2 stream crossing (T43N, R11W, Section 24) in Newton Township, Mackinac County. Sixteen additional specimens were collected over a 3-day period (3-5 August 2004) approximately 12 miles southeast of Sault Ste. Marie (T46N, R1E, Section 34) in Bruce Township, Chippewa County. The habitat at both collection sites was similar. The cumulative degree-day value (Base 10°C) using the Baskerville-Emin method (Baskerville and Emin 1969) was calculated with the assistance of staff from the agricultural weather office at Michigan State University (MSU) for Manistique and Barbeau, Michigan. These were the closest Upper Peninsula weather stations to the capture locations. The cumulative degree-day calculated values for Manistique and Barbeau were 394 and 385, respectively. *S. sigmoidea* was later collected in southern Ingham County starting on 26 August 2004, when the cumulative degree-day calculated value (Base 10° C) for East Lansing was 1061. This important pheromone and degree-day information should help collectors target *S. bolteri* and *S. sigmoidea* in the future.

I would like to thank Jeff Andresen at the MSU agricultural weather office for providing the temperature data used to calculate the degree-day accumulation information. Also, many thanks to Stewart Gage of MSU for calculating the actual degree-day numbers and to Thomas D. Eichlin, Sarah Wolf and Mogens C. Nielsen for helpful suggestions and reviewing this paper.

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FIGURE 1. *S. bolteri* collected southeast of Ralph on 23 July 1984, Dickinson County, Michigan. (Photo Credit: P. Carrington)

FIGURE 2. *S. bolteri* collection site. Note the numerous willow shrubs interspersed within the sedge meadow habitat found along the Rock River, Mackinac County, Michigan. (Photo Credit: Wm. Taft)

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