



PHYCIODES (PHYCIODES): NEW DISCOVERIES, NEW SUBSPECIES, AND CONVERGENCE

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Abstract. The paper presents new discoveries in *Phyciodes* (*Phyciodes*). New life history information is given for *P. mylitta arizonensis*, *P. pallida pallida*, *P. pallida barnesi*, *P. tharos tharos*, *P. cocyta selenis*, *P. cocyta diminutor*, *P. batesii lakota*, *P. b. apsaalooke*, *P. b. anasazi*, *P. pulchella camillus*, and *P. picta picta*. *P. batesii anasazi* was found to significantly converge toward *P. cocyta* in western Colorado in appearance of some adults larvae and pupae, and *P. cocyta selenis* from the same area was found to converge a little toward *anasazi* in adult wing pattern and larval head pattern, so some individuals of these two taxa are difficult to distinguish. The nomenclatural identity of *P. tharos* form *marcia* is clarified. Five new subspecies are named: *P. tharos orantain* has orange antenna nudum and is somewhat intermediate between *P. tharos tharos* and *P. cocyta*. *P. cocyta diminutor* is multivoltine with late-flying summer generations that are small like *P. tharos*, and might possibly even be a separate species from the sympatric univoltine larger *P. cocyta selenis*. *P. pulchella deltarufa* has oranger ups than ssp. *pulchella*. *P. pulchella owimba* differs from ssp. *pulchella* by having an orange antenna nudum and some different wing pattern details. *P. phaon jalapeno* has paler median ups bands.

INTRODUCTION

Scott (1994) reported on the systematics and biology of *Phyciodes* (*Phyciodes*), described numerous new life histories, named five new taxa, and corrected prior nomenclature. This paper continues that project with more recent findings and more new taxa.

METHODS

Larval segments are labeled T1-3 on thorax and A1-10 on abdomen. Larval scoli are named by prefixing B- (for branching spine) to the name of the nearest primary seta, thus BD1 is the scoli near seta D1 (primary setae are present on 1st-stage larvae but are mostly lost among numerous secondary setae on older larvae, whereas scoli are present on 2nd-stage to mature larvae). Upf=upperside of forewing, unf=underside of forewing, uph=upperside of hindwing, unh=underside of hindwing, ups=upperside, uns=underside. All times are given as 24-hour standard time.

DISCUSSION OF CHARACTERS

EGG. Scott (1994) indicated that multivoltine *Phyciodes* species that are polyphagous on numerous asters including small rough asters (*P. tharos* and *pulchella*), lay more eggs per cluster than species that are univoltine and specialize on large lush asters at the best time of year (*cocyta* and *batesii lakota*). But an exception has been found. The average number of eggs per cluster is 62 for the multivoltine *P. tharos orantain* and 60 for multivoltine *P. pulchella camillus*, versus 49 for the univoltine Colorado *P. cocyta selenis* and 42 for univoltine Neb. *P. batesii lakota* (but three clusters of univoltine Ontario *P. batesii batesii* had 50-80 eggs, so this low average might not be true for *P. batesii batesii* or even for *P. batesii lakota* from other regions). However the exception is that the average is about 91 for *P. batesii anasazi* (mean 91 for egg clusters, 57 for 1st-stage larva clusters), and about 84 for *P. batesii apsaalooke* (mean 84 for egg clusters, 60 for 1st-stage larval clusters). Both *P. b. apsaalooke* and *P. b. anasazi* are univoltine and feed on fairly large asters at the best time of year, specifically *Aster glaucodes*, which grows in very large clumps often many meters wide (the largest biomass I have ever seen of any aster); evidently, females lay many eggs per cluster on this aster because its giant clumps can feed very many larvae. The extra eggs laid by *tharos* and *pulchella* is traditionally interpreted as "R-selection" for more eggs laid on worse hosts, the logic being that a greater number of eggs must be laid to account for poorer survival on worse hosts. But a better explanation is that Colorado *cocyta selenis* and Nebraska *batesii lakota* lay

fewer eggs on a large tall few-leaved aster (*Aster laevis* var. *geyeri*) in the hope that some can survive on a single plant, rather than forcing a large number of larvae to attempt to move to other plants after they defoliate that single plant, because *A. laevis* generally does not grow in large clusters, and especially in Nebraska often grows as single plants or a small cluster of just a few plants. Likewise, females can lay a large number of eggs on *Aster glaucodes* and on the *tharos* and *pulchella* hosts because each plant cluster of those aster species usually has a greater biomass of leaves. The same explanation may also fit *P. mylitta*, because its hostplants (various thistles) generally are large and lush when compared to the average aster (*P. mylitta* subspecies laid 115, 50, and 52 eggs, averaging 72). *P. picta* may also lay a rather high number of eggs per cluster (averaging 55), and is multivoltine and has some small non-lush weedy hosts.

Oviposition leaves are mostly at middle heights on the hostplants in *P. cocyta* and *P. batesii*, although they vary from low to high on the plant, whereas in *P. tharos* and *P. pulchella camillus* and *P. pallida* and *P. picta* eggs are mostly laid fairly low on the plants, though in the case of *tharos* and *camillus* this may be because most of their hostplant asters are rather low plants rather than the tall succulent asters preferred by *cocyta* and *batesii*. *P. pallida* evidently oviposits low on the plants because the hostplants are frequently biennial and females oviposit on the first-year seedlings (which are low) rather than the second-year flowering plants.

LARVAE (Tables 1-2). The age of the 1st- and 2nd-stage larva is important for studying their color pattern.

Further study of **1st-stage larvae** of all species of the *tharos*-group proves that non-molting 1st-stage larvae have a fairly-strong pattern of brown bands only in *P. pulchella* (including a weak middorsal tan line, a nearby tan line, a conspicuous wide brown dorsolateral band, and a tan sublateral line), whereas this pattern is absent (rarely weak) in all *P. batesii* subspecies and *P. cocyta*, and absent in *P. tharos tharos/riocolorado* (note that the **molting** 1st-stage larva appears to have a brown pattern in **all** taxa, because the 2nd-stage larva has a fairly-strong brown pattern of lines/bands in all taxa, so when the 1st-stage is molting and the 2nd-stage head is visible as a bulge in the prothorax of the 1st-stage larva, the 2nd-stage body pattern is also visible through the soon-to-be-shed 1st-stage skin).

The 2nd-stage larva is similar in all species and undergoes the same color change: the young larva is greenish-tan with middorsal and nearby darker-green lines and dorsolateral wide lighter-brown band and sublateral darker-green line; but 2nd-stage larvae later turn browner (tan) and the lines become tan and the dorsolateral band becomes brown.

1st-stage larvae always eat their eggshells, and then they remain together while spinning some **silk web** on the leaf. The strongest webs are made by clusters of young larvae preparing to molt. This web is very conspicuous in *P. batesii* (all four subspecies) and most *P. pulchella camillus*, about half the *P. cocyta selenis* families, and a few *P. tharos orantain* families, while the web is absent thus far (though may be conspicuous rarely) in *P. cocyta diminutor* and *P. tharos tharos*. Most larvae rest on top of the silk web, but occasionally some larvae may rest and feed beneath part of it. 1st-stage larvae eat small pits on leaf undersides and stick their heads into these pits, often beneath a cuticle overhang, to feed on the internal leaf tissue. 2nd-3rd-stage larvae continue to eat pits in the leaf, bigger pits by older larvae, and only the older larvae (~4th-stage-mature) eat the leaf completely through by excising chunks of leaf from the edge.

HIBERNATION STAGE AND DURATION OF LARVAL STAGES. Unfed 4th-STAGE LARVAE hibernate in *P. tharos tharos*, *P. cocyta selenis*, *P. cocyta diminutor*, *P. batesii batesii*, *P. batesii lakota*, *P. batesii apsaalooke*, *P. b. anasazi*, *P. pulchella camillus*, *P. pallida pallida*, and *P. orseis orseis*.

Additional rearing of various species proves that length of **lab diapause** does not differ between species or subspecies (as Table 4 of Scott 1994 suggested). Actually, for every taxon, if one collects eggs or 1st- or 2nd-stage larvae in nature, or collects postdiapause larvae, almost none of them will diapause when reared in the lab. But if one collects 3rd-stage larvae in nature, many will diapause, and of course if pre-diapause 4th-stage larvae are collected in nature most of them will diapause in lab. Obviously, the larvae diapause only if they have experienced a photoperiod in nature that triggers diapause, and the 3rd-stage larva must be the stage that is affected by photoperiod in nature. Thus, the various subspecies of *P. batesii* do not differ in length of lab diapause.

HABITS OF POSTDIAPAUSE LARVAE. Further study continues to show that post-diapause larvae are very difficult to find in nature, which proves that older larvae spend most of the day hiding at the base of the plant. The only way to find postdiapause larvae seems to be to notice feeding damage on the aster leaves (excision of leaf tissue from leaf edges), then laboriously search the litter below that plant; using that method I have found some older larvae of *P. pallida pallida*, *P. cocyta selenis*, *P. pulchella camillus*, and *P. picta*. So postdiapause larvae seem to rest in litter below the hostplant during the day, then feed on the host at night. In contrast, young larvae (prior to 4th-stage diapause) remain on the hostplant all day and night. 1st-stage larvae form a cluster and remain very close to the eggshells, and in some species they cling tightly to a silk-web.

LIST OF NAMES, TYPES, and TYPE LOCALITIES
OF *PHYCIODES* (*PHYCIODES*)
(In addition to Scott 1994)

A. *mylitta* species-group

- 1a. *mylitta mylitta* (W. Edwards) 1861, neotype CAS (=California Academy of Sciences), TL (=type locality) Stanyan Hill, San Francisco.
= *epula* (Bdv.) 1869, female syntype is supposed to be in BMNH (=British Museum Natural History), but is not there according to Philip Ackery; location unknown.
- 1b. *mylitta arizonensis* Bauer 1975, type in David Bauer collection (Ferris, ed., 1989).
- 1c. *mylitta mexicana*
- 1d. *mylitta arida* (Skinner) 1917. The ups of a pseudotype male is figured on plate LIX fig. 22 of Holland's 1931 Butterfly Book. The actual type is in CM (=Carnegie Museum) (photo sent by John Rawlins).
- 1e. *mylitta thebais*
- 2a. *pallida pallida*
- 2b. *pallida barnesi*
- 3a. *orseis orseis*
- 3b. *orseis herlani* Bauer 1975, type in David Bauer collection (Miller and Brown 1981), holotype male and allotype male figured by Howe (1975, plate 45).

B. *tharos* species-group

- 4a. *tharos riocolorado*
- 4b. *tharos tharos* (Drury) 1773, type sold and lost, but may be in Macleay collection in Macleay Museum, Sydney Australia, because Macleay bought many specimens from Drury.
= *distincta* Bauer, 1975, type LACM (=Natural History Museum Los Angeles County) (Ferris, ed., 1989).
= *marcia* (W. Edwards) 1868 (preprint issued 1868, so Higgins' [1981] date 1869 is wrong), invalid lectotype=pseudotype CM, labeled "marcia male / A. Hunter / type" (photo proves lectotype is female, not male), TL Hunter, Greene County, New York. This lectotype is declared invalid below, because it cannot be identified to species, does not fit the original description, is the opposite (and unidentifiable) sex, was collected at the fringe of the stated range, and was probably collected after the original description so could not be a valid syntype or lectotype. TL declared in current paper to be Coalburgh, Kanawha Valley, West Virginia.
- 4c. *tharos orantain* (or *cocyta orantain*, or *orantain orantain*) Scott 1998 (current paper), holotype BMNH, TL Barr Lake, Adams County, Colorado.
- 5a. *cocyta diminutor* (or *orantain diminutor*) Scott 1998 (current paper), holotype BMNH, TL NE Conger, Freeborn Co., Minnesota.
- 5b. *cocyta selenis* (Kirby) 1837, type evidently lost, TL Cumberland House, 54⁰ N Lat., Saskatchewan.
= *pascoensis* Wright 1905, lectotype CAS, TL Pasco, Franklin County Washington.
- 5c. *cocyta cocyta* (Cramer) 1777, neotype AMNH, TL Black Rock, Cape Breton, Nova Scotia (locality of neotype)
= *arctica* dos Passos 1935, holotype AMNH (=American Museum Natural History), TL Table Mtn., Port au Port, Newfoundland.
- 6a. *batesii batesii*
- 6b. *batesii lakota*
- 6c. *batesii apsaalooke*
- 6d. *batesii anasazi*
- 7a. *pulchella pulchella*
- 7b. *pulchella deltarufa* Scott 1998 (current paper), holotype BMNH, TL N Davis, Yolo County, California.
- 7c. *pulchella montana*
- 7d. *pulchella owimba* Scott 1998 (current paper), holotype BMNH, TL Pattee Canyon, Missoula County, Montana.
- 7e. *pulchella tutchone*
- 7f. *pulchella camillus*
- 7g. *pulchella shoshoni*

C. *phaon* species-group

8. *pallescens*
- 9a. *picta picta*
- 9b. *picta canace*
- 10a. *phaon phaon* (W. Edwards) 1864, neotype CM, TL St. Simons Island, Glynn County, Georgia.
- 10b. *phaon jalapeno* Scott 1998 (current paper), holotype BMNH, TL Mesa, Maricopa County, Arizona

10c? *phaon maya* Hall 1928, holotype Booth Museum (Brighton, England), TL Lake Amatitlan 1260 m, Guatemala. Perhaps a subspecies, as the holotype is very dark according to Gerardo Lamas Müller. Or, the holotype could merely be aberrant.

INDIVIDUAL SPECIES ACCOUNTS

A. *PHYCIODES MYLITTA* SPECIES-GROUP

CHARACTERS (in addition to Scott 1994). The pupal cones in general are wider than those of the *P. tharos* group, although there is some variation in this trait. The cones do seem wider in *P. orseis herlani* and *P. mylitta mylitta* and *P. pallida barnesi*, while they seem not quite as wide in *P. pallida pallida* (and the cones seem a little lower in this subspecies), and only some individuals seem wider in *P. orseis orseis* and *P. mylitta arizonensis*. The one family of *P. mylitta arizonensis* reared had small transverse dorsal ridges on A2-3, which are generally lacking in other *Phyciodes* taxa.

1B. *PHYCIODES MYLITTA ARIZONENSIS* BAUER

Early stages have now been reared, and seem to closely resemble published accounts of subspecies *mylitta*.

HOSTPLANTS. Adults associated with *Cirsium vulgare* and *C. undulatum*, Questa, Taos County New Mexico, 6750', Aug. 13, 1996, female laid 52 eggs **in lab** on *Cirsium incanum* Aug. 15, hatched Aug. 23, reared on *C. incanum*, adults emerged Sept. 21-29, 1996.

EARLY STAGES. SILK WEB. 1st-stage larvae spun an extensive strong silk web over a bend in a leaf in lab by their third day, and most (50) older 1st-stage larvae rested under the web (only 2 were on top of it) and ate the leaf surface under the web; 2nd-stage larvae spun no web in lab. **EGG** yellowish-greenish-cream, after 7 days turning blackish as black heads become visible through clear eggshell, about 20 or perhaps 21 vertical ribs; duration 8 days. **1st-STAGE LARVAE** uniform pale dull yellow, after feeding the green food makes anterior 3/4 of body bluish-green, with no body pattern; when about to molt (when 2nd-stage head creates a bulge in prothorax) a weak pattern of light-brown lines and bands appears including a middorsal line and a line near it and a subdorsal band and a sublateral line; pinaculi brown, setae black; collar and suranal plate and head blackish; duration 4 days. **2nd-STAGE LARVAE** gray-green, with some dark-brown bands, including a middorsal dark-brown line, a row of dark-brown dashes, a creamy subdorsal band, a wide dark-brown band, some slightly-creamy dots in a row above level of spiracles, a creamy lateral band edged below by a weak sublateral brownish line; the lateral BL1 scoli creamy, the other (dorsal and subdorsal) scoli brown; older (molting) 2nd-stage larva tan, a dark-brown heart-band joins dark-brown middorsal BD1 scoli, subdorsal dark-brown BD2 scoli lies in a tan circular area between a dark-brown hourglass-shaped spot (one spot between each scoli) so that subdorsal area is dark-brown except for the circular area, the cream subdorsal band present in *Phyciodes tharos* group is absent and represented only by a creamy incursion into the neck of the hourglass spot, a dark-brown continuous line above the BSD dark-brown scoli edges the bottom of the hourglass spots, the spiracular/supralateral area is dark-brown except for a square tan area around BSD scoli, a tan line is above a light-brown line edging tops of BL1 creamy scoli, a lateral cream band includes BL1 scoli, a light-brown sublateral area; head black. **3rd-STAGE LARVAE** almost solid black, with some cream markings, specifically a narrow cream line beside black heart-band that touches lateral edge of BD1 scoli, two small V-shaped cream checks (or joined into one mark shaped like the greek letter pi) in front of BD2 scoli and two more behind this scoli, a long cream dash that has spiracle at its center, a fairly-wide lateral cream band includes BL1 scoli and above this scoli angles dorsoposteriorly to a point at spiracle, this wide lateral cream band is interrupted briefly near posterior edge of segment, a cream dash ventroposterad of spiracle widens as it nears the band interruption; upper three scoli (BD1-2, BSD) blackish, BL1 scoli cream; legs blackish; head blackish, with a small cream crescent just dorsoposterior to upper eyes, a cream dash on vertex (side of top of head) as in *P. tharos*. **4th-5th-STAGE LARVA** same as mature larva but BL1 scoli orangish-tan. **MATURE LARVA** black with a few scattered tiny cream or tan dots, except dark-brown on side of body (between spiracles and BL1 scoli), and there are various cream markings, including a very weak cream subdorsal band running between BD2 scoli consists of a few tiny cream dots, a tiny dash of brownish-orange immediately behind each BD2 scoli (as part of the cream subdorsal band), a row of cream dots runs above spiracles and edges the top of the dark-brown area, a cream ring surrounds each spiracle, some cream dots occur in the dark-brown area, an irregular lateral cream band edges the bottom of the dark-brown area and connects bottom of BL1 scoli, BL1 scoli and ring around those scoli are brownish-orange (the dorsal BD1-2 and BSD scoli are black), a blackish area is below the lateral cream band, underside blackish-brown, collar and suranal plate and proleg plates and legs black, the tiny SV scoli (above level of prolegs) are black with brownish-orange tips; head black (and frontoclypeus black), except a cream crescent dorsoposterad of upper eyes, and the usual cream stripe on vertex (which often has a satellite spot at its anterior end on upper part of forehead). The mature larva has the same basic pattern as the

tharos-group, but the dorsal pattern is obscured by the blackening of the body. Mature larvae seem very similar to Charles Dammers' painting of California subspecies *mylitta*, except the underside is darker than the drawing. Duration of larval stages about 22 days.

PUPA. About 50% of pupae are light-brown, some are slightly-grayish brown, some are slightly-orangish tan, some pupae are tan, some are medium-brown, and one pupa is blackish- (lightened only by some dark-brown areas on wing base and near wing margin and some dark brown mottling dorsally--this pupa was live and produced an adult and was not blackened by disease); wing cases are very weakly mottled, only the discal spot is present but it is weak, wings have the usual ~6 tiny postmedian creamy dots and tiny marginal creamy dots; pattern details are the same as those of the *tharos*-group, including a row of brown dots near middorsal axis, a dorsolateral row of brown dots on abdomen (one toward front of segment, one near rear), a weak row of brown dots anteroventral to spiracles on A5-9, a ventrolateral row of brown dots on abdomen, another supraventral row of brown dots on abdomen, a midventral row of brown dots on abdomen; the ridges and wing base have the usual anterior brown edging and posterior brownish-orange edging; the anterior rim of emergence flap (on head) has the usual brown anterior edging and creamy rim edge, side of T1 has usual paler area; appendages and antenna checkering as usual; the usual weak middorsal ridge occurs on A2-4 as in *tharos*; the cones on abdomen are moderate in height (like those of *P. batesii*) and are not much wider than *tharos*, but the transverse dorsal ridges on abdomen are fairly weak (smaller than those of *P. tharos/coccyta*, a little smaller than those of *P. batesii*, and slightly larger than those of *P. pulchella*), the ridge on A4 is strongest, A5-7 have fairly weak ridges, and A2 has a weak ridge, A3 a fairly weak ridge (these ridges on A2-3 are present on more than 90% of pupae of the single family reared, a rather unique trait because A2-3 ridges are nearly always absent in other *Phyciodes*, for instance they are absent in the *tharos*-group, absent in *P. mylitta mylitta*, absent in *P. orseis*, absent in *P. pallida barnesi*, and present but weak in only some *P. pallida pallida*). Duration of pupa 10-11 days; from oviposition to adult 40.5 days in lab.

1D. *PHYCIODES MYLITTA ARIDA* (SKINNER) 1917

Scott (1994) surmised that the male figured and labeled as the "type" of *arida* by Holland (1931 pl. LIX fig. 22) was the true type, because Holland worked in the Carnegie Museum where the type was stated to be located. However, a male labeled "type" in Carnegie Museum (a white label states "Cochise Co. May. Arizona", a red label states "type Melitaea arida Skin. 7020") is not the same specimen as Holland's figure, based on antenna position and wing details on a slide of it kindly sent by Dr. John Rawlins. I will consider the male in the slide to be the true type; it closely resembles both the male figured by Holland and the male from Morelia figured by Scott (1994), except that it has the median band of ochre uph spots narrower than Holland's and Scott's figures. Scott's figure differs from the other two by having the postmedian upf spots a little larger. But all three males seem to represent the same taxon, as all have the forewing margin not indented much, the ups rather dark, and the hindwing margin less scalloped. So this type fits the figure and description and concept of Scott (1994). Gerardo Lamas Müller (pers. comm.) states that a female syntype labeled "type" in Carnegie Museum resembles *thebais*; I have not seen it, but I will ignore it and treat the above male as the true type.

Further field collecting is needed to determine whether *arida* is a good subspecies or species; it may prove to be just a local phenotype from Morelia and vicinity that is intermediate between *mexicana* and *thebais*.

2A. *PHYCIODES PALLIDA PALLIDA* (EDWARDS)

EARLY STAGES. LARVAL FEEDING. Just before diapause (4th-stage, and evidently also 3rd-stage) larvae mostly rest on upperside of leaves, and eat the leaf surface, leaving craters on the leaf surface (usually on the upperside) that do not go through to the other side. **DIAPAUSE STAGE.** 4th-stage larvae diapause, including at Indian Peak, Jefferson County Colorado, Sept. 5, 1991 (not 3rd-stage as stated in Scott 1994 page 17).

2B. *PHYCIODES PALLIDA BARNESI* SKINNER

DIAGNOSIS. Older larvae are evidently much blacker than those of subspecies *pallida*, based on my western Colorado larvae and two descriptions from Oregon/Washington, including a new description from Washington by Jonathan Pelham. Adults, however, can seldom be identified.

HOSTPLANT RECORDS. Reared from *Cirsium undulatum*, Wawawai, Whitman County Washington by Jonathan Pelham (pers. comm.). Two ~3rd-stage larvae found on *Cirsium neomexicanum* leaf tops, Sewemup Mesa, Montrose County Colorado, 5000', July 18, 1996, reared in lab on *Cirsium incanum*, 2 adults emerged Aug. 9, 1996. *Cirsium arizonicum* has been documented as a hostplant in Washington Co. Utah by Clyde Gillette (pers. comm.); this thistle is roughly similar to *C. undulatum* but has long spines and red flowers.

EARLY STAGES. OLDER-MATURE LARVA (Sewemup Mesa Colorado), some heads have a small ochre spot on frontoclypeus, which is new for the species. Color photos of ssp. *barnesi* and *pallida* are in the CD-ROM version of my book (Scott 1997). **OLDER-MATURE LARVA** (Wawawai Wash, reared from *C. undulatum* by J. Pelham, who sent description) black, with unevenly-distributed small cream-white spots, a longitudinal subspiracular band formed by intersegmental white crescents to the 2nd thoracic segment; another pale supraspiracular line is less defined and broken; the subspiracular row of spines have orange at their base; supraspiracular spines have little or no orange at their base; the dorsal spines and the adjacent subdorsal spine row have large orange spots at their bases; these [subdorsal scoli] are connected to each other by a white line (composed of concentrated white dots); these also connect with the dorsal orange spot row; middorsal line black, punctuated by the orange spot row and flanked by concentrated white spots that form two parallel creamy dorsal lines [weak or absent on Mesa County larvae]; head black with faint orange near mandibles and faint pale crescents dorsally. The Washington older larva differs from Colorado *barnesi* larva by having a line of cream dots beside the heart-band.

PUPA in Colorado in 1996 is the same as described by Scott (1994) (uniform fairly-light-brown), except the two young pupae had a moderately-blackish supraspiracular (dorsolateral) band (incorporating the brown dots mentioned by Scott 1994) below a slightly-paler tan band (the remnant of the cream subdorsal band of larva), and had some darker transverse areas on top of abdomen segments. Duration of Colorado male pupa 10 days. **PUPA** (Wawawai Washington) similar to Colorado pupa.

B. *PHYCIODES THAROS* SPECIES GROUP (Tables 1-5)

So many additions and improvements have been made to this group in this paper, that Tables 1-5 of Scott (1994) are revised and repeated here.

4A. *PHYCIODES THAROS RIOCOLORADO* SCOTT

ANTENNA CLUB SHAPE. The antenna club of this subspecies is short (oval) like that of subspecies *tharos* (see below). **RANGE** Now known to occur in Grand, Emery, Wayne, and San Juan Counties Utah, and Mesa, Delta, Montrose Counties Colorado, in lowland weedy habitats, even on a golf course lawn. It occurs all along the warm lowlands of the Colorado River valley as far downstream as Lake Powell, and possibly extends as far downstream as the Grand Canyon. **GENERATIONS.** Evidently three generations (at least late May, late July, late Aug.-early Sept.).

4B. *PHYCIODES THAROS THAROS* (DRURY) 1773 (=“Black-antenna variety”) (Fig. 2)

ANTENNA CLUB SHAPE. The antenna club of *Phyciodes* varies greatly in shape between individuals, from oval (fig. 2) to elliptical (fig. 1), and occasionally even more elongate. Catling (1997) thought that in Ontario, the *tharos tharos* “black-antenna variety” has more club-shaped [oval] antenna clubs than does *P. cocyta*. I examined club shape of all *tharos*-group taxa, and found that they vary considerably in shape, and all have about the same average shape in all taxa (usually elliptical), except that the *tharos tharos* (“black-antenna variety” of Scott 1994) (and subspecies *riocolorado*) does seem to have oval-shaped clubs significantly more often (usually, fig. 2) than do the other taxa. These other taxa have elliptical clubs most often (fig. 1) and oval-shaped clubs sometimes (*P. cocyta* sometimes has clubs that are slightly more elongate than elliptical), whereas *tharos* black-antenna var. and *riocolorado* usually have oval but sometimes elliptical clubs. This is an interesting finding, because even the *tharos* orange-antenna variety (named *P. tharos orantain* below, fig. 1) differs by usually having elliptical clubs like the other taxa and unlike the black-antenna variety (part of the reason why I name the orange-antenna variety a new subspecies below). Other black-nudum taxa have usually-elliptical clubs (*P. batesii batesii*, *P. b. lakota*, *P. pulchella pulchella*, *P. p. camillus*), so the club shape is evidently not genetically linked to the nudum color.

DIAGNOSIS. This subspecies has an oval antenna club. Also, its antenna club nudum is black, though some males are reported to have orangish nudum in northern Ohio and southern Ontario etc., and females sometimes have the entire nudum orangish; the nudum typically has black border and black lattice, while the steps are mostly brown in males and brown or orange (usually orange on distal third of club) in females. In Pendleton County West Virginia, 82% of the apparent *tharos* males have black nudum, 18% orange nudum, while only 17% of females have black nudum, 83% orange nudum (NMNH=USNM series collected by Paul Opler, examined by Adam Porter, pers. comm.) (at the same site all *P. cocyta* have orange nudum). The older larval ground color is darker. In addition there are a few weak traits: the unf black spots (esp. the black median spot on rear of unf) seem to average a little smaller than on subspecies *orantain*; the uph orange area nearly always

has a black postmedian line through it (this line is interrupted in 10-20% of *orantain* males); dark-upf females are rare (occasional in *orantain*); and young larvae may make silk webs slightly less often. It shares various traits with subspecies *riocolorado* and *orantain*, including relatively small size (some Arizona-Mexico males are quite small, and some NE U.S. adults are larger, and the usual individual variation exists), black line crossing the orange uph area on most males, etc. (see the tables). In eastern North America, some males seem to have slightly shorter (more square) forewings. Subspecies *tharos* thus is transitional between *riocolorado* and *orantain* in some traits.

FORM *MARCIA*. Scott (1994) stated that the name *marcia* was a valid name for the orange-antenna variety of *P. tharos*. But examination of the original description, and Paul Catling's recent discovery (Catling 1997) that orange-antenna *tharos* do not prevail in the east, force a reappraisal of the name *marcia*. William Henry Edwards named *marcia* in 1868 (preprint issued 1868, so Higgins' [1981] date 1869 is wrong). F. Martin Brown (1966) designated a lectotype *marcia* in the Carnegie Museum, labeled "marcia male / A. Hunter / type" (however Brown's photo proves the lectotype is female, not male), type locality Hunter, Greene County, New York. The name is nomenclaturally available to be used for a species or subspecies under the ICZN Code (*marcia* is "subspecific", not "infrasubspecific", using the terminology of the Code), and Scott (1994) thought that *marcia* applied to the orange-antenna populations, which someone might eventually treat as a subspecies. But further investigation into the name *marcia* proves that this name cannot apply to the orange-antenna populations, because the original description of *marcia* lists the range as only New York to Louisiana (and the lectotype type locality is New York), whereas the orange-antenna variety *P. tharos orantain* is now known to occur only from Manitoba westward. Furthermore, numerous questions have arisen as to the validity of Brown's lectotype of *marcia*. Both *P. tharos* and *P. cocyta* occur in the Catskills where the locality of the lectotype (Hunter, Greene County, New York) is located, so the lectotype could be either species. Brown's lectotype lacks an antenna (see photo in Brown 1966) so its nudum cannot be examined to determine its species; and the lectotype is a female (not a male as Brown thought) making it difficult to identify (even if it had an antenna); the combination of missing antenna and female sex means that Brown's lectotype cannot be identified as either *tharos* or *cocyta*. Furthermore, Edwards' original description of *marcia* describes its underside as "purple-grey (or pearly-grey in some specimens)", a description that fits only the spring form of *P. tharos*, and does **not** fit Brown's lectotype. Edwards also described the range of *marcia* as New York to Louisiana, and common on the Kanawha River West Virginia (Coalburgh, where Edwards worked as the president of a Coal Company), a distribution that suggests *marcia* should apply to *P. tharos*, not to *P. cocyta* which does not occur in Louisiana or anywhere near Louisiana. Edwards' original description states that the *marcia* male antenna club was fulvous below (black above), suggesting that *marcia* could belong to *P. cocyta*, whose club is orange than that of *P. tharos*, though occasional *tharos* males do have orange nudum in eastern U.S. as noted above, and females of both species vary even more in this trait. But Edwards' described the male uph as having "a line more or less distinct expanded on costal margin into a long triangular patch" basal to the six submarginal black spots, which fits *P. tharos*, **not** *P. cocyta*. And Edwards described a "greyish-white crenated line from one angle to the other" on uph submargin, a trait more typical of *P. tharos*. Edwards described the male wing expanse 1.3 to 1.5 inches (=33-38 mm), which translates to a forewing length of 17-19 mm, which would match a large *P. cocyta*. But Edwards described the female wing expanse of 1.7 inches (=43 mm), which is equivalent to fw length of about 24 mm, and this is far larger than any *Phyciodes tharos/cocyta* I have ever seen (43 mm is nearly 5 mm larger than the wing expanse of the largest *cocyta* female that I possess, even if the forewings were mounted in airplane-wing position to achieve maximum wingspan). Therefore Edwards' measurements are much too large, and cannot be trusted. Worst of all, Brown's lectotype was probably collected after *marcia* was named so could not be a valid lectotype (a lectotype by definition must be a syntype--a specimen that was examined by the original describer when he described the taxon): the specimen was probably not a syntype, because it was collected at Hunter in New York (a small town in the Catskills probably named for A. Hunter or his relatives) in 1875 or later, as Edwards (Can. Ent. 9:1-10, 51-) mentioned that he went to the Catskills only in 1875, and a quick perusal of Edwards' other publications suggests that he may not have gotten Catskills specimens as early as 1868 when *marcia* was named. Brown (1966, p. 433) himself stated "that it [this lectotype] belonged to the original type series cannot be proven or disproven now. I accept it as Edwards's selection for lectotype." Brown proved that William J. Holland (who bought Edwards' collection) often asked Edwards to write various "type" labels and send them to Holland, and Holland would then attach them to specimens that were not the actual types; thus Brown documented numerous specimens labeled "type" in the Carnegie Museum that are actually pseudotypes, not true types (Brown 1966 mentioned nine pseudotypes among the Melitaeinae alone, and there must be nearly a hundred for all the butterflies named by Edwards). Thus Brown's *marcia* lectotype could just be another pseudotype, even though it is labeled "type." Therefore, there are numerous reasons to believe that Brown's lectotype is invalid, as it does not fit the description and lacks diagnostic parts and cannot be identified to species and probably was not even a syntype. I could declare this specimen to be a neotype, but considering that it is a female and lacks abdomen and lacks the diagnostic antenna so cannot even be identified to species, it should not be declared to be anything except trash. Declaration of lectotypes/neotypes must be done to clarify--not confuse--the nomenclature. Therefore I hereby declare Brown's *marcia* lectotype to be **INVALID**. A *marcia* lectotype **should** be a male specimen of carefully-identified *P. tharos* from

Coalburgh West Virginia in the Carnegie Museum, with intact antennae and abdomen, which has the unh strongly mottled with brown and pearly spots. But because *marcia* obviously is the infrasubspecific mottled-unh spring form of *tharos*, a lectotype is not needed now. I hereby designate the type locality to be Coalburgh, Kanawha Valley, West Virginia.

RANGE. The range of the “black-antenna variety” as stated by Scott (1994) was too small. Catling (1997) has found that throughout southern Ontario (north to the northern limits of the species’ range at Ottawa, where it may be a recent immigrant because all records are after 1990) and adjacent extreme southern Quebec and northern New York, the antenna club nudum is generally black, not orange as Scott (1994) wrote. This area is large and extends west to the Michigan state line, suggesting that orange-antenna *tharos* does not occur in the east. Scott concluded that *tharos* in the Northeast had orange antennae based on Charles Oliver’s statements in letters (pers. comm.) that some Pennsylvania colonies have orange antennae. And Adam Porter reports (pers. comm.) that northwestern Ohio *tharos* usually have orange antennae also. However I have not seen these specimens, and these orange-antennae populations may represent *P. cocyta diminutor* (named below) rather than *tharos*, so further research is necessary. Thus black-antenna *tharos* evidently occupies southeastern Canada (including southern Ontario and extreme southern Quebec) and eastern U.S. as far west as southern Minnesota (Freeborn County), Iowa (Franklin, Story, Pottawattamie Counties), eastern Neb. (Omaha- Lincoln southward; although there is some variation in antenna color in the eastern 2/3 of Neb. esp. among females), eastern and south-central Kansas (Barber, Montgomery, Elk, Douglas Counties), most of Okla. (Woods County), south to the Gulf coast, and westward across Texas to Arizona and southeastern California, south to central Mexico. The orange-antenna *P. tharos orantain* (named below) is evidently limited to Saskatchewan & Alberta, southward through the Dakotas and Montana to Neb. (most of the state), Wyoming, Colorado, extreme western Okla., and probably NE New Mexico; and it may also occur in southern Manitoba, as Klassen et al. (1989) state that the antenna clubs in Manitoba are usually black with some orange ventrally. The presumed blend zone between the black- and orange-antenna subspecies evidently extends roughly from near Amarillo Texas to NE Neb., then due north to Winnipeg Manitoba; the exact course of this blend zone of course needs more investigation.

NUMBER OF GENERATIONS. *P. tharos* always has more than one generation. There are three generations in southern Ontario-extreme southern Quebec (peak populations in early June, mid July-early Aug., and late Aug.-early Sept.; and extreme dates May 22-Oct. 23, Catling 1998a), evidently three in southern Minnesota (late May-Sept.), and there may be six or more generations in southern Florida (where adults have been recorded every month of the year) and Mexico.

HOSTPLANTS. Oviposition of at least three egg clusters of 52-64 eggs on undersides of leaves of seedling *Aster ciliolatus* at Aylmer in Quebec and Metcalfe and Dwyer Hill Siding in Ontario, reared to adults on *A. ciliolatus* (Paul Catling 1997; this Catling host was previously mentioned by Jeffrey Crolla 1996, Trail and Landscape 30:51-57). Adults associated with *Aster pilosus* and *Aster oolentangiensis* (= *azureus*) at several other Ontario sites (Catling 1997). Adults associated with *Aster simplex*, 3 mi. NE Alden, Freeborn County Minnesota, June 11, 1995, June 20, 1996. Theodore Mead also found larvae in nature in the Catskills New York on *Aster novae-angliae* (Can. Ent. 7:161), which would be a valid hostplant record, **unless** the larvae found were actually *P. cocyta*, so the record is uncertain.

EARLY STAGES described by Scott (1994). **SILK WEB.** Young larvae evidently never make extensive silk webs (according to W. Edwards, Can. Ent. 9:1 and 16:109, and Oliver 1982), whereas some families of subspecies *orantain* do make extensive webs. **DIAPAUSE STAGE.** 4th-stage (Scott 1994). **EGG.** Clusters of 33 and 56 laid in eastern Ontario (Catling 1998a).

MATURE LARVA very dark in southern Minnesota (brownish-black, Scott 1994), the dorsal brown area as dark as subdorsal band (whereas it is paler in most *tharos orantain*), the subdorsal cream band narrow and somewhat interrupted in most larvae (band varying from strong [90% complete and 10% interruptions] in some larvae to nearly absent [30%] in other larvae); larvae are darker than those of *P. tharos orantain*; details in Scott (1994). In Ontario, Paul Catling (pers. comm.) has found that older larvae are also very dark, dark-chocolate-brown with the subdorsal creamy band weak. In Pennsylvania, Oliver (1979) stated that *tharos* larvae were dark-chocolate-brown. So this dark larva is evidently characteristic of black-antenna subspecies *tharos*, though more rearing needs to be done (esp. in southeastern and southern U.S.) because *Phyciodes* are rather variable and individual families often differ greatly, apparently genetically. **DURATION** of eggs 6-7 days, egg-larvae-pupae 32 days in Ontario (Catling 1998a).

PUPA in southern Minnesota (Scott 1994) orange-brown, except one pupa brown-orange (the wings slightly reddish), wing mottling weak except for moderate brown discal cell spot.

4C. PHYCIODES THAROS ORANTAIN SCOTT 1998
(OR *PHYCIODES COCYTA ORANTAIN*,
OR *PHYCIODES ORANTAIN*),
NEW SUBSPECIES
(Figs. 1, 3-4)

DIAGNOSIS. This subspecies was called the “orange-antenna variety” by Scott (1994), but is here renamed as a separate subspecies, because several new distinguishing characters have been

discovered: Its antenna club (fig. 1) is usually elliptical (longer than oval--technically an ellipse can range from very elongate thus rod-shaped, to circular, depending on the lengths of its two perpendicular axes, but here I will use the word elliptical in its most popular usage, to mean more elongated than oval), versus most often oval in subspecies *tharos* (fig. 2). Its antenna club nudum is orange in males of course, versus black in subspecies *tharos*. Its older larva has a paler ground color than the blacker *P. tharos tharos*. Young larvae construct conspicuous silk webs sometimes, evidently more often than subspecies *tharos*. The black postmedian line crossing the orange uph patch averages a little weaker than subspecies *tharos*, so a greater percentage of males resemble *P. cocyta* by having an undivided orangish uph patch. It did not seem reasonable to name a new subspecies based on only the color of the antennal nudum, but these other differences seem valid, so it seems worth naming now. As noted above, the name *marcia* does not apply to this taxon (nomenclaturally, it belongs to the spring form of subspecies *tharos* from eastern U.S.), so this taxon lacked a name until now. **ORIGIN OF NAME:** the name *orantain* is formed from ORange-ANTenna plAINs dweller, as this butterfly occupies the colder parts of the Great Plains. **TYPES** all from type locality Barr Lake, Adams County Colorado (the privately-owned cattle pastures and ditches below the dam of this reservoir), holotype and allotype (both British Museum Natural History) from type locality emerged Oct 11, 1985, numerous paratypes reared and collected from this locality (*P. cocyta* does not occur here, and only occurs in the Front Range more than 30 km to the west).

PHYLOGENETIC ORIGIN. One interesting speculative theory is that *orantain* does not belong to *P. tharos* at all, and is actually a Great Plains subspecies of *P. cocyta*. This theory would explain why it is basically allopatric to *cocyta*, as it occurs on the northern Great Plains while *cocyta* occurs in the mountains nearby (Rocky Mts., Black Hills, Cypress Hills) and in the Canadian forests. The theory would also explain Scott's (1986) otherwise inexplicable finding that this Great Plains taxon and *P. cocyta* are not reproductively isolated in nature in central Colorado (released reared univoltine *cocyta selenis* females mated with wild *orantain* males in nature and produced numerous reared hybrid adults). This theory would explain its orange antenna nudum, its elliptical antenna club, its somewhat-more-frequent possession of a large undivided orange uph space (like that typical of *cocyta*), and its paler larval color.

Another even more speculative theory is that *Phyciodes orantain* might be a full species—distinct from *P. tharos*—and contains a subspecies, namely the multivoltine *P. orantain diminutor* that ranges from southern Minnesota to southeastern Manitoba and eastward to northern New York and southward. This theory would explain the limited sympatry of *orantain* with *cocyta selenis* in the west, and would explain the sympatry of *diminutor* with *cocyta selenis* in Ontario. But orange-antenna *tharos* and multivoltine *cocyta* are reported sympatric in southern Manitoba (Klassen et al. 1989), so if the former is *orantain* and the latter is *diminutor* they cannot be the same species. But the ranges of each subspecies in Manitoba should be investigated further, as--for instance--*orantain* perhaps occurs only in southwestern Manitoba and *diminutor* only in southeastern Manitoba.

The two taxa *orantain* and *diminutor* do share the elliptical antenna club, orange antenna nudum, and a paler mature larva than that of *P. tharos tharos*. But *orantain* is similar to *tharos* in adult size, the black line dividing uph center, the stronger uph pale submarginal line, pupa color, pupal wing streaks, and color of BL1 scolus base. The mature larva of *riocolorado* is paler like *orantain*, even though *riocolorado* is clearly derived from *tharos*. And the orange or black color of the antenna nudum does vary within other species such as *P. batesii* and *P. pulchella*. So, when the characters supporting one placement of *orantain* are compared to those supporting the other placement, most support placing it into *tharos*. But perhaps some characters are more important than others.

Paul Catling (pers. comm.) suggests that *orantain* is a subspecies of *cocyta/diminutor*, as it has the important trait of the elliptical antenna club shape of *cocyta*, and shows several other similarities to *diminutor*. And admittedly, I have listed *orantain* as a ssp. of *tharos* here partly because of taxonomic inertia.

Further research will have to be done to investigate these speculations. I place *orantain* in *P. tharos* now, because more characters favor that placement, and because of the slight sympatry between *orantain* and *cocyta* at the edge of the range of *orantain* from southern Alberta to Larimer County Colorado (they overlap slightly at Horsetooth Mountain Park, Lory State Park, and Turkey Creek in Larimer County, Paul Opler, pers. comm.), east to southwestern Manitoba and northwestern Nebraska (in the Pine Ridge of northwestern Neb. *orantain* is common, and *P. cocyta* is usually scarce but is sometimes common), and the reported sympatry between *orantain* and *tharos* in southern Manitoba.

Ignoring such speculations, the characteristics of *orantain*--some of which are transitional between *P. tharos tharos* and *P. cocyta*--are most easily explained as historical relicts from its distribution between the ranges of *P. tharos tharos* (black antenna) and *P. cocyta*. Some of its intermediate traits--formed when all these taxa were one species ranging across the entire area--remained after the genes for presumed reproductive isolation spread and divided the prototype into several species *tharos* and *cocyta*. The other simple (and similar) explanation, is that introgression from occasional hybridization spread genes for antenna characters etc. that happen to be linked to traits useful for adaptation to the Great Plains area.

Apparently much work still remains to be done in this group. The eastward range of *orantain* needs to be studied (in Manitoba for instance), and more series must be studied to determine

whether the antenna color and shape and larval ground color etc. intergrade into the black-antenna subspecies *tharos* as would be expected if they are subspecies, and as they seem to intergrade now based on small samples (Scott 1994 noted that northwestern Nebraska males have the antenna nudum slightly less orange than those from westward in Colorado etc., but the nudum remains orange eastward in Neb. toward the eastern end of the state, and then black antennae start to predominate in eastern Neb.). And the relationship between *orantain* and *tharos* should be studied where they probably meet in central New Mexico, Oklahoma, Kansas, Nebraska, etc. northward. The multivoltine ecotype of *P. cocyta* should be studied further, in order to determine its relationship to the univoltine *cocyta* ecotype to the north and to this orange-antenna “*tharos*” *orantain* taxon to the west. The immatures of *P. tharos tharos* (black antenna) should be studied in more families, as I have studied them only from one location in southern Minnesota (although Paul Catling has reported larval ground color from southern Ontario, and Pennsylvania larvae are also stated to be darker), and subspecies *tharos* has not been reared from southern U.S. or Mexico.

RANGE. As noted above, *orantain* does not occur in eastern North America, and evidently occurs only in the colder part of the Great Plains (the north, and high-altitude west), from southern Manitoba (where it is probable in southwestern Manitoba and perhaps intergrades with subspecies *tharos* in southeastern Manitoba) and Saskatchewan westward to Alberta, southward through Montana and the Dakotas to Wyoming, Neb., Colorado, extreme western Okla., and probably NE New Mexico. I have a male that is probably this from Sweet Grass Co. Montana (Swamp Creek Road, 5400 feet, July 2, 1966) but might possibly be an odd *P. cocyta*. It occurs over all of South Dakota (I have examined adults from Fall River, Pennington, Jackson, Hughes, Spink, Deuel Counties). It occurs over most of Neb., specifically the counties of Sioux, Sheridan, Lincoln (some have black nudum), Dawson (some have black nudum), Greeley & Merrick (half the adults from these two counties have a little brownish shade on the orange nudum), and Cedar. Then the subspecies start to blend in eastern Neb. near Iowa (orange and black nudums are about equally common in Stanton County, two females from Platte County have one black and one orange nudum, in Seward Co. one male is orange the other male mixed orange/black). Extreme SE Neb. evidently has mostly black nudum so is ssp. *tharos* (Dodge Co. has a female with black nudum, Lancaster Co. two males and one female with black nudum and one female with orange, Jefferson Co. one male with black nudum, Gage Co. one female with black nudum). Adam Porter reports some mostly-orange-antenna *tharos* in northwestern Ohio, and Charles Oliver reported orange-antenna populations in Pennsylvania, but further work will be necessary to decide whether these are truly variants of subspecies *tharos* or are *P. cocyta diminutor*.

Subspecies *orantain* is one of the few butterflies endemic to the Great Plains, which has a rather depauperate butterfly fauna. The most notable plains endemic is *Hesperia dacotae* in the NE Great Plains (mixed-grass and tall-grass prairies). *Lethe eurydice fumosus* occupies plains wetlands (and is now common in roadside ditches). *Oarisma powesheik* occurs in the NE tallgrass prairie and ranges eastward to Mich. *Speyeria idalia* is basically a plains (mixed-grass and tall-grass) species, which expanded to the Atlantic in meadows and pastures when the eastern deciduous woodland was heavily logged, and is now retreating westward as the forest is regrowing and development proceeds and its habitat is becoming fragmented into too-tiny remnants for this fast- and far-flying species (this species cannot exist permanently in tiny remnants because adults fly far and cannot find their way back). *Chlosyne gorgone* is to a considerable extent a Great Plains species, but ranges beyond especially eastward (where it is reduced to a few local colonies at its eastern limits in Ontario and Georgia).

NUMBER OF GENERATIONS. There are two generations northward in southern Alberta (May 3-Aug. 28), Saskatchewan (May 24-Aug. 10), and southern Manitoba (June 5-Aug. 27), and about three southward in Colorado (May-Sept.).

HOSTPLANT RECORDS (in addition to Scott 1994). Three males associated with *Aster ascendens* (= *adscendens*) (common, the probable host) and *Aster glaucodes* (common, but doubtfully a host) and *Aster foliaceus* (frequent along creek, probably not a host); west of Hidden Basin Campground, Bighorn County Wyoming, Aug. 17, 1993-Aug. 1-2, 1995.

EARLY STAGES. These were detailed by Scott (1994) for “orange-antenna variety.” Young larvae of occasional families make extensive silk webs.

5A. *PHYCIODES COCYTA COCYTA* (CRAMER) 1777 (= *arctica* dos Passos 1935)

DIAGNOSIS. Newfoundland-Nova Scotia populations have only one yearly flight, are smaller than the boreal univoltine ecotype (*selenis*), have a darker-orange uns, and often have more brown and white unh mottling, as noted by Scott (1994). But size and unh mottling are strongly influenced by temperature/photoperiod, so many more specimens should be examined from eastern Canada to determine whether this taxon is a distinct subspecies, although the darker unh color would seem to be a consistent difference at the current time. The *cocyta* type locality is Nova Scotia, so this is the nomenclaturally “typical” subspecies. It flies from late June to late Aug. in a single generation in Newfoundland, and flies June 12-Aug. 11 in Nova Scotia (with sometimes a partial second generation in the fall, Ferguson 1954).

**5B. *PHYCIODES COCYTA SELENIS* (KIRBY) 1837
(UNIVOLTINE ECOTYPE)**

DIAGNOSIS. This boreal forest Canadian and Rocky Mts. variety has only one yearly flight, and is large in size. The name *selenis* is available for it. The Rocky Mts. populations are also large and univoltine, and wing pattern appears similar to Canadian populations, so the name *selenis* can be used for both areas. It might have a weak second generation in southern Ontario (Paul Catling, pers. comm.), although this generation might actually be *P. cocyta diminutor* (described below).

RANGE. The dot in Warner Mts. NE CALIFORNIA on the map of Stanford and Opler (1993) is based on only one specimen in an eastern museum, so I will consider it a mislabeling **ERROR**, because the Warner Mts. have been collected enough to find this species if it were actually there. The range in southern Wyoming-western Colorado-Utah-Arizona-northwestern New Mexico is somewhat uncertain due to confusion in the past with *P. batesii anasazi*. In WYOMING, this ecotype occurs in the major mountain ranges, including the major ranges in the northwest, the Bighorn Mts. in the north, and the Laramie Range and Snowy Range in the south. On the western slope of COLORADO, *cocyta* is evidently limited to montane areas with much aspen: I have seen *cocyta* from Summit, Grand, Jackson, Routt, Eagle, Gunnison, and Garfield (? Grizzly Crk.) Counties. A prior record from Mineral County is probably correct, while former county records from lower-altitude areas (including county records from Mesa, San Miguel, Dolores, Montezuma, and La Plata Counties), must be reexamined because they may include *anasazi* or *cocyta* or both species. What some people thought was a different subspecies of *cocyta* from western Colorado/Utah has mostly proven to be *P. batesii anasazi*. In UTAH, I have seen probable *cocyta* from Morgan County (1 male, 10.1 mi. south of Morgan, June 11 1986, Ray Stanford) and Wasatch County (1 male, 12 mi. north of Heber City, June 11, 1986, R. Stanford), although a confident identification will have to await more specimens or reared families. In northern NEW MEXICO I have seen adults from the mts. of Rio Arriba, Sandoval, Union, and Colfax Counties. I have not seen adults from the White Mts. ARIZONA, though the absence of the *P. batesii anasazi* host (*Aster glaucodes*) there probably means that reported specimens from the White Mts. are *P. cocyta*.

HOSTPLANT RECORDS (in addition to Scott 1994). Adults associated with common *Aster laevis* var. *geyeri* (although one clump of another *Aster* species with blue flowers and pointed leaves was found along road), Tongue Canyon, Sheridan County Wyoming, Aug. 1, 1995. Adults associated with *A. l.* var. *geyeri*, Mosier Gulch Picnic Area, Johnson County Wyoming, Aug. 4, 1995. Mature larva found rolled in ball at very base of *A. l.* var. *geyeri* that had eaten spots on ~6 of 20 leaves, pupated June 18, male emerged June 28; several other clumps had eaten spots; Tucker Gulch, Jefferson County, Colorado, June 15, 1995. Adults associated with *A. l.* var. *geyeri*, near Indian Creek Campground, Douglas County Colorado, July 6, 1995. ~Three 2nd-stage larvae found on leaf uns ~30 cm up on 50 cm plant; ~80 1st-stage larvae found under leaf ~25 cm up on 50 cm plant; ~10+ older 1st-stage larvae found under leaf curled with strong silk web, ~40 cm up on 60 cm plant; all on *A. l.* var. *geyeri*, Tucker Gulch, Jefferson County Colorado, July 25, 1996. 35 2nd-stage larvae found under *A. l.* var. *geyeri* leaf ~25 cm up on 40 cm plant (much silk web and 1st-stage head capsules found on 1 cm² of this leaf uns); Tintytown, Jefferson County Colorado, July 31, 1996. Cluster of 2nd-stage larvae found 60 cm above ground on 75-cm-tall plant, cluster of young larvae found ~55 cm above ground on 70 cm plant, all on *A. l.* var. *geyeri*, reared to adults; Tintytown, Jefferson County Colorado, Aug. 13, 1997. Three 2nd-stage larvae (25 cm up on 45 cm plant) found on *A. l.* var. *geyeri* leaf uns (leaf curled under due to moderate silk web at curled spot); Tintytown, Jefferson County Colorado, Aug. 8, 1996. ~35 2nd-stage larvae found on *A. l.* var. *geyeri* leaf uns, with much silk web; start of Rollins Pass Road, Gilpin County Colorado, 9400', Aug. 5, 1996, reared on *geyeri*, adults emerged Sept. 1-9, 1996; pupal ridges only moderate in size (few large, some small). ~25 2nd-stage larvae found on uns of 4 leaves of a 15-cm-tall basal rosette plant (the eggshells were 4 cm above ground); egg cluster of 97 eggs (40 still present, 57 eggs missing—evidently eaten by some unknown predator such as ants—but their former presence marked by 57 dark-green indentations on the leaf surface noticeable using a microscope) found on leaf uns 40 cm above ground on 85-cm-tall plant; egg cluster of 97 eggs (70 present, 27 indentations of former eggs present) found on leaf uns 20 cm above ground on 95-cm-tall plant; cluster of 42 eggs found on leaf uns 3 cm above ground on 40-cm-tall plant; cluster of 61 1st-stage larvae (a little silk web present made by newly-hatched larvae) found on leaf uns 45 cm above ground on 60-cm-tall plant; cluster of 68 1st-stage larvae found on leaf uns 37 cm above ground on 75-cm-tall plant (a strong sheenlike silk web present over eggs); all on *A. l.* var. *geyeri*; all southwest of Morrison, Jefferson County Colorado, June 30, 1997. ~14 larvae (two 1st-stage, 12 2nd-stage) found on uns of about six *A. l.* var. *geyeri* lower leaves (3-10 cm above ground on 35 cm plant), reared to identifiable older larvae; NNE Idledale near pass, Jefferson County Colorado, Aug. 8, 1997. *A. l.* var. *geyeri* plant 60 cm tall mostly defoliated by now-absent larvae; Tintytown, Jefferson Co. Colo., Sept. 4, 1997.

EARLY STAGES were described by Scott (1994) based on extensive material from the Colorado Front Range. **EGG.** Eggs are laid on underside of leaves, mostly toward the upper middle of the plant in Colorado (averaging 50% of the distance from ground to tip of plant, and averaging 30 cm above ground on an average 54-cm-tall plants, based on 14 clusters of eggs and young larvae from the E and W slope of Colo.). An average of 49 eggs per cluster is laid in Colo. (based on average of 43 for 10 clusters of eggs, and 54 for 12 clusters of 1st-stage larvae).

MATURE LARVA (Ontario, Paul Catling) brown, brighter than *P. tharos*, subdorsal cream band and lateral cream band both present, scoli bases orangish. **PUPA**. A high-altitude family reared in 1996 from Rollins Pass Road, Gilpin Co. Colorado was unusual because the transverse abdominal ridges were small (other pupal and larval traits of this family were ordinary). The cremaster is usually moderately rugose, although some are very rugose, for instance most pupae of a 1997 family from Tinytown were very rugose. The cremaster width averages smaller than *P. batesii* evidently, but varies considerably, for instance a 1997 family from Tinytown averaged 1.03 mm (n=12).

**5C. PHYCIODES COCYTA SELENIS,
W COLO.-WYO. ASTER FOLIACEUS VARIETY
(Figs. 18-23)**

This “variety”, which I reared from *Aster foliaceus* on the western slope of Colo., is the same as *P. cocyta selenis* from the Front Range of Colorado, except most males of the three reared families are slightly two-toned on upf (the median band being a little creamier-orange than the orange postmedian band, fig. 19)(these two bands are usually largely fused together on male upf, though they may differ in color). This variety may not prove to be significantly distinct, but I separate it here to simplify reporting new data on it. The slightly two-toned upf makes males even harder to distinguish from *P. batesii anasazi* than are other *P. cocyta*. Perhaps past introgression with *anasazi* is responsible for creating these two-toned adults and the few larvae with blackish frontoclypeus (see below under *anasazi*). But most traits clearly show that this taxon belongs to *P. cocyta*, and not to *P. batesii anasazi*: specifically, young-larvae spin very little silk web, like *cocyta*; the hostplant is most similar in appearance to the hosts of *cocyta*; the older-larval frontoclypeus most resembles *cocyta*; the older-larval scoli tips are creamy like *cocyta*; the pupal ridges are moderate/large like *cocyta*; the pupa is creamier like *cocyta*, and females have a slightly darker postmedian uph area. The unh marginal crescent color is intermediate but a little closer to *anasazi*; the male upf is intermediate in two-toning. **DIAGNOSIS**. A few males have the upf quite two-toned (fig. 19), and some males have the upf unicolorous (not at all two-toned, fig. 18), but most are slightly two-toned. The unf black spots are similar to those of other *P. cocyta* (and similar to many *P. batesii anasazi*): the unf black tornus spot is medium in size (few large, few small); the unf black median spot on rear margin is medium in size (few small). On the larva, the frontoclypeus patch is large and cream varying to small and tan, and a few larvae have the frontoclypeus black with a brown spot in the center or black with three brown spots in the corners. The older larval scoli tips are quite cream or merely cream-tan. Females are orange on ups (no dark-upf females were found), and are quite two-toned; they are rather difficult to distinguish from *anasazi* females, although the orange uph area is not quite as large as *anasazi* so the postmedian uph orange rings are more distinctly ringlike. Adults are the size of other *selenis*. The crescent in the unh brown marginal patch is more often creamy than in other *P. cocyta* varieties: in males, the crescent was cream in 9, yellow in 5, half yellow-half brown in 7, and brown (absent) in 11; in females, the crescent was cream in 21, yellow in 3, half yellow-half brown in 4, brown in 8. In contrast, the wild-caught non-reared *P. cocyta* from other montane aspeny areas of western Colo. had the crescent mostly brown (in males, 2 cream, 1 yellow, 40 brown; in females, 9 cream, 3 yellow, 15 brown). There is evidently only one yearly flight. **RANGE**. This ecotype occurs in the lower Montane Zone at middle-altitudes of western Colorado, and evidently also occurs in the same habitats in western Wyoming. In **WYOMING**, I have examined 5 males 4 females from south of Daniel on the Green River and south of of Pinedale on the New Fork River (a tributary of the Green River), all from montane lowland willow/moist meadowy river banks, Sublette County Wyoming, Aug. 1-3, 1990 (Andrew Warren), which have the upf somewhat two-toned (the median band paler than postmedian band) on four of the five males, and the unh crescent is gray or gray-brown; they seem to be this *P. cocyta* taxon. The willow-meadow habitat of these Sublette Co. adults fits *P. cocyta*, and not *P. batesii anasazi*, whose hostplant grows on sliding dirt which is generally found only in gulch/canyon areas.

HOSTPLANT. *Aster foliaceus* seems to be the main hostplant on the western slope of the Colorado mountains. This aster is extremely common in montane aspeny areas of western Colorado, where *Aster laevis*—the hostplant in the Colo. Front Range and Bighorn Mts. and western Neb.—is scarce. *A. foliaceus* ranges northwest to Montana & Alaska and south to California and New Mex., so is likely to be the main or a major host in this area. **Records**: Lot A, 58 2nd-stage larvae found on uns of leaf 33 mm wide, 10 cm above ground on 27-cm-tall *Aster foliaceus* plant, in partly-shaded nook beside log in valley bottom, no silk web under this non-egg leaf and no web found under adjacent 32-mm-wide oviposition leaf (which had many shed 1st-stage head capsules), reared to adults emerged Sept. 14-23, 1997, except three **4th-stage larvae diapaused**; lot D, 18 2nd-stage larvae found on leaf uns of two leaves 20 cm above ground on 35-cm-tall *A. foliaceus* plant, little web noted and no web noted later in lab, on SE-facing slope base, reared to adults emerged Sept. 17-21, 1997, one **4th-stage larva diapaused**; E part of Vail, ~8300 ft., Eagle Co. Colo., Aug. 22, 1997. Lot H, cluster of 83 1st-stage larvae found on uns of 22 mm wide by 20 cm long leaf 8 cm above mud on 10 cm-tall *A. foliaceus* plant, no web noted then or later in lab, in shade under two *Salix monticola* bushes in valley bottom, reared to adults emerged

Sept. 22-Oct. 6, except six **4th-stage larvae diapaused**; 7.4 mi. N of I-70, N of Silverthorne, Summit Co. Colo., Aug. 25, 1997.

EARLY STAGES. The **SILK WEB** spun by youngest larvae is absent, or very little is spun. **DIAPAUSE STAGE** 4th-stage larva. **1ST-STAGE LARVA** yellowish-cream with the usual cream bumps near setae, innards appear green; head black. The usual color change when molting to 2nd stage. **MATURE LARVA** body color is dark-brown, but a few individuals are blackish-brown. The body is almost as dark above the subdorsal cream band as below it (as is true of most *P. cocyta* and *P. batesii*). The subdorsal cream band is complete on most larvae, 90% complete on some. The band beside the BD2 scoli has an orangish (brownish-orange in some individuals, orangish-brown in few) dash. Near BD1 scoli the orangish area is nearly absent (just a touch of brown) or has a tiny area of orangish-brown. Just below the BSD scoli is a tiny area of orangish-brown or orangish-tan. The BL1 scoli are orange-brown, sometimes light-brown. The ring around BL1 scoli on most larvae is brownish-orange, on many orangish-brown. The frontoclypeus of head has a large cream spot in many adults, varying to a smaller cream spot, and a few larvae have only a small tan or brown spot, and three larvae had a solid black frontoclypeus, except for three tiny brown spots at top corner and near each lower corner of the triangular frontoclypeus. **PUPA** color of most individuals is cream-tan, but some are orangish-tan, a few light-orange-brown, a few gray, rarely orangish-cream, rarely creamy-&-black. Pupa wing mottling is weak/moderate, often moderate, often strong. Pupal ridges/cones are moderate/large in size. Pupal cremaster is winged in nearly all adults. Cremaster varies somewhat in width (from .75 to 1.2 mm): lot A averaged .99 mm (n=25), lot D averaged 1.12 mm (n=6), lot H 0.94 mm (n=48). (In contrast, *P. cocyta* from the Front Range averages 0.9-1.0 mm, and one lot reared in 1997 averaged 1.03 mm [n=12].)

5C. *PHYCIODES COCYTA SELENIS* (= *PASCOENSIS* WRIGHT 1905)

Several generations from June to early Sep. are reported for *P. cocyta* from southeastern Washington and adjacent Oregon. However, little information is available about this population, and few specimens have been collected, so (for instance) populations from this area could possibly be primarily univoltine, and Aug.-Sept. adults specimens may be merely abnormal. The name *pascoensis* is available for this entity if it differs significantly. However the few adults of it that I have seen do not seem to differ in appearance from the univoltine ecotype, so there is no good evidence that it is significantly different from the univoltine ecotype. This taxon—if it differs at all—could be related to the *Aster foliaceus* ecotype discussed above, but the few specimens seen do not seem to be two-toned.

HOSTPLANT RECORDS (in addition to Scott 1994). Prediapause larvae (of *cocyta*?) were found on *Aster frondosus* (Columbia Basin, Washington, Jon Pelham pers. comm.), but were not reared, so these larvae might have been another species, such as *Chlosyne acastus*.

5D. *PHYCIODES COCYTA DIMINUTOR* SCOTT 1998 (OR *PHYCIODES ORANTAIN DIMINUTOR*), NEW SUBSPECIES (Fig. 5-17)

DIAGNOSIS. This subspecies has smaller wingspan, and several generations. The first generation is fairly large (figs. 12-17), but the later generations (figs. 7-11) are small in size, about the size of *P. tharos*; thus adults diminish in size late in the season. I name it here because in some places in NE U.S.-southeastern Canada it occurs almost sympatrically with the *P. cocyta* univoltine ecotype (*selenis*), so this subspecies might even prove to be a distinct species. In eastern Ontario, Paul Catling (1998a) found *P. tharos tharos* and the small *P. cocyta diminutor* on a limestone plateau (the latter during second week of June), and the larger boreal univoltine *P. cocyta selenis* ecotype in nearby wetlands after mid June. In northern New York (St. Lawrence County), Catling (1998b) has found *diminutor* populations which seem to be similar to the multivoltine *diminutor* population in southern Minnesota discussed by Scott (1994), and have three flights (at least mid June, mid July [perhaps part of the first flight?], and mid to late Aug. [Aug. 13-27]), that occur in drier habitats (such as scrubby abandoned pasture), and in some places fly near the larger univoltine variety of *P. cocyta* that occurs in wetlands in mid June. In southern Minnesota there are at least two flights and perhaps three, flying at least in early to late June, July 13 (one male of a poorly-sampled second flight which might fly mostly late July-early Aug., as no adults were seen there July 8-13 1997, a late year), and Sept. Adults in both areas are larger in June and small in Aug.-Sept.: in northern New York fw length is 16.7 mm for males (18.4 females) in June, ~16.1 for males (~17.2 females) in Aug. (based on a small sample); in Minnesota fw length is 17.4 for males (18.7 females) in June, 15.8 for males (18 for one female) in Sept. The adults I reared in lab from Sept. Minnesota females were even larger (17.8 males, 19.4 females) than June adults, suggesting that Aug.-Sept. adults may be smaller because the hot summer weather experienced by their larvae in nature somehow retards their growth, whereas the cooler fall and spring weather experienced by larvae producing the June brood somehow produces bigger adults. Many butterflies have smaller adults in

the spring than in the summer generation (*Papilio multicaudata*, *Colias philodice*, *Pieris protodice*, etc. etc.), but those spring generations fly in April-May, and June flights of butterflies in general are not smaller. Thus the size difference between *P. cocyta diminutor* and *P. cocyta selenis* and *P. tharos* is probably genetic, since some of these taxa are larger despite flying only a few weeks apart in the season, and *P. tharos* is small during all three of its flights throughout the season from spring to fall. And the difference in voltinism is probably genetic as well, caused by genetic adaptation to the climatic conditions that prevail in most of its range (boreal Canada in the case of *selenis*). Further research will be needed to determine more precisely the genetic and environmental influences on this taxon, and to determine how distinctive is this taxon, but naming it will undoubtedly encourage lepidopterists to map its range and study it further. This taxon of course was confused with *P. tharos* when *P. cocyta* was thought to be synonymous with *tharos*, and even now the first generation of *diminutor* may be confused with *selenis*, and the small later generations may be confused with *P. tharos*, so careful study will be needed (the characters of antenna nudum color, presence of black line across uph orange space, size, mature larva color, etc. will have to be carefully examined). And the relationship of *diminutor* with the Great Plains *P. "tharos" orantain* must be investigated, as noted above under *orantain*, as one hypothesis considers both taxa conspecific (perhaps as *P. orantain orantain* and *P. orantain diminutor*). **RANGE.** This multivoltine subspecies evidently (I have not seen most of the relevant specimens) occurs all across the southern part of the range of *P. cocyta* in the east, from southern Manitoba and Minnesota to southern Ontario and New York, evidently southward to Pennsylvania where Charles Oliver (pers. comm.) reported some multivoltine populations, and probably to the southern limit of the range in West Virginia. Northward in Canada (Nova Scotia, Quebec, the middle of Ontario, northern Manitoba, Alberta, British Columbia etc.), the boreal larger ecotype (*P. cocyta selenis*) is just one generation, and the southward extent of *selenis* still needs to be determined. **ORIGIN OF NAME.** The name *diminutor* is named from later generations becoming smaller (more diminutive) in wingspan. **TYPES:** Male holotype and female allotype (both BMNH), from type locality NE Conger, Freeborn County Minnesota, eggs found *Aster simplex* Sept. 12, 1994, holotype male emerged Oct. 25, 1994, allotype female emerged Oct. 27, 1994, numerous paratypes from there and other locations in Freeborn County from May-Sept. during many different years. 2 male 1 female paratypes, all from 2 km north of Helena, St. Lawrence County, New York, Aug. 13, 1995; 2 female paratypes same site Aug. 27, 1995; 1 male paratype, 1 km NE Helena, St. Lawrence County, New York, Aug. 13, 1995; all New York paratypes collected by Paul Catling.

HOSTPLANT RECORDS (in addition to Scott 1994). Oviposition 108 eggs on leaf uns of basal rosette of *Aster lateriflorus* var. *lateriflorus*, east of Massena, St. Lawrence County New York (Catling 1998b). Adults associated with *Aster simplex* var. *simplex*, 3 mi. NE Alden, Freeborn County Minnesota, Sept. 13, 1994, June 11, 1995. Preoviposition 11:30 near *Aster simplex*, 3 mi. NE Alden, Freeborn County Minnesota, June 20, 1996. Females collected at 3 mi. NE Alden, Freeborn County Minnesota, June 20, 1996, laid eggs in lab (clusters of 3, 31, 38, 94, 122 eggs) that were reared (mostly on *A. laevis*); egg stage took 6 days (family 94) and 7 days (family 122); family from 38 eggs had no silk web June 29, slight silk web July 4; family from 94 eggs had slight silk web July 2; family from 122 eggs had some silk web June 29; five larvae diapaused as 4th-stage.

EARLY STAGES from southern Minnesota. Six families were reared from southern Minnesota in 1994 (briefly reported by Scott 1994) and 1996. **SILK WEB.** Young larvae make very little silk web, but some web was noticed above leaf surface on several leaves. **DIAPAUSE STAGE** 4th-stage larva, based on five larvae of three families. **EGG** pale green, lab duration 6-7 days in Minnesota, 7 in New York. **1st-STAGE LARVA** ochre-cream or ochre-tan, becoming greener anteriorly after feeding, the usual faintly-creamier low wide mounds, with no pattern until molting when the pattern of 2nd-stage larva becomes visible as a browner middorsal line and a weak browner line near it, a slightly-creamier subdorsal band, a wide band of brown subdorsal patches, a slightly-creamier lateral band edged below by a browner line, suranal plate brown; head black. **2nd-STAGE LARVA** greenish-cream when young, middorsal and nearby lines weakly brown, a wide brown subdorsal band, a weak lateral brown line, older 2nd-stage become browner, with middorsal and nearby brown lines, a creamier subdorsal band, a wide subdorsal band of large brown patches, a creamier lateral band edged below by a brown line; head blackish. **OLDER-MATURE LARVA** dark-brown to blackish-brown, the ground color nearly as dark above subdorsal cream band as below it; the cream subdorsal band generally complete (but slightly interrupted so only 85% complete on a few larvae); the ring around BL1 scolus is orange-brown on most larvae, brownish-orange on many; the orangish dash beside BD2 scolus (in cream subdorsal band) is usually brownish-orange (extending farther from scolus in a few oranger-tinted larvae) but is orange-brown on some larvae and orange or pale-orange on a few; the area just below base of BD1 scolus is usually brown but sometimes has a tiny brownish-orange dash; ventroposterad beside BSD scolus there is sometimes a very small brownish-orange (sometimes brown) dash; BL1 scolus orangish-tan, sometimes light-brown, dorsal scoli (BD1-2, BSD) blackish; scolus tips cream (esp. on thorax and on rear), but on many larvae the tips are brown on middle 2/3 of body; head black, the cream vertex stripe always present, always a cream crescent above/behind eyes that extends sinuously back to neck, frontoclypeus usually has a fairly large cream spot but sometimes has a small cream spot or rarely a dark-brown spot. Larval duration 42-43 days in cages in New York (Catling 1998b).

PUPA most often orangish-tan, but many are cream-tan, some are creamy, some are orange-tan, a few are brown or gray; the wing cases are usually moderately mottled, sometimes rather weakly

mottled, rarely strongly mottled (some pupae are creamy and rather strongly mottled with gray-black); ridges and cones large, though they were mostly moderate in several families; cremaster 0.99 mm wide on average, cremaster of most pupae winged, but ~20% are tapered; pupal duration 10-11 days in lab in New York (Catling 1998b).

6A. *PHYCIODES BATESII* (REAKIRT) 1865

DIAGNOSIS. Scott (1994) should have mentioned in text (this was listed in the tables) that *P. batesii* has large gnathos hooks (nearly always larger than those of *P. pulchella*), although the hooks of the western subspecies *apsaalooke* and *anasazi* vary from large to slightly less large. All subspecies generally oviposit on plants with aerial stems rather than low stemless seedlings, though the western subspecies *apsaalooke* and *anasazi* may oviposit a little lower down on the plant (the data available suggest that subspecies *batesii* oviposits about in the middle of the plant, subspecies *lakota* mostly in the upper part of plant, subspecies *apsaalooke* and *anasazi* about a third of the way up the plant).

6A. *PHYCIODES BATESII BATESII* (REAKIRT) 1865

CLINE OF UNH MARGINAL PATCH. Since Scott (1994), I have examined two more males from Syracuse New York, and both have very tiny brown unh marginal patches (one with a silver crescent, the other with yellow crescent). Near Ottawa in extreme eastern Ontario, this brown marginal patch is also usually weak, especially in males: it is totally absent in 2 males examined, almost absent in 7 males 1 female, weak in 5 males, a small area in 2 males, larger (about half-size) in 5 males 1 female, and fairly large (almost full size and fairly reddish-brown) in 2 males 4 females. In contrast, the biggest patch on a North Carolina adult is a female with an almost-half-sized marginal brown patch. The crescent on unh margin near Ottawa is yellow in 9 males, yellow-cream in 4 males, gray in 2 males, and cream in 8 males 6 females. Thus Ottawa adults seldom have a strong patch, so are definitely *P. batesii* near *batesii*, and do not belong to subspecies *lakota*. Some adults from Manitoulin Island Ontario have the brown marginal patch, and some lack it.

HOSTPLANTS. Paul Catling (1998c) found three egg clusters of 50-80 eggs (on leaf undersides on middle part of plant) and three clusters of young larvae on silk webs on *Aster cordifolius*, and found two clusters of young larvae on silk webs on *Aster ciliolatus*, on a semi-open dry limestone ridge in the Marlborough Forest area of eastern Ontario, in June-July 1996, and reared some of each family to *batesii* adults (adults identified as *batesii* by he and I), so these asters are evidently frequent hostplants or are the usual hostplants in Ontario/Quebec. That colony had common adults and a recent history of fire, wood cutting, and cattle grazing, suggesting that fire suppression and “environmental protection” is harmful to this species (unfortunately many ignorant “environmental nuts” and “tree huggers” and “Gaia worshipers” want to ban all logging and fires and want to create dense mature forest everywhere, and want to outlaw all grazing and logging (and hunting), because they have little knowledge of biology and do not understand that most animals require an earlier stage of forest succession, and die in mature forest). Paul Catling (pers. comm.) guesses that subspecies *batesii* has declined in eastern North America because of fire suppression, loss of habitat due to alien weeds and urban development, overgrazing, pesticides, etc., perhaps even climatic warming. Catling also visited the Aylmer, Quebec site (near Ottawa) where McDunnough (1920) found a cluster of 1st-stage larvae on “Aster with heart-shaped leaves”, and Catling found *A. cordifolius* common in open areas there, so it was probably also McDunnough’s host. *A. cordifolius* has perfectly-heart-shaped leaves, and narrow petioles that do not connect broadly to the stem; it is found in open woods, thickets and clearings. *Aster ciliolatus* is very similar to *cordifolius*, differing by having fewer taller heads and more-acute not-appressed phyllaries, the leaves a little thicker and a little less heart-shaped; it is found in open areas and thickets, and ranges to Alberta and the Mackenzie District so could be a hostplant all across Canada for *P. b. lakota* as well as for *P. b. batesii*. *Aster undulatus* could not have been McDunnough’s host, because it does not occur anywhere near his Aylmer locality; it occurs only at one site in Ontario, just north of Lake Erie; it is found in dry soil, in dry open woods, thickets and clearings. (However, *A. undulatus* is a hostplant farther south, in North Carolina.) *A. macrophyllus*—another heart-shaped-leaf species—grows in shade, so is less likely to be a *P. batesii* host than these other asters; it occurs in dry to moist open woods, thickets and clearings. *A. cordifolius* often occurs in clearings, but in southern Minnesota is usually found under moderate shade at the edge of small woods (but moderate shade near a sunlit area is no barrier to oviposition because I have found that eggs/larvae of the western subspecies *P. b. lakota*, *P. b. apsaalooke*, and *P. b. anasazi* are most likely to be found in partial shade under bushes or trees).

Evidently the known hosts of *P. b. batesii* differ from those of the other three *P. batesii* subspecies by being non-glaucous (the three known hosts *A. cordifolius* and *A. ciliolatus* and *A. undulatus* are not glaucous, though *undulatus* is “pale or hoary”), and by having the leaf petioles not as broadly connected to the stem (*A. undulatus* has the petioles fairly wide at stem but narrow otherwise, *A. ciliolatus* has the petioles slightly winged at base but narrow otherwise, and *A. cordifolius* has the petioles narrow throughout). Perhaps more undiscovered aster species are used

by *P. batesii batesii* as hostplants. But the three known hostplant asters (*cordifolius*, *ciliolatus*, and *undulatus*) all have heart-shaped lower leaves, and all are evidently closely related taxonomically, as all are placed near each other among the asters described in floras, and the botanist Semple placed all three asters in the same section *dumosi* and subsection *heterophylli* of genus *Aster*. Therefore, I currently conclude that *P. batesii batesii* prefers this group of *Aster* species.

EARLY STAGES in Ontario (Paul Catling): **HIBERNATION STAGE** 7-10 mm larva (no doubt 4th-stage). **EGG** pale-green, duration 7 days. **LARVAL** stages duration 30-50 days in lab. **PUPA** ridges and cones barely moderate (fairly small) in Ontario; duration 5-7 days in lab.

6B. *PHYCIODES BATESII* LAKOTA SCOTT 1994

EARLY STAGES. OVIPOSITION. Females oviposit on the underside of leaves, usually on upper leaves (though not the topmost leaf) of plants with vertical stems (not on seedlings) that grow roughly 15-40 cm tall, except one egg cluster was found on a lower leaf, and 2nd-3rd-stage larvae were found lower on the plants, probably because those plants with 2nd-3rd-stage larvae had grown taller since oviposition. Eggs are laid preferably on a plant that is in partial shade.

VARIATION BETWEEN FAMILIES. Considerable variation occurs, both within and between families, in Nebraska. The subdorsal cream band is absent in most larvae of several families, usually fairly complete but more or less interrupted in most families, and always complete or nearly complete in several families. The BL1 scolus is orangish in most families, reddish to orangish in a few families, brownish-orange to orange-red on one family, orangish-tan in some families, orangish to slightly-orangish-black in one family, orange-tan to brown in one family, and orangish-brown in one family. The frontoclypeus is black in all larvae of some families, black with a few larvae brown-spotted in some families, black on most larvae but brown- or cream-spotted in some larvae in most families, and quite variable with some black and many tan/brown-spotted and many cream-spotted in a few families. Pupae are most often (the commonest coloration) orangish-tan in most families, but most are grayer-tan in one family, most are dark-gray-tan in a few families, most are orange-brown or brown in one family, and in the darkest family most were brown (a few orangish-tan). Pupal wing mottling also varies individually within families, but was usually absent (moderate on some) in one family, weak in many families, weak but sometimes strong in many families, moderate in some families, and moderate to strong in one family. Scott (1994) listed variation between families in adult pattern, including amount of ups orange, size of unf black spots, ochre line on unh margin (present in some *P. b. anasazi* also), black median band on upf of females (present and exaggerated in one *P. b. anasazi* family), unh brown marginal patch, and presence and absence and color of the crescent in unh marginal brown patch.

6C. *PHYCIODES BATESII* APSAALOOKE SCOTT 1994

DIAGNOSIS AND STATUS. The unh marginal brown patch is of course another trait that is similar between the three western subspecies (*lakota*, *apsaalooke*, *anasazi*) and different in the eastern subspecies *batesii*. Thus subspecies *lakota* bridges the gap between *batesii* and *apsaalooke* to the extent that *lakota* is more similar to *apsaalooke* in unh brown patch, host, larval frontoclypeus pattern, larval scolus color, dark larval ground color, and weak A4 pupal ridge near wing. Additional rearings have improved knowledge of the variation of *apsaalooke*. The median black spot on rear of unf is large, but averages a little smaller than subspecies *lakota* and *batesii*. The unf black tornus spot and other unf black spots are rather large and vary little, compared to the great variation in these spots in subspecies *anasazi*. The unh pale crescent (in the brown marginal patch) is cream or yellowish in about 2/3 of adults, and brown (absent) in about 1/3 of adults.

RANGE. Undoubtedly widespread in the Bighorn Mts. in Wyoming (I recently found it in Sheridan County on the eastern side of the range) and adjacent Carbon County Montana (where it will no doubt be found in the future). And it probably occurs westward in the lower canyons of the east side of the Absaroka Range, and the canyons on the east side of the Wind River Mts., because the river that drains the west side of the Bighorn Mts. (the Bighorn River) also drains the east side of the Wind River Mts. (where the same river is oddly renamed the Wind River).

HOSTPLANT RECORDS. The hostplant *Aster* (*Eucephalus*) *glaucodes* has somewhat variable leaf shape, and further examination suggests that the leaves of Bighorn Mts. plants are not greatly different from those in Colorado. Newly-emerged female (still-floppy just-expanded wings, could not fly more than 5 cm) found resting on *A. glaucodes* in patch of this plant at 13:00, so the larva evidently fed to pupation there; many eggs and larvae found on *A. glaucodes*, adults reared: lot J, 91 new eggs found Aug. 2 on *A. glaucodes* leaf uns 5" above ground in partial shade of *Populus angustifolia* near creek, on Aug. 9 larvae had hatched and were eating leaf, Aug. 10 a little silk web along edge of leaf and in dung ball, Aug. 12 all were still in 1st stage, much web including web at edge of small leaf, moderate web over midrib of smaller-than-average leaf, moderate web over small leaf and some web over tip, Aug. 14 much web along leaf edge of large leaf, much web over midrib and some underneath cut base of large leaf, some web under large leaf, Aug. 16 most were 3rd-stage, much web between leaves, later no web seen; lot K, 60 new eggs found Aug. 2, 2" above ground under lower green *A. glaucodes* leaf, in partial shade of *Populus angustifolia* near

creek, hatched Aug. 4, on Aug. 6 all were young 1st-stage larvae with no web on egg leaf or other leaf, Aug. 8 extensive web on fairly-large leaf, ~Aug. 9 all molted into 2nd-stage, Aug. 10 not much silk web, Aug. 12 strong web along leaf edge of medium leaf, Aug. 14 most 2nds, no web seen, later no web seen; lot L, 95 older eggs found Aug. 2 morning, 3" above ground under green *A. glaucodes* leaf (25 cm from lot K), in partial shade of same *Populus angustifolia* near creek, hatched mid-afternoon of Aug. 2, by Aug. 6 older 1st-stages had made strong web over eggs and near eggs and on another leaf, Aug. 8 all were 2nd-stage, no web on three new leaves, Aug. 10 most 2nd-stage and some 3rd-stage, some web over midrib of small leaf and silking one leaf to another, Aug. 14 they were 3rd-stage, no web seen, later no web seen; lot M, cluster of 58 1st-stage larvae found 2" above ground (3" from base of plant) on *A. glaucodes*; lot N, cluster of 50 1st-stage larvae found 1.5" above ground (2" from base of stem) on *A. glaucodes* leaf, made strong silk web over eggshells that larvae rested on; lot O, cluster of 72 1st-stage larvae (~8 resting underneath a strong web) found 3" above ground (5" from base of stem) on *A. glaucodes* leaf in partial shade of *Populus angustifolia*; lots M+N+O of 1st-stage larvae were combined in one jar in lab, and on ~Aug. 4 their egg leaves were checked for web made previously (perhaps spun July 30-Aug. 3) and 1st egg leaf (perhaps made by lot M) had heavy web over eggs and moderate web on rest of leaf, 2nd egg leaf (perhaps made by lot N) had strong web over and near eggs, 3rd egg leaf (perhaps made by lot O) had strong web over and near eggs, by Aug. 6 all were 2nd-stage larvae except one older 1st-stage, the combined group of larvae made a good silk web on one part of large leaf (not an egg leaf), Aug. 8 some web under two large leaves, Aug. 10 most just molted to 3rd-stage and no web noticed, Aug. 14 some 3rd-stage some 4th-stage, no web seen, later no web seen; all west of Hidden Basin Campground, Bighorn County Wyoming, Aug. 2, 1995, adults reared from all lots. Three clusters were laid in lab by four females caught in nature at same locality: lot F, 91 eggs laid in lab Aug. 3? (cluster seen Aug. 8) by one of 4 females, Aug. 10 eggs turning brown about to hatch, hatched Aug. 11, Aug. 12 no web seen, Aug. 14 moderate web over midrib of tiny leaf, some web over midrib of medium-sized leaf, Aug. 16 2nd-stages made much web under and at edge of small leaf, more web leaf to leaf, Aug. 18 2nd-stages much web between 3 leaves, Aug. 22 2nd-stages molting to 3rd-stage no web seen, Aug. 24 most 3rd-stages and no web seen, later no web seen; lot G, 109 eggs laid in lab Aug. 3, Aug. 10 turning brown about to hatch, hatched Aug. 11, Aug. 12 moderate web in corner of bottle and slight web on leaf uns, larvae ate the eggshells as all eggshells gone, Aug. 14 very extensive sheen web noted between leaves in jar and some remained stuck to one leaf (extensive web between two medium leaves), Aug. 16 all were now 2nd-stage, now much web at edge of several leaves incl. small leaf, Aug. 18 many 2nds and more 3rd-stage, much web between three leaves and moderate web on uns at middle of medium-sized leaf, sheen web on side of bottle where molting occurred, Aug. 20 only a bit of web seen (along leaf edge), Aug. 22 some 2nd-stage many 3rd-stage no web seen, Aug. 24 nearly all 3rd-stage no web seen, later no web seen; lot H, 110 eggs laid in lab Aug. 3, Aug. 10 eggs turning brown about to hatch, hatched Aug. 11, Aug. 12 moderate web in curl of leaf as it was curled into trough of medium-sized leaf (web above trough)(egg leaf had no web), Aug. 13 much web between leaves and between leaf and glass, Aug. 14 much web over midrib of medium leaf and much web over small leaf and moderate web over larger leaf, Aug. 16 all 2nd-stages, much web between leaves and glass and some web at edge of small leaf, Aug. 18 most 3rd-stage, a little web along leaf edge, Aug. 20 most 3rd-stage, no web seen, Aug. 22 most 3rd-stage, no web seen, later no web seen; all west of Hidden Basin Campground, Bighorn County Wyoming, Aug. 2, 1995, adults reared.

ADULT BEHAVIOR. Males evidently patrol canyon bottoms all day to seek females, perhaps a bit slower than *P. pulchella* near *camillus*, and were observed chasing others there (mate-locating behavior) at 13:00, 15:00, and perhaps 15:50. One male sipped mud. Many adults visited various flowers: 5 males 3 females were seen on blue *Medicago sativa*, 1 male on blue-white *Aster glaucodes*, 1 male on yellow *Grindelia squarrosa*, 1 female on white *Achillea lanulosa*. Adults fly from mid June-mid Aug. (known dates June 26-Aug. 17), the peak probably early-mid July.

EARLY STAGES. OVIPOSITION. Average number of eggs/cluster is about 84 (combining eggs and 1st-stage larvae, 33-110, n=10; this includes seven clusters of eggs averaging 84 per cluster, and three clusters of 1st-stage larvae averaging 60 per cluster; the means for eggs and 1st-stage larvae are usually similar in *Phyciodes*, though longer exposure to mortality such as ant attack would be expected to reduce the average for 1st-stage larvae below that for eggs). *P. b. apsaalooke* evidently lays many more eggs per cluster than *P. batesii lakota* (which averages 42), because the hosts grow in very large clusters often many meters wide, a much greater amount of aster biomass than that of any other aster I have seen. Eggs were found on undersides of leaves 4-13 cm above ground (averaging 7 cm above ground, and averaging 8.5 cm from base of stem) on plants that were mostly roughly 15 (a few 20-25?) cm in height (exact heights were not recorded). Eggs are mostly laid on plants that grow in partial shade. **EGG** pale green when laid, turning creamy, then turning brown when about to hatch, shaped like other *Phyciodes*, with ~20-21-22 ribs on conical upper portion of egg (20 ribs in a good count); duration 8 days for three clusters. **SILK WEB.** All families have a silk web (rather strong except in one family, often strong enough to appear as a strong sheen) made by young larvae (1st-stage larvae always make a web, over the eggshells and nearby where they feed, 2nd-stage larvae often make a web, 3rd-stage larvae sometimes make a web; but no web was noticed for 4th-stage to mature larvae). Some 1st-stage larvae were noted resting under the silk web, but most larvae rest on top of the web. Subspecies *apsaalooke* is like subspecies *lakota* in web construction. **LARVAL STAGES AND HEAD WIDTHS.** Widths of

larval heads indicate six larval stages, with these head widths: 1st-stage 0.27-0.28 (n=2), 2nd-stage 0.35-0.4 (mode 0.4), 3rd-stage 0.6-0.8, 4th-stage 0.9-1.3, 5th-stage 1.4-2.0 (mode ~1.6), 6th-stage 2.0-2.4 mm (mode 2.3). **DIAPAUSE STAGE.** 4th-stage larvae hibernate, because head widths of nearly all larvae that died (mostly during diapause) were 0.95-1.3 mm. In 1995, one lot K and one lot L and one lot M larva diapaused 4th-stage (two larvae had 1.0 mm-wide head capsules, the lot M larva had 1.3 mm capsule). Lab diapause was frequent and long in 1993, resulting in much mortality, but in 1995 very little diapause occurred because immatures were collected at an earlier stage (as eggs and 1st-stage larvae) and had not yet been programmed to diapause by natural photoperiod. **1st-STAGE LARVA** yellowish-cream when young, after feeding the front half of body becomes slightly greener due to bluish-green innards from intestinal food, lacks color pattern, later the body is slightly-bluish-cream on top and yellowish-cream laterally (with at most a weak pattern of a slightly-darker greenish subdorsal band, and three very faint dorsal lines due to slightly-greener heart-line and tiny brownish seta bases), then body becomes creamier after larva stops feeding; near the end of the larval stage before molting (when the 2nd-stage larval head becomes visible as a bulge in the prothorax of 1st-stage larva), the body is greenish-yellowish-cream with green innards, and the body develops a pattern (because the second-stage larva becomes visible through the 1st-stage integument), as a slightly-darker greenish subdorsal band often appears, weak narrow brown lines appear running between BD1 setae; still later a weak narrow brown middorsal line develops, and the subdorsal band becomes wide and brown, a weak supraspiracular brown band appears (above L1-2 setae), a slightly-brown narrow sublateral line develops (the weakest of all these bands and lines), and the uns becomes slightly-darker ochre (in developing this pattern at molting, larvae resemble subspecies *lakota*); body (like other *Phyciodes*) has the usual slightly-creamier bumps (a creamier bump above/at D1 seta, a larger creamier bump below D1 and above D2, a fairly large slightly-creamier bump between L1-2); setae dark-brown, setal lengths like other *Phyciodes*, spiracles brown, suranal plate blackish, proleg shields light-brown (brown on A10), legs dark-brown, collar dark-chitin-brown with slightly-paler spot at bases of usual 3 long 1 short setae; head blackish with only primary setae, head width ~0.27-0.28 mm. **2nd-STAGE LARVA** when young is greenish-cream (or greenish-tan)(bluish-greenish-yellowish-cream with green innards), with a weak narrow brown middorsal line (more like a line of dashes) and a similar weak narrow brown line near it, a wide brown subdorsal band below a creamier band, weak brown supralateral dashes, a greenish or slightly-brown weak sublateral line below a creamier lateral band, some slightly-creamier bumps below that; when older the larva is tan with brown lines and the same two creamier bands (middorsal line dark-brown, line beside it reddish-brown, a wide dark-brown subdorsal band, brown supraspiracular dashes, a brown sublateral line); BD1-2 and BSD scoli brown or dark-brown, BL1-3 scoli orangish-tan (greenish-cream with tan tips when young), scoli tips not noticeably paler; suranal plate solid dark-brown, proleg plates light-brown (darker light-brown or brown A10), legs dark-brown; collar dark-brown with a paler bump carrying each of 4 primary setae (anteromedial bump sometimes dark), or collar has a dark-brown patch (enclosing an anterolateral tan bump) that extends laterally around anterior rim of collar then jogs medially to behind lateral 2 primary setae (where it may be dark-brown or light-brown); head unmarked blackish, ~6 secondary setae on each side, head width 0.35-0.4 mm. **MATURE LARVA** variable, the palest larvae are dark-brown with strong cream subdorsal band and orangish areas around some scoli, while the darkest larvae are quite black with the subdorsal cream band absent (black) and the only paler markings being the lateral ochre band and ochre BL1 scoli (and even the head is almost solid black with perhaps a tiny creamy vertex spot). Body ground color is usually blackish-brown; many larvae are dark-brown, and many are quite black. This ground color is just as dark above the subdorsal cream band as below it, but was a little paler above the band in a few larvae of one family. The subdorsal cream band is usually fairly complete but slightly interrupted (~3/4 complete), and varies from completely solid to absent. The orangish dash in this subdorsal cream band beside the BD2 (subdorsal) scoli is usually orange or brownish-orange, but is orange-brown in some, pale-orange in a few, rarely absent. The small orangish dash beside the BD1 (middorsal) scoli is blackish, brown, or orange-brown about equally often, and is sometimes brownish-orange. The orangish dash posterolaterad beside the BSD scoli is absent (being the ground color, usually blackish), brown, or orange-brown about equally often, less often brownish-orange, sometimes orange. The orangish ring around the BL1 (lateral) scoli is usually brownish-orange, frequently orange-brown, but varies from rarely orange to rarely brown or dark-brown. The BL1 scoli is usually orangish-tan, but is brown in some larvae, rarely black in others. The BD2 scoli is nearly always black, but is dark-brown at base in some larvae, and dark-brown in rare larvae. The BD1 and BSD scoli are always black. The scoli tips were all black in most larvae (in contrast to *P. b. anasazi*, in which the tips are paler in many larvae esp. of some families), except a few larvae have pale scoli tips (esp. on thorax). On the head, the frontoclypeus is completely black in about 80% of larvae, and the remaining 20% have a tan, ochre, or cream spot; but all the reared families had some variation of the frontoclypeus (the palest frontoclypeus is like the usual *tharos* frontoclypeus with a large cream triangle [and these larvae have a cream V on the bottom of the adjacent gena], but the palest frontoclypeus in some families merely has a brown spot). **PUPAE** most often creamy (or grayish)-tan or creamy-brown, but are often creamy/gray or orange-tan or brown, and few are orange-brown or dark-blackish-brown or black with mottling/streaks of creamy. Pupal wing mottling is mostly moderate to strong, but is sometimes weak. **LARVA-PUPA DURATION** in lab averages 38 days males, 40 days females, average emergence lag 2.5 days in lab.

VARIATION BETWEEN FAMILIES. The **older larva** body color varies from dark-brown to black between larvae of the same family in most families, but is dark-brown in most larvae of some families, and is black (some larvae merely blackish) in one family. The larval subdorsal band was complete in nearly all larvae of one family (70% complete in the larva with the weakest band), most families had the band mostly-complete, but several families often had incomplete bands (averaging only 50% complete in one family, and a few larvae of a similar family had the band totally absent). The orangish dash beside the BD2 (subdorsal) scolus in this subdorsal cream band is paler (all orange) in one family, and darker (all brown-orange) in one family. The small orangish dash beside the BD1 (middorsal) scolus varies somewhat within most families, but is absent (blackish) in several families, and is brownish-orange in the palest-dash family. The orangish dash posterolaterad beside the BSD scolus also varies in color within most families, but was always orange in one family, and absent (blackish) in several families. The orangish ring around the BL1 (lateral) scolus was brownish-orange or orange-brown in larvae of most families, but also varied to brown in some families, was always orange in one family, and was orange-brown or brown in one dark-ringed family and was brown (some dark-brown, some brownish-orange) in the other dark-ringed family. The BL1 scolus is always orange-tan in most families, but some larvae of many families also include individuals that are tan or brown (rarely black), and all larvae of one family had this scolus brown to tan. The larval scolus tips are totally black in some families, many families have the tips black in most larvae but pale in some, and one family had the tips slightly-paler but black in some larvae. The larval frontoclypeus of the palest-head families had a cream or tan spot on about a third of larvae of each family, and a black frontoclypeus on most larvae, whereas the darkest-head family had a black frontoclypeus on nearly all larvae but a brown spot on a few larvae. **Pupae** show some variation in color between families: in most families the commonest pupae are cream-tan, but in some families the commonest pupae are grayish-brown, and in some families the commonest pupae are creamy-orangish-tan, or creamy, or tan to brown. Many families have rather strongly mottled pupal wings, many are moderately mottled, and few families have weakly-mottled wings. **Adults** also vary between families. The unh crescent (in the marginal brown patch) is cream in all males of several families, cream in most males of many families, and brown in most males of many families. Other adult traits show much less variation, compared to *P. b. anasazi*. The amount of ups orange varies a little, mostly between individuals but slightly between families. All families have the unf black spots of males rather large, though some individuals have these spots (such as the tornus spot) only moderate in size.

6D. *PHYCIODES BATESII ANASAZI* SCOTT 1994 (Figs. 24-33)

DIAGNOSIS. Considerable variation has been found in adults and immatures of this taxon, making it harder to identify, so a redefinition is needed here. Adults almost always are very orange on ups, and usually have a large orange space on uph, making them similar to *P. cocyta*. (Although Paul A. Opler [pers. comm] notes that males from Grand Canyon National Park Arizona and from eastern Zion National Park Utah are frequently darker on ups.) Males usually (~80% of males) have a conspicuously two-toned upf, the median band being creamier than the oranger postmedian band. The unf has very large black spots in some adults, but this character has proven to be very variable, and mostly genetic, so that some families have these spots very large (figs. 24-26), other families have smaller spots on the average (figs. 27-29), and some families have the black spots rather small, as small as those of *P. cocyta* (rarely even smaller on average, figs. 30-33). The black unf tornus spot and the black unf median rear spot of males vary from small to giant. The crescent in the unh brown marginal patch is also variable, being creamy (whitish or white) in about a third of males, yellow in about a third, brown in about a third (females usually have a creamy crescent, and only about a quarter have a brown crescent). Most characters of larvae and pupae are also variable. About a third of older larvae have the frontoclypeus solid black (this character is also genetic and varies greatly between families). The scolus tips of older larvae vary from blackish to cream (they are dark in other *batesii* subspecies) The larval body varies from black to fairly-orangish brown (most are blackish or dark-brown). The subdorsal cream band on larval body is nearly always strong, rarely very narrow or only 80% complete; thus this band averages stronger than in subspecies *apsaalooke* and *lakota*. The BL1 (lateral) scolus varies greatly in color: most are tan or orangish-tan, but some are light-brown or ochre, a few are brown, orange, orange-brown, or creamy. The orangish ring around BL1 scolus is most often orange-brown, but is commonly orangish-brown or brownish-orange, seldom orange or brown. The orangish dash beside BD2 scolus is most often brownish-orange, commonly orange-brown, sometimes orange. Pupae are most often orangish-tan, often creamy-tan, sometimes creamy-gray or creamy, rarely orange-brown, pale-brown, brown, red-brown, blackish, mottled black, or gray. The brown mottling on pupal wings is weak or moderate, sometimes strong. The pupal ridges and cones are most often moderate in size, but almost as often are small, sometimes are strong. The antenna club is orangish: the nudum of males has dark-orange (sometimes orange or brown) borders, orange-brown (rarely dark-orange or brown) lattice, the steps yellow-orange (sometimes orange); females have brown (rarely dark-orange or black) borders, brown (sometimes black) lattice, and orange (sometimes brown) steps. Subspecies *anasazi* differs from *P. batesii apsaalooke* by having much oranger adults, the uph

orange center is seldom divided by a black line, and many adults have smaller unf black spots. **GAME CREEK FAMILY** (figs. 30-33). One family reared from *Aster glaucodes* from Game Creek, Minturn, Eagle Co. Colo., 8050 ft., was especially puzzling as it superficially appears to intergrade between *anasazi* and *P. cocyta*, and its adults especially are similar to the latter in several traits. The unf spots are small, even smaller than the average *cocyta* (figs. 31-32); the unh marginal crescent is like *cocyta* (the crescent is brown on 6 males, gray-brown on one, brown on 2 females, cream on one), though this trait varies between families considerably; the older larval frontoclypeus spot varies from large and cream to small and ochre, most like *cocyta*; the older larval scoli tips are weakly to strongly cream, most like *cocyta* (or somewhat intermediate) in appearance; however, the silk web spun by young larvae was strong like *anasazi*; the two-toned upf of males is rather strong (fig. 30) like most *anasazi*; the hostplant is that of *anasazi*; the pupal ridges are moderate (few small, some large) like *anasazi*, and the cremaster is very rugose like *anasazi*. So overall, counting these traits, the verdict is 5 to 3.5 traits in favor of *anasazi*, and the traits nearer to *cocyta* are traits that vary greatly within *anasazi*, so I will conclude that this family belongs to *anasazi*, and merely is one of the families nearest to *cocyta*. But this family was from the upper end of the altitudinal range, near *cocyta*, so the possibility exists that this family has some genes from introgression from *cocyta*. **IDENTIFICATION:** Adults are easily distinguished from *P. pulchella camillus* by having a large black subapical spot on the unf costa, whereas *P. pulchella* has only a small orangish or brown spot there with at most only a tiny blackish-brown mark within the spot; *camillus* is also much darker on ups, etc. The great variation within *anasazi* makes it more difficult to distinguish from *tharos/cocyta*. The only subspecies of *P. tharos* that occurs within the range of *anasazi* is *riocolorado*, and *P. tharos riocolorado* is easily distinguished because it is smaller, has a black antenna nudum, lacks a two-toned upf, and has the unh marginal crescent generally brown. Distinguishing *anasazi* from *P. cocyta* is the most difficult task, because both taxa are very orange on ups and are about the same size, males of both have a large orange space in middle of unh, etc. Some males are easy to identify because they have very large unf black patches (like those of *apsaalooke*, including a large spot in the outer part of cells M_{1-2} and a large tornus patch that sandwich a pale marginal crescent). But many males, especially at higher altitudes, have smaller unf black spots, and only two characters offer much help for distinguishing them from *cocyta*: the upf ground color of *anasazi* males is still usually two-toned (the postmedian ochre band is conspicuously paler than submarginal orange band on 80% of males, though they are about the same color on some males); and the unh marginal brown patch of males contains a cream (whitish or white) or yellow crescent on most (two-thirds) *anasazi* males (the crescent is brown on a third), whereas in *cocyta* the crescent is nearly always brown (rarely yellow or cream in males; in female *cocyta* more than 50% are brown but some are yellow and many are cream). Most female *anasazi* (about 75% or more) have the uph orange area (the central orange area not divided by the black line of *tharos*) a little larger than that of *P. cocyta*, so the postmedian orange rings are less distinct as they are more engulfed in the orange patch in middle of wing. Larvae are also variable, but many can be easily distinguished from *tharos/cocyta* by having the frontoclypeus darker (solid black in a third or half of larvae, and the cream frontoclypeus patch is small in most of the remaining larvae, though the cream patch is large in some families); some larvae are dark enough to be confused with *P. pulchella*.

RANGE. In **COLORADO**, I have reared or seen adults from Summit County (all around Green Mtn. Res.), Grand County (Radium and vicinity), Eagle County (near Basalt, Deep Creek, Edwards, Avon, Minturn), Garfield County (Grizzly Creek), Mesa County (near Gateway, and West Creek, and Paul Opler [pers. comm.] found it in Big Wash south of Cameo), Montrose County (Sewemup Mesa), San Miguel County (San Miguel River), and Ouray County (Chaffee Creek) (most collected by J. Scott, some collected by Ray Stanford, Andrew Warren, Scott Ellis). The butterfly is recorded from Mesa Verde National Park in Montezuma County (Paul Opler). It evidently occurs continuously all along the valleys of the Colorado River system and all its tributaries, so *anasazi* no doubt also occurs along the Yampa and Green Rivers in Dinosaur National Mon. in Moffat County, and along the Gunnison River. The hostplant occurs mainly on the west slope of the continental divide in Colorado, including the Black Canyon of the Gunnison, so *anasazi* no doubt occurs there (in Montrose County) and downstream in Delta County. The hostplant also occurs at Durango in LaPlata County and at Pagosa Springs along the San Juan River in Archuleta County (according to Rydberg's Flora of Colorado), so *anasazi* probably occurs there also, as well as downstream along the San Juan River in New Mexico. The hostplant also occurs in Ouray County at Ouray and on the chaparral hills southeast of Ouray, occurs in Pitkin County along the Roaring Fork River northwest of Aspen, and occurs in Grand County at Grand Lake beside Rocky Mtn. National Park (although the butterfly may not range this far upstream). The hostplant occurs at very few places east of the continental divide (Rydberg): "Larimer Co." (perhaps along the Cache La Poudre River), in Boulder County in the mts. between Sunshine and Ward, and in Clear Creek County at the headwaters of Clear Creek including "Gray's Peak" (Gray's Peak at 14,274 feet altitude is much too high for the plant, which may have occurred northward in a gulch at Bakerville)(in this area I have seen it only along Clear Creek, specifically at Georgetown Lake and at Silver Plume, although it may have occurred more widely in the past there before reforestation and Interstate Highway 70 exterminated it in the valley bottom west to Bakerville). The male of *Phycodes "batesii"* illustrated by Brown Eff and Rotger (1957, p. 88), was collected in Clear Creek County at Loveland Pass Road 10,200', which is just a mile or two west of Bakerville, but the photo

shows a male that I cannot confidently identify, which has an upf with large black spots like *P. batesii* and a two-toned melanic upf blacker than any *anasazi* I have seen, and has an uph with a black line dividing the orange area unlike *anasazi* or *P. cocyta*; it might be an odd *P. b. lakota*, but is best considered an unidentifiable oddity. In **WYOMING**, *anasazi* probably continues northward from the Colorado state line along the Green River system in canyons, but I have seen no specimens yet. *P. batesii* may have extended its range west to form ssp. *anasazi* by populating the Green River system from the east, because the Green River drains the west side of the Wind River Mts., and a short distance across the low continental divide at South Pass at the south end of this range is the Platte River and Bighorn River drainages, only a few miles from each other, the latter upstream from the Bighorn Mts. home of *P. batesii* *apsaalooke*. So *P. batesii* probably occurs east of the Wind River Mts. along the Wind River system (which downstream is renamed as the Bighorn River), but subspecies *apsaalooke* instead of *anasazi* may occur on the east side of the Wind River Mts. The host occurs at the northern end of the Laramie Range just south of Casper in Natrona County, so *anasazi* or *apsaalooke* could occur in this range. I have not examined specimens from Carbon County Wyoming where *P. batesii* may occur. In **ARIZONA**, *anasazi* occurs in Coconino County in the canyons below the North Rim of the Grand Canyon, undoubtedly occurs in South Rim canyons also, occurs in Oak Creek Canyon near Sedona (Paul Opler pers. comm.) and undoubtedly occurs northeastward along the Colorado River into Utah. The hostplant, as *A. glaucodes* var. *pulcher*, occurs only in the northern part of Arizona according to the Kearney and Peebles Arizona Flora, including "Beclabite" (Biklabito) 6000 feet near the San Juan River in Apache County in extreme NE Arizona, probably occurs in extreme northern Navajo County, and occurs in Coconino County on the Kaibab Plateau (including Sunset Crater near Flagstaff far south of the Grand Canyon, 8000 feet) and on both rims of the Grand Canyon (including Havasu Canyon on the south rim, 3000 feet). In **NEW MEXICO**, neither the butterfly nor the hostplant has been recorded so far, but both should be present along the San Juan River in San Juan County, and some specimens from the Chuska Mts. seen by Paul Opler may be *anasazi*. In **UTAH**, I have seen adults from Millard County (Oak Creek Forest Camp.), Sevier County (ESE Salina), Sanpete County (ENE Sterling), Wayne County (south of Grover), Emery County (Rilda Canyon), Carbon County (U.S. 191 NE of U.S. 6), Duchesne County (West Tavaputs Plateau), and Washington County (near Zion National Park) (most collected by Ray Stanford, some by J. Scott). It evidently also occurs in San Juan County Utah, based on published paintings (figs. 9-10 in Howe [1975] pl. 77, 1 male 1 female from Buckboard Flat, Abajo Mts., July 16, 1969, NMNH, look like *anasazi* to me, as the male has the characteristic two-toned upf, the female unh has a cream crescent, etc.). In Utah the hostplant *A. glaucodes* occurs in the Uinta, Stansbury, Bear River, and Wasatch Mts., south in the Utah plateaus to Zion National Park etc., eastward interruptedly to Colorado (no doubt all along the Colorado River system, from the Grand Canyon to western Colorado); so *anasazi* probably occurs in all of these areas, except perhaps the Stansbury Mts. In **IDAHO** *P. batesii* is probable (but not yet discovered) in Bear Lake County, because the host *Aster glaucodes* occurs in that county (presumably along the lower part of the Bear River). In **NEVADA** it may occur in the mts. in eastern White Pine County or Lincoln County, as George Austin's discovery of the more-two-toned upf of males of a *Phyciodes* species from White Pine County might approximate *anasazi* (I have not seen these specimens), and suitable habitat may be mostly continuous from Washington County Utah to at least Lincoln County Nevada; however the floras make no mention of *Aster glaucodes* occurring in Nevada, but this aster might possibly occur there.

Many of the published/mapped records of *P. cocyta* from western Colorado-Wyoming-Utah-Arizona may actually be *anasazi*. *P. cocyta* seems to be limited to higher altitudes in western Colorado, in aspen habitats or oak groves etc., so it may have a smaller range in these states than *anasazi*.

INTROGRESSION? Scott (1994) dismissed the possibility of introgression between *anasazi* and *P. cocyta*, which share some similarities (both are very orange, have a large orange uph space on males, have orange antennal nudum, etc.). But the current paper demonstrates even closer resemblance between these two, in both adults and larvae, especially at the upper altitudinal limit of *anasazi* in areas where their ranges are close together. For instance, the *anasazi* from Green Mtn. Res. in Grand County, from Minturn in Eagle County, and some from the San Miguel River in San Miguel County, are most similar to *cocyta*, whereas those from Mesa and Montrose County are quite different from *cocyta* (*anasazi* from the latter counties [and from Grand Canyon National Park, Paul Opler, pers. comm] have whiter unh marginal crescent, for instance). And *Phyciodes cocyta selenis* reared from *Aster foliaceus* in W Colorado seems closer to *anasazi* in male upf two-toning and slightly closer in larval frontoclypeus color than the usual *cocyta*, as noted above. Perhaps this convergence could be due to past hybridization (introgression) between the two species. Or, the convergence could possibly be due to some of these genes being linked to genes that are important physiologically in adapting to greater moisture and lower temperatures etc. at higher altitudes, causing appearance to differ with habitat. But there is little hope of proving these high-tech introgression and linkage hypotheses with the nonexistent funding available for butterfly research. And opposing the idea is Oliver's (1979) finding that *P. batesii batesii* (from Pennsylvania) is strongly reproductively isolated from *P. cocyta* (from Syracuse New York), especially in the cross *cocyta* male X *batesii* female, the cross which would be necessary to introduce genes from *cocyta* into the *batesii* population. Oliver also found that matings would not occur in lab cages between *batesii* and *cocyta*, whereas matings would occur in lab cages between

tharos and *cocyta*, implying that *batesii* has a pheromone barrier to mating. Furthermore, the *anasazi* reared from Deep Creek in Eagle County are very different from *cocyta*, even though this locality has habitat that appears suitable for *cocyta*. And Grizzly Crk. in Garfield County has *anasazi* that is rather distinctive, as well as adults that are not so distinctive and adults that look like ordinary *cocyta*. So perhaps this is not introgression, but just another case of local convergence, which is annoying to human lepidopterists who want to conveniently pigeonhole the identity of the butterflies they find. This case of convergence could also be due to virus transmission of genes between species. Viral transmission seems to best explain the many convergences between sympatric species of *Speyeria* in western U.S. And there is still the Batesian mimicry theory (Scott 1994), which suggests that *anasazi* has become orange in order to mimic the very orange *Euphydryas chalcedona wheeleri* (Hy. Edw.), which is presumably distasteful to predators.

HABITAT. Gulch bottoms and canyon bottoms, and steep gullies etc. descending to the canyon bottom, the surrounding vegetation being wooded with pinyon/juniper or ponderosa/spruce, or covered with oaks or sagebrush. The gulch bottom can be dry, or a stream with cottonwoods and willows at its edge. The hostplant prefers to grow on sliding dirt or mixed dirt and small rocks (resting at the angle of repose, next to a creek or gulch bottom or on a highway cut or a railroad cut or at the bottom of a cliff on a hillside, etc.). Males fly near the host along the canyon bottom and steep side gulches and to some extent on adjacent hillsides. **HOSTPLANT.** The hostplant is evidently *Aster glaucodes* only. Furthermore, other *Phyciodes* evidently do not eat this plant, as everything I have reared from *A. glaucodes* has proven to be *batesii*, except for *Chlosyne acastus* larvae reared from *A. glaucodes* Minturn in Eagle County Colorado and the Bighorn Mts. Wyoming. Additional hostplant records follow. Adults associated with *Aster glaucodes*; southeast and northwest ends of Green Mtn. Reservoir, Summit County Colorado, July 11, 1996. Adults associated with *Aster glaucodes*, NE Radium, Grand County Colorado, 7300', July 11, 1996; three females from here laid eggs in lab on *A. glaucodes* on July 12 that hatched July 19, all reared on *Aster laevis* and *glaucodes*: lot 3, cluster of 3 eggs, adults emerged Aug. 19-24, 1996; lot 43 (laid by same mother as lot 3), cluster of 43 eggs, adults emerged Aug. 17-23; lot 98; cluster of 98 eggs, slight silk web noticed on July 21, adults emerged Aug. 19-27; lot 128, cluster of 128 eggs, slight silk web noted July 21, some web on two leaves and much silk web on two leaves made by 1st-stage larvae July 23, adults emerged Aug. 19-27. Adults associated with *Aster glaucodes*, just east of Avon, Eagle County Colorado, 7800', July 17, 1996. 30 1st-stage larvae (later died) found on *Aster glaucodes* leaf uns in shade in gulch bottom, much silk web formed a sheen; west side Avon, Eagle County Colorado, 7500', July 17, 1996. 51 1st-stage larvae (lot A)(later died) found on *Aster glaucodes* leaf uns (20 cm up on 40 cm stem), in shade of bushes, nearby leaves chewed and two had strong silk web; 137 1st-stage larvae (lot B) found on *Aster glaucodes* leaf uns (22 cm up on 50 cm stem), in shade of bushes, much silk web July 19 and strong sheen silk web July 21 made by 1st-stage larvae, much silk web July 21 made by 2nd-stages, some web July 23 made by 2nd-stages, reared on *Aster laevis*, some 4th-stage larvae diapaused, adults emerged Aug. 19-28, 1996; WNW up Deep Creek, Eagle County Colorado, 6500', July 17, 1996. Five 3rd-stage and 4th-stage larvae found on *Aster glaucodes* leaf tops, Sewmup Mesa, Montrose County Colorado, 5000', July 18, 1996, reared on *Aster laevis*, adults emerged Aug. 19-23, 1996. 22 1st-stage larvae (lot C) found on uns of two *Aster glaucodes* leaves, two leaves had much silk web (so thick it formed a sheen) and some larvae were under the web on one leaf, some 4th-stages diapaused, adults emerged Aug. 16-20, 1996; 39 1st-stage larvae (lot D) found on *Aster glaucodes* leaf uns, much silk web on uns of oviposition leaf and on tiny leaf at top of stem, some 4th-stages diapaused, adults emerged Aug. 16-21, 1996; 25 2nd-stage larvae (lot Misc.) of three family clusters found on *Aster glaucodes* leaf uns, some silk web on leaf uns including a sheen of thick silk on 2 cm² of one leaf, 8 produced older larvae with black frontoclypeus and adults emerged Aug. 14-18, 1996, 17 produced older larvae with cream frontoclypeus and adults emerged Aug. 13-23, 1996; oviposition leaves (leaves containing eggshells) at this site were found 15 cm up on 30 cm stem, 10 on 25, 8 on 25, 3 on 35; all reared on *Aster laevis*; all found in shade under Englemann Spruce; San Miguel River east of Norwood, San Miguel County Colorado, 6470', July 18, 1996. Extensive larval feeding damage noted on very common *Aster glaucodes*, including one oviposition leaf that had a strong silk web all over uns and had ~30 1st-stage and ~15 2nd-stage larval head capsules and some shed larval skins; the *glaucodes* host and strong silk web suggest that these larvae were *P. batesii anasazi*; some *A. laevis* and many *A. ?ascendens* also present; 1 male adult found that resembles *cocyta* (unf black spots small, upf not two-toned; but unh crescent is dark-gray), but is most likely *anasazi*; Chaffee Creek, Ouray County Colorado, July 18, 1996. Eight 2nd-stage larvae (lot A) found on *Aster glaucodes* leaf uns, adults emerged Aug. 23-Sept. 5, 1996; 62 1st-stage larvae (lot B) found on *A. glaucodes* leaf uns, a little silk web found on uns of oviposition leaf containing eggshells, a little silk web July 29, adults emerged Aug. 27-Sept. 5, 1996; 24 1st/2nd-stage larvae (lot C) found on *A. glaucodes* leaf uns, much silk web found on oviposition leaf which contained some uneaten eggshells, adults emerged Aug. 27-Sept. 5, 1996; all larvae of lots A, B, and C found on underside of leaves ~5-10 cm up on 30-35 cm-tall *A. glaucodes* plants; all reared on *Aster laevis*; all just ESE Avon, Eagle County Colorado, 7800', July 27, 1996. 55 2nd-stage larvae found on *Aster glaucodes* (egg leaf was ~18-20 cm up on 38 cm branch)(egg leaf had many empty 1st-stage head capsules; egg leaf and nearby leaf had strong silk web, a third leaf had some web), reared on *Aster laevis*, one 4th-stage diapaused, adults emerged Sept. 30-Oct. 8, 1996; Game Creek, northern edge Minturn, Eagle County Colorado, 8050', Aug. 24, 1996.

EARLY STAGES (supplementing Scott 1994). Duration of egg-larva-pupa in lab ~41 days. **OVIPOSITION.** Average number of eggs per cluster is about 91 (among 3 egg clusters and six 1st-stage larva clusters, the count was 22-137, N=9; the three egg clusters averaged 91 eggs, the six 1st-stage clusters averaged 57, as perhaps some mortality occurred among 1st-stage larvae). Females oviposit on leaf undersides, preferably on a stem that is in partial shade (eggs are less often laid on stems that get a full day's sun). The oviposition leaves are low on the plant to about halfway up (as low as 9% above ground to top, as high as 50% from ground to top), averaging 35% of the distance upward from ground to the uppermost stem tip (in other words, ten clusters of eggs/hatched eggs occurred an average of 12 cm above ground on plants that averaged 34 cm in height) (the stems at this time of year only have immature flower buds or none, plus a dozen or several dozen leaves, because the flowers tend to bloom later). **EGG** greenish-cream, with ~22 vertical ribs, duration ~7 days in lab. **LARVAL HABITS.** Older larvae tend to move higher on the plants in part because the basal leaves turn brown and dry up; older larvae were on top of leaves of 20-50 cm plants, and older larvae tend to spread to other nearby plants. 1st-stage larvae skeletonize leaf underside near eggshells, while 2nd-3rd-stage larvae eat pits on leaf undersides; 4th-mature larvae eat leaves from the edge. **SILK WEB.** 1st-stage larvae always spin a strong silk web on the underside of the leaf on or beside the eggshells and where they feed. 2nd-stage larvae nearly always spin a strong silk web, but silk web was not noticed for later larval stages. **DIAPAUSE STAGE.** 4th-stage larvae hibernate. New research shows that few larvae hibernate when eggs or 1st- or 2nd-stage larvae are collected then reared in lab; only when 3rd-stage larvae are collected, have they experienced natural photoperiod which has programmed many of them to diapause; thus many of the larvae of Scott (1994) diapaused, because many of those larvae were collected in the 3rd-stage. Thus there does not seem to be any difference between lab diapause of the species of *Phyciodes* (*Phyciodes*), so I have removed that character from the table.

LARVAL STAGES AND HEAD WIDTHS. Duration of larvae-pupae in lab ~34 days. Head widths of numerous head capsules and larvae indicate six larval stages, with these head widths: 1st-stage ~0.28-0.3 mm, 2nd-stage ~0.4, 3rd-stage 0.6-0.8 (mode 0.7), 4th-stage 0.85-1.5 (mode 1.2), 5th-stage 1.5-2.0 (mode 1.7), 6th-stage 1.9-2.65 mm (mode 2.3). **1st-STAGE LARVA** yellowish-cream (ochre-cream in some darker families) when young, developing green innards after feeding (so the top of body in dorsal view takes on a slightly bluish-green tint), with the usual slightly-creamier elliptical (longer anteroposteriorly) bumps (one small middorsal bump above D1 seta, one larger subdorsal bump below D1 and in front of D2 and above SD1, one supralateral bump above L setae, one smaller lateral bump between L1-2, and perhaps a tiny sublateral one; these bumps seem to occur near where scoli appear in the 2nd-stage), with no trace of brown bands or lines, though some larvae have a weak subdorsal brown band; when about to molt larva becomes tan or ochre-tan (the innards still a little greenish so top looks greenish) with some brownish (light-brown on some paler families, to red-brown on dark families) bands (one middorsal line, one adjacent line, a wide subdorsal band, a lateral line), the creamy bumps are now smaller and round (the subdorsal cream bumps are connected by a weak creamy band on abdomen the, same band conspicuous on mature larvae), (some of these older larvae are rather colorful with a greenish top and slightly ochre sides and red-brown subdorsal band and creamy bands and bumps); collar and head black. **2nd-STAGE LARVA** when young greenish-cream, with fairly-weak or stronger pattern including a middorsal brown (sometimes greenish when young) line, a brown line near it, a dark-brown or brown subdorsal band, and a lateral brown line, body becomes greenish-tan, then becomes light-brown with the same bands and lines being dark-brown, many larvae have slightly-creamier bands in the same positions as older larvae (subdorsal and lateral); scoli are now present, BD1 and BD2 scoli brown-tan, BSD scoli brown with cream tip, BL1 scoli cream-tan; collar and suranal plate brown; head brownish-black, with paler vertex streak, some larvae have a paler (brown) frontoclypeus spot, head width 0.4-0.55 mm.

OLDER-MATURE LARVA. Most characters of larvae are quite variable. The larval body varies from black to fairly-orangish brown (most are blackish or dark-brown); larvae from Mesa and Montrose Counties were more orangish-brown. The subdorsal cream band on larval body is nearly always strong, rarely very narrow or only 80% complete; this band averages stronger in *anasazi* than in subspecies *apsaalooke* and *lakota*. The BL1 (lateral) scoli varies greatly in color: most are tan or orangish-tan, but some are light-brown or ochre, a few are brown, orange, orange-brown, or creamy. The orangish ring around BL1 scoli is most often orange-brown, but is commonly orangish-brown or brownish-orange, seldom orange or brown. The orangish dash beside BD2 scoli is most often brownish-orange, commonly orange-brown, sometimes orange. The scoli tips of older larvae vary from blackish to cream (they are dark in other *batesii* subspecies) About a third of older larvae have the frontoclypeus black (this character is also genetic and varies greatly between families).

PUPA. In overall appearance, pupae are most often orangish-tan, often are creamy-tan, sometimes are creamy-gray or creamy, and rarely are pale-brown, orange-brown, brown, reddish-brown, gray, mottled blackish, mottled slightly-orangish-black, or black-and-cream. Pupae average slightly more orangish than *apsaalooke*. But the main difference from *apsaalooke* is the somewhat weaker brown mottling on pupal wings. This mottling is weak or moderate, sometimes strong; the wing usually has only a weak browner spot near end of discal cell, the area along anal margin dorsal to 1A is only slightly brown, and the streaks near apex and near tornus are absent or very weak; these pupae were from many mothers so this difference from *apsaalooke* seems real. The pupal

ridges and cones are most often moderate in size, but almost as often are small, sometimes are strong. Cremaster very rugose in nearly all pupae, a few moderately rugose. Pupal duration in lab ~9-10 days males, ~10-11 days females. **EMERGENCE LAG** 3.3 days (=average number of days that lab-raised females emerge after males).

BETWEEN-FAMILY VARIATION. Amazing variation was found between families, in most traits of adults and immatures. Among adults, large black unf spots occurred with high frequency in families from Mesa and Montrose Counties, and a family from Deep Crk. in Eagle County had large black spots and even had a blackish postmedian upf band on females. Some families had small black unf spots, including one of three families from Avon in Eagle County and a family from Game Creek at Minturn in Eagle County. The posteriormost black median unf spot on Deep Creek adults (both sexes) had an hourglass-shaped distal margin (indented in the middle) which was not noticed on other families. The color of the crescent in the unh marginal brown patch of males varied greatly also: the more heavily black-spotted families had the crescent mostly cream or yellow, whereas one family from San Miguel County had the crescent brown in all 5 males yet another family from there had 8 males with cream and 5 males with yellow crescents, and the same difference occurred between two families from Radium in Grand County, and between two families from Avon in Eagle County. The frontoclypeus of older larvae had a large cream spot in all larvae of one family, other families had a cream spot or small orangish spot, in other families the frontoclypeus was black or had an orangish or cream spot in different individuals within the family, and lastly in the families with the largest black spots the frontoclypeus was most often black but sometimes had a small orangish spot. The tips of larval scoli were blackish in families with large black unf spots on males, but creamy in families with small black spots. The larval body color varies somewhat between families, as does the shade of orangish near the scoli bases. Pupal color varies somewhat between families also, as does the height of pupal ridges and cones. The pupal wing mottling seems to be weaker on the families that have the largest unf black spots on male adults, but otherwise there seemed to be no correlation between the two characters. Some families had some adults with a paler unh margin on males.

7. *PHYCIODES PULCHELLA* (BDV.) 1852

NOMENCLATURE. William Henry Edwards was first reviser in making *campestris* a synonym of *pratensis*, in his Synopsis of North Amer. Butterflies (Edwards, 1873).

Gerardo Lamas Müller wrote to me that the "Hofer" on the *pulchella* neotype/lectotype label (this neotype/lectotype has labels "Type *pulchella* Bdv. a/c Hofer.", "EX MUSAE ODRIS BOISDUVAL", and "Oberthur Collection") was probably the frenchman Maurice Hofer. This seems correct, because: 1) Maurice Hofer wrote an obituary of a frenchman Ernest Dollfus (Petites Nouvelles Entomologiques 1:201-212, 1872), 2) Dollfus was from Alsace, an area of France where Oberthur also lived (in Rennes France), and 3) Boisduval's collection went to Oberthur probably shortly after Boisduval's death in 1879, so Hofer apparently lived at the same time as Oberthur. William Barnes purchased the North American species in the Oberthur collection (Mallis 1971). Charles Oberthur lived 1845-1924, and William Barnes lived 1860-1930 but did not graduate from medical school until 1886 and sold his collection about 1922. Thus, the *pulchella* specimen must have taken this route: it was collected in California by Pierre J. M. Lorquin, sent to Boisduval who named it *pulchella*, Boisduval died and his collection was sold to Oberthur and around this time Maurice Hofer wrote or had something to do with the label "Type *pulchella* Bdv. a/c Hofer", Oberthur sold the specimen to William Barnes probably between 1886-1922, and finally the Smithsonian purchased Barnes' collection about 1922. I still do not know what "a/c" means on the label; probably it is written in french, as the word "type" on the same label is the same in french and english so the whole label could be written in french, so "a/c" might NOT mean "according to" or "accessioned by" or "acquired from collection of" Hofer. Regardless of how this label was written, the specimen remains the neotype/lectotype, and *pulchella* remains the valid name.

I must reemphasize that when Boisduval wrote in his publications a species name immediately preceding the name of an author, he was absolutely NOT stating specifically that that person named that species! He was merely stating that that person wrote a paper that had something to do with that species which usually was originally named by someone else! Boisduval's citations have absolutely nothing to do with homonymy. We must not pretend that our current customs of citation and nomenclatural practice bear any resemblance to those practiced six generations ago (146 years ago), when western civilization was still in the steam age.

Interestingly, 121 years ago W. H. Edwards (1877) listed *pulchella* Bd. (as well as *campestris*) as a synonym of *Phyciodes pratensis*, so even at that time some respected lepidopterists believed that the name *pulchella* belonged to *pratensis*, and did not belong to *P. tharos*.

7A. *PHYCIODES PULCHELLA PULCHELLA* (BDV.) 1852

DIAGNOSIS. The orange-antenna portion of what Scott (1994) called subspecies *pulchella* is split off and named as a new subspecies *owimba* below, so a rediagnosis of subspecies *pulchella* is needed here. The antenna club nudum is black (Scott 1994). Adults from the central Coast Range

of California (including the type locality of *pulchella*, San Francisco, and nearby areas in Contra Costa County such as Point Richmond, etc.) are a little larger in size (the largest in the species), and the male forewing is a little more truncate (less pointed). Males from there have a more strikingly two-toned blackish ups wing pattern, in which the ups ground color is a little darker (blackish-brown), and the submarginal orange upf and uph bands are a little smaller, both features producing a darker appearance, yet the upf discal cell spot and upf median band and (most noticeable) the uph median band average a little larger and paler (ochre-yellow in color). The contrast between the darker ups ground color and submarginal areas and the lighter median bands creates more of a two-toned appearance of males, which is somewhat reminiscent of the two-toned appearance of *P. orseis orseis*, which also occurs in the northern Coast Range of California; this similarity evidently adds still another example of convergence to the many examples of convergence already documented in *Phyciodes*. Other distinguishing features: the uns is almost uniformly orange mottled with yellowish, the black unf spots are small (only two are present, on inner margin, and these are usually small although variable [the posterior median black spot varies from absent to fairly large, but averages smaller than *owimba* and larger than *montana*]), the marginal unh patch and crescent are weak (the patch is light in color--orange-brown--when present, and averages smaller than *owimba* and larger than *montana*, and the crescent is yellow so contrasts little with the ground color), and the unf discal cell bar is yellow.

SUISUN MARSH POPULATION. Arthur Shapiro has studied this population and compared it to subspecies *deltarufa* (named below). It occurs at Suisun (Solano County California, at the west edge of the Central Valley near an eastward finger of San Francisco Bay). Adults are large and are very dark like coastal subspecies *pulchella*, but have a strange pattern of voltinism: adults are often not seen until Aug. or Sept., but in some years there are three full generations as in subspecies *deltarufa*. **HOSTPLANT:** *Aster chilensis lentus* at Suisun (Shapiro, pers. comm.). This plant *lentus* is listed as endangered, and is treated as a separate species in the new Jepson flora, but grades into *A. chilensis* according to both the Jepson flora (Allen 1996) and Arthur Shapiro (pers. comm., see below), so I will list it as a subspecies.

7A. *PHYCIODES PULCHELLA PULCHELLA* small variety

DIAGNOSIS. Adults from northern California, the low-altitude Sierra Nevada (up to rather high elevations in the southern Sierra), and southern California, all resemble subspecies *pulchella* by having a blackish antenna club nudum (the nudum is black throughout California, except probably for some orange individual variants in extreme N California), blackish ups, unspotted orange uns, and similar slightly-two-toned wing pattern on both ups and uns, but these adults are small in size (like subspecies *owimba* and *camillus*) and the forewings are not as truncate.

EARLY STAGES. These were reported by Scott (1994) from high-altitude Inyo County California.

7B. *PHYCIODES PULCHELLA DELTARUFA* SCOTT 1998, NEW SUBSPECIES (Figs. 34-35)

DIAGNOSIS. This taxon occurs in the Sacramento River delta area of California. Adults resemble subspecies *pulchella* in black antenna nudum color and uns color and size of ups spots, but are smaller in size (the size of *montana*) and have the ups usually oranger or yellower, with the uph pale submarginal line stronger. Thus in color *deltarufa* seems to be somewhat intermediate to the high-altitude subspecies *montana*, even though its habitat is near sea level. But considering all traits, *deltarufa* seems to be a low-altitude *pulchella* that has simply become oranger, so that traits such as the yellow unf discal cell bar remain as in subspecies *pulchella*. If the oranger color of *deltarufa* does have a phylogenetic origin from introgression from subspecies *montana*, the genes that help subspecies *montana* thrive at high altitude evidently did not transfer to *deltarufa*. Arthur Shapiro (pers. comm.) notes that *deltarufa* exhibits a striking seasonal diphenism (unknown elsewhere in the genus), with the summer generations very orange, in contrast to the lack of seasonal diphenism in coastal adults (including the subspecies *pulchella* population at Suisun Marsh to the west, which has large very black adults). The delta home of *deltarufa* is hotter than coastal areas such as San Francisco and Point Richmond where the large black subspecies *pulchella* thrives. The amount of orange is somewhat variable in *deltarufa* and some adults are as dark as subspecies *pulchella*, but most adults are much oranger, so this set of populations is visually quite distinctive and thus seems to be a valid subspecies. The antenna club is mostly rather elliptical, and the club nudum is mostly dark: in males the nudum is brown or mostly brown in most males and orange-brown in some males, orangish in a few (the border and lattice are brown or dark-brown, but the steps are always narrowly orange in most males, to widely orange in some); in females the nudum is mostly brown in about half the females, mostly orangish in about half, and intermediate in some (the border and lattice vary from brown to orange-brown, and the steps are narrowly orange in some to widely orange in most). **RANGE:** So far known from in and near the Sacramento River

delta, in the bottom of the Central Valley east of the Coast Range, from Bethel Island in Contra Costa County, to Davis in Yolo County, to Grizzly Island in Solano County. **NAME** is from the delta locality and oranger coloration (rufus is the latin word for orange, so I have taken the letters “ruf” from rufus and added –a to make the word euphonius, so the ending is intended to be pronounced nicely and is not intended to be latin or the latinized feminine form, so the name should NOT be emended to *deltarufus*). **TYPE LOCALITY**: Willow Slough just north of Davis, Yolo County California. Adults were common there and fed on *Medicago sativa* flowers, and courtships were observed about these flowers (mating pairs were found at 12:31, 13:30, 14:00, one female of which flew toting the male, as is typical of *Phyciodes*). **TYPES**: Holotype male and allotype female (both BMNH) and numerous paratypes from type locality Aug. 31, 1974, many paratypes from type loc. Sept. 2, 1974, paratype female from Bethel Island, Contra Costa County California, Aug. 31, 1968. **GENERATIONS**: three generations occur at the type locality (A. Shapiro pers. comm.) and evidently everywhere in the range, at least May to late Sept. **HOSTPLANT**: At the type locality the host is *Aster chilensis*, which is very variable but does not show characters of *Aster chilensis lentus* (A. Shapiro pers. comm.). At Grizzly Island the host is an *Aster chilensis-lentus* hybrid swarm (Shapiro pers. comm.; *lentus* is listed as a species in the new Jepson flora [Allen 1996], but would seem to be a subspecies of *chilensis* as Shapiro and the Jepson flora both mention intermediacy); this island is just southeast of the subspecies *pulchella* population at Suisun, yet its population is mostly like *deltarufa*.

7C. *PHYCIODES PULCHELLA MONTANA*

DIAGNOSIS. The antenna club nudum is dark as in subspecies *pulchella*, despite the very orange wings. The uns is mostly-unmarked orangish like subspecies *pulchella* but is even less marked, with the unf black spots even smaller (usually almost absent), and the unh marginal orange-brown patch even weaker (usually absent), and even the unf discal cell bar is usually orange (thus absent against the surrounding orange). It also shares the same basic two-toned ups pattern of *pulchella*, except the ups is **much oranger**, making *montana* very different in appearance. Adults are smaller than the central Coast Range variety of *pulchella*, but are the same size as subspecies *pulchella* (small variety) from the rest of California. The uph submarginal orangish line is rather strong. **INTERGRADATION.** Arthur Shapiro (pers. comm.) found a blend zone between *montana* and *pulchella* in Plumas and Sierra Counties in the northern Sierra Nevada: wildly variable intergrades are abundant at Caribou, near Butterfly Valley, and all through that part of the Feather River country. In addition, Shapiro found intergrades abundant in Sierra Valley in the 1970s and 1980s, but not recently so they possibly have become depopulated or rarified by development etc. there.

7D. *PHYCIODES PULCHELLA OWIMBA* SCOTT 1998, NEW SUBSPECIES (Figs. 36-37)

DIAGNOSIS. This subspecies is defined by its antenna club nudum, which is orange as in subspecies *tutchone* (whereas it is blackish in subspecies *pulchella* and all other subspecies), and by other less-distinct characters: Adults are smaller and the forewings seem a little more extended than the topotypical California central Coast Range variety of *P. pulchella pulchella*, but are the same size and shape as subspecies *pulchella* from the remainder of California. The male ups averages less two-toned than subspecies *pulchella*, because the postmedian ups orange bands average a bit larger, and the upf discal cell bar and upf and uph paler median bands average a little less conspicuous (the discal cell bar averages smaller) and average oranger than subspecies *pulchella*. The uns resembles subspecies *pulchella*, being rather uniform orange with few spots and these are small, except the unf black tornus dash and unf posterior median black spot average larger than subspecies *pulchella* (the posterior median black unf spot varies from absent to large in individual *montana*, *pulchella*, and *owimba*, but the average spot size increases from *montana* [usually absent] to *pulchella* [averaging small] to *owimba* [usually a long but narrow black streak], then is smaller again in *tutchone* [averaging small]), and the unh dark marginal patch averages stronger (this patch when present is only orange-brown in all these subspecies, paler than the brown/dark-brown patch of *P. tharos*/*P. cocyta*). Subspecies *owimba* is thus somewhat intermediate between subspecies *pulchella* and the Yukon-Alaska subspecies *tutchone* when all traits are considered; *owimba* is a little bigger than *tutchone*, has less neat rows of paler ups spots, the pale bar in the upf discal cell is bigger, the upf base averages slightly darker, the posterior median unf black spot tends to be larger, and the unh marginal crescent tends to be yellower. Subspecies *owimba* was called “near-*pulchella*” by Scott (1994), although a better name would have been “*P. pulchella* orange-antenna variety”; it is raised to subspecies status in the current paper, because it differs in several characters (antenna color, size, wing shape, ups and uns pattern) from topotype *pulchella*, and because the other geographic taxa with differently-colored antennae in other species have also been raised to subspecies status (the two western orange-antenna subspecies of *P. batesii* were named separate subspecies by Scott 1994, and the orange-antenna subspecies of *P. tharos* is named subspecies

orantain in the current paper). **RANGE.** I have examined this subspecies from Oregon (northern Oregon at least; subspecies *pulchella* may occur in southwestern Oregon, and occasional adults in the Cascades resemble subspecies *montana*), Washington, Idaho, Montana, southern British Columbia, southern Alberta, and it is also known to extend barely into the Cypress Hills of Saskatchewan. It occurs throughout Montana, where adults from just north of Yellowstone Park (Falls Creek Campground, Sweetgrass County) also have orange nudum and are mostly typical *owimba* (they are not intergrades to *camillus* as I wondered in Scott 1994). **NAME.** The name is from the main range Oregon Washington Idaho Montana British Columbia Alberta. And the letters of the name could also signify Orange-Within-Matrix-of-Brown Antenna. Therefore this is not a latinized name and the final letter -A is not a latin suffix, so the misguided anachronistic nomenclatural pedants who enjoy emending suffixes to make each genus-species combination either male-homosexual or lesbian, but never heterosexual, should not emend this name to "owimbus." (Those mindless nomenclatural pedants can change the name of this subspecies when they succeed in changing the name of the province of Alberta to Usberta.) **TYPES and TYPE LOCALITY.** Holotype (BMNH) male Pattee Canyon, 3500', Missoula County, Montana., June 23, 1962, 8 male 1 female paratypes same site June 22-23, 1962.

7E. *PHYCIODES PULCHELLA TUTCHONE*

DIAGNOSIS. This subspecies is related to *pulchella* and *owimba*, as the uns is quite orangish with uns black spots nearly absent (being small on tornus and median inner margin of unf). The antenna club nudum is orange like *owimba*, not black as in *pulchella*. Adults are a little smaller in size than ssp *owimba* and *pulchella*, and the ups is more uniformly mottled with neat rows of more unicolorous orangish spots (the postmedian upf band has more-uniform-sized orangish spots). The upf paler discal cell spot is less conspicuous (smaller and oranger) than subspecies *owimba* and *pulchella*, and the upf base is oranger. The male fw is moderately pointed, but not as pointed as subspecies *camillus* and not as truncate as San Francisco *pulchella*. The unf discal cell bar is yellow or orange. The unh has a fairly-strong orange-brown marginal patch whose crescent is usually cream but sometimes yellow.

7. *PHYCIODES PULCHELLA OWIMBA/CAMILLUS* INTERGRADE POPULATIONS

ADULTS. Subspecies *camillus* is evidently the same species as *P. pulchella*, as there seems to be some intergradation in the higher mountains of northern Wyoming. Adults in low-altitude Bighorn Mts. Wyoming have antenna and underside like *camillus*, but average a little darker on the ups, and larvae are a little darker, as discussed in Scott (1994). Since then I have collected adults from the higher-altitude Bighorn Mts., which seem to show intergradation. All adults from the foothills seem to have black antenna club nudum. But at upper altitudes, 9 males 5 females have black nudum, 4 males 3 females have orangish-black nudum, and 4 males have orange nudum. Wing pattern varies considerably in these upper mountains also, from like *camillus*, to like *owimba*, with many intermediate. A few specimens from the higher-altitude Wind River Mts. Wyoming suggest that there is some *owimba* influence in this range also. (A series of 5 males from Falls Creek Campground, Sweetgrass County Montana [in the mts. next to Yellowstone Park], a locality mentioned by Scott [1994], are mostly subspecies *owimba* with little influx of *camillus*.)

7F. *PHYCIODES PULCHELLA CAMILLUS EDW. 1871*

HOSTPLANT RECORDS (in addition to Scott 1994). Many *Aster fendleri* plants were searched but had no eggs, so *fendleri* is probably not a host (or is a very rare host) because its leaves are too small and narrow; 1 mi. east of Morrison, Jefferson County Colorado, Oct. 10, 1995, Sept. 16, 1996. Five older larvae (two 6th-stage, three 5th-stage) found resting in litter under *Aster porteri* (found by noticing feeding damage on leaves), these larvae found at 15:00 in sunny weather, so the larvae evidently feed at night; preoviposition 13:30 *A. porteri*; Green Mtn., Jefferson County Colorado, May 7, 1996. Oviposition 11:29 of 35+ (I disturbed her twice) eggs on *A. porteri* leaf uns, Lookout Mtn., Jefferson County Colorado, June 10, 1996. Oviposition, she fluttered and landed on *A. porteri* seedlings from 11:00-11:02 then settled on one *porteri* seedling and laid cluster of 119 eggs from 11:20-11:45 on leaf uns 2.5 cm above ground, hatched June 12; Ralston Butte, Jefferson County Colorado, June 3, 1997. Oviposition 10:46, female flew out from *A. porteri* seedling clump as I walked near, and 32 eggs were found on leaf uns there, hatched June 15; Green Mtn., Jefferson County Colorado, June 6, 1997. 19 late-2nd-stage and 3rd-stage larvae found on leaf uns on about 5 stems of one *Aster foliaceus* clump; Maloit Park, south edge Minturn, Eagle County Colorado, 8200', Aug. 24, 1996, reared on *Aster laevis*, adults emerged Oct. 4-10, 1996. ~30 1st-stage (and a few 2nd-stage) larvae in dense silk web covering distal 3 cm of tender basal shoot (among mature stems) of *Aster ericoides* var. *ericoides* (stem hairs appressed, involucre 3-4 mm tall, but petal count 20, 20, 20, 22); Barr Lake, Adams County Colorado, 5075', Sept. 9, 1996; reared on *Aster laevis*, *hesperius*, and *porteri*, adults emerged Oct. 20-Nov.2, 1996; one larva

diapaused as 4th-stage (head width 1.4 mm) for several weeks. Adults associated with *Aster ascendens*; south of Cucharas Pass, and east of Stonewall, Las Animas County Colorado; Sept. 1, 1996. Adults associated with *Aster glaucodes*; southeastern end Green Mtn. Res., Summit County Colorado, July 11, 1996 (5 adults), July 19, 1996 (1 adult). Lot B, 75 2nd-stage larvae and two 1st-stage larvae found on leaf uns 9 cm above ground on 15-cm-tall *Aster foliaceus* plant, a very strong sheen silk web on uns of oviposition leaf, and much web noted later in lab through Sept. 2, in sunny meadow in valley bottom, reared to adults; lot C, 17 2nd-stage larvae found on leaf uns 15 cm above ground on 39-cm-tall *A. foliaceus* plant, much web noted on uns of this and two adjacent leaves, in sunny meadow in valley bottom, reared to adults; lot E, four 2nd-stage larvae found on leaf uns 8 cm above ground on 8-cm-tall *A. foliaceus* seedling, some silk web noted under a tiny 2 cm leaf and a strong sheen web noted later in lab, on S-facing slope base, 60 cm from lot C (and 60 cm from *P. cocyta* lot D), not reared to adults but identified by larval color pattern; E part of Vail, ~8300 ft., Eagle Co. Colo., Aug. 22, 1997. Lot G, cluster of ~65 2nd-stage larvae and one 1st-stage larva found on leaf uns 15 cm above ground on 25-cm-tall *Aster ascendens* plant, much web noted on leaf uns and later in lab, adults reared; on NE-facing slumping bank of mesa, 3.7 mi. N of I-70 (=Dillon Res. dam), 8550 ft., Summit Co. Colo., Aug. 25, 1997. Adults assoc. *Aster porteri*; Mt. Zion, Jefferson Co. Colo., Sept. 1, 1997. **HOSTPLANT SUMMARY.** *Aster foliaceus* is a popular host; it is a somewhat wide-leaved rather lush-looking species, so is an exception to Scott's (1994) rule that *P. pulchella* chooses small-leaved rough and hairy asters, although the previously-known host *Aster chilensis* looks a little lush as it has somewhat tender leaves that are about half as wide as *A. foliaceus*. But even this butterfly will not eat a truly rough and dry very-small-leaved species such as *Aster fendleri*.

EARLY STAGES. **EGG** duration 9 days. **SILK WEB** of 1st/2nd-stage larvae is strong in all families. **MATURE LARVA.** The frontoclypeus of larvae from Minturn in Eagle Co. was usually black as usual, but a few larvae had a **brown spot**. Also, a second family from Eagle Co. (Vail, lot C) had one larva with a tan spot, and a third family from nearby Summit Co. (N of Dillon, lot G) had two larvae with a brown spot. These larvae are the first I have seen with a non-black frontoclypeus in the species *P. pulchella*. All three families were reared from the same host (*Aster foliaceus*) from nearby counties in the western slope of central Colorado. So it is tempting to surmise that introgression from *P. cocyta selenis* populations that eat the same host at the same localities might have occurred to transfer genes for a paler frontoclypeus, but of course actual proof of introgression will be difficult to obtain (I have reared some larvae from the plains of Colo. that had a slightly paler frontoclypeus on pickled molted head capsules, so some of those larvae may have had a paler [brown] frontoclypeus on live larvae also). The larval body ground color of these families varied from dark-brown to blackish. **PUPA** from Minturn tan, the wing cases very weakly mottled, with no spots at all. Pupae from Eagle Co. in 1997 were mostly brownish-tan, but pupae from Summit Co. were mostly darker (brown), and some were dark-brown, some tan-brown. Wing mottling of all these *Aster foliaceus* pupae was weak.

C. THE *PHAON* SPECIES GROUP

Another trait of this group is that males of all species always patrol to seek females.

9A. *PHYCIODES PICTA PICTA* (EDWARDS) 1865

RANGE. *P. picta* evidently does **not** extend as far south as Michoacan (Andrew Warren, pers. comm.), and the record of *picta* from Pedernales Michoacan by Balcazar L. (1993) was a misidentification.

HOSTPLANT RECORDS (in addition to Scott 1994). The aster *Machaeranthera phyllocephala* (=Haplopappus annuus=Aster phyllocephala=A. annuus=Aplopappus phyllocephala=A. annuus in various floras) is a new host; but oddly, its congener *M. canescens* is not a host. Adults very local and flew only near *M. phyllocephala* seedlings (4-17 cm tall, most ~5 cm tall) and were not found away from this plant (one male remained at *M. phyllocephala* patch at least 3 hours), *Convolvulus arvensis* absent, *Aster ericoides* and *Machaeranthera canescens* scarce; Fort Morgan, Morgan County Colorado, June 14, July 17, 1995. Oviposition seen, female preoviposited 13:00 as she landed often on green-vegetated area near *M. phyllocephala* and fluttered to mowed *Artemisia filifolia* and fluttered over it and landed on it several times after circling and landing, at 13:10 she bent abdomen on it while crawling through clump, she rested on it in between crawling and bending abdomen, from 13:20-13:25 she oviposited 20 eggs on underside of tender *A. filifolia* leaves low in plant, then I interrupted her and took her 10 m away in net to see what else she would oviposit on and let her go on bed of *M. phyllocephala*, she flew fast and ignored *M. phyllocephala* and landed twice, and within 5 minutes she had found the same mowed *A. filifolia* plant (the only *filifolia* plant present at locality except 80 m away) and landed on it and crawled and bent abdomen and rested, and from 13:39-13:52 she laid 77 eggs on that *A. filifolia* then flew away (thus she laid 97 total eggs on it, which hatched Aug. 4); two other clusters of 7 and 67 new (yellowish-green) eggs (but no larvae)(hatched Aug. 3) were found on same mowed *A. filifolia* plant, which was 5, 20, 20, 35, 40, and 40 cm (common 50 cm onward) from *M.*

phyllocephala plants; adults associated only with *M. phyllocephala*; Fort Morgan, Morgan County Colorado, July 28, 1995. A female bagged on transplanted *M. phyllocephala* in garden laid cluster of 48 eggs on leaf uns (hatched Aug. 8), and the young larvae survived well and skeletonized about 6 lower leaves, but on Aug. 25 I opened net bag and found only one live 3rd-stage larva (the others evidently escaped out a hole in net), I rebagged that 3rd-stage larva and 10 ~4th-stage lab larvae onto same branch, and these larvae lived a week or so and molted since many head capsules were found, then all but one shriveled and died (due to moisture loss from being forced to be up on the plant during the day?). In lab jars, older larvae ate none of *Artemisia filifolia*, ate none of *Artemisia scopulorum*, ate much of *Machaeranthera phyllocephala*, ate a lot of *Aster laevis*, and ate a lot of *Convolvulus arvensis* (their favorite--when *C. arvensis* is in a jar with *A. laevis* and *M. phyllocephala* and *A. filifolia* and *M. canescens*, larvae eat all the *arvensis* and less of *laevis* and *phyllocephala*, and eat none of the *filifolia* or *canescens*). Therefore *M. phyllocephala* seems to be the host at Fort Morgan (even though lab larvae like it less than *C. arvensis* and *A. laevis*). No adults were seen at Fort Morgan, Morgan County Colorado June 23, 1996, but adults were common there July 15, 1997; at this site in 1996-1997 *M. phyllocephala* grew only near the road intersection and not westward where ovipositions and most adults were found in previous years, though a few plants were found in 1997 near the *Artemisia filifolia* bush; the plants were not mowed in 1996 or 1997, so mowing/grazing may not be absolutely necessary to support populations of this species. Adults associated with *C. arvensis*, north of Penrose, Fremont County Colorado, Aug. 31, 1996.

HOSTPLANT SUMMARY. *M. phyllocephala* is a sticky annual weed (it resembles *Grindelia squarrosa* closely, and both have yellow flowers), and it is somewhat surprising that this sticky plant is a hostplant. *M. canescens* is also a little sticky and has similar leaves, but is not a host. Evidently some biochemical(s) in these two plants are used by the butterfly to discriminate between them. *M. phyllocephala* may be a host in many areas of the Great Plains, because its range (NE Colorado, western Nebraska, south to C Okla., Texas, and New Mexico, but absent in Arizona) fits the plains range of *P. picta*. *M. phyllocephala* was probably also an original host (before *Convolvulus* was introduced, which is the favorite host now).

EARLY STAGES (a new rearing from Fort Morgan; which corrects the frontoclypeus color).
SILK WEB. Young larvae make **very little** silk web: some 1st-stage larvae spun some web on a leaf that was not the oviposition leaf, and some 2nd-stage larvae made a little web on large *A. laevis* leaf and several days later made very little web (a small amount on one spot of one leaf).
DIAPAUSE STAGE. 4th-stage larvae undoubtedly diapause, based on other *Phyciodes*. **EGG:** pale-yellowish-green when laid, turning yellowish-cream, with with 23 or 24 (some counts were 22, 26) vertical ribs on upper half; averaging 55 eggs/cluster (range 6-140, N=18); duration 7 days in Colorado. **1st-STAGE LARVA** ochre-cream with a very slight pinkish tint, the innards becoming greenish due to food, a subdorsal band formed of brown pinaculi (seta bases), setae blackish, collar and suranal plate brown; head blackish; duration 5 days. **2nd-STAGE LARVA** cream-tan with some brown bands, the scoli arise from broad tan mounds, a slightly-brown line between tan bases of BD1 and BD2, an irregular (narrow between BD2 and BSD scoli, broad elsewhere) brown band runs between BD2 and BSD scoli, a very slight irregular browner line below BSD scoli, a weak browner line below BL1 scoli; head dark-brown. **3rd-STAGE LARVA** tan, with dark-brown bands; when young a slightly-brown heart-band, a wide tan band, a small slightly-brown area between the wide bases of BD1 and BD2, a slightly-creamier subdorsal band contains BD2 scoli, a dark-brown line connects bottom of BD2 scoli, a wide brown dorsolateral band encloses BSD scoli on its lower part, a tan band, a slightly-browner slightly-irregular line just above BL1 scoli, a creamier lateral band runs between BL1 scoli, a brown line just below BL1 scoli, underside light-brown; head blackish-brown. The older 3rd-stage larva body is browner, with a brown heart-band including tan BD1 scoli, a tan band, a sinuous brown line, a cream-tan subdorsal band includes tan BD2 scoli, a wide dark-brown band includes some paler small blotches near its lower part and includes tan BSD scoli in the bottom part, a broad tan area includes a very sinuous weak brown "line", a slightly-cream lateral band includes tan BL1 scoli, a light-brown line below BL1 scoli, underside brownish-tan except for the tan BL3 scoli; head solid brownish-black.

4th-STAGE LARVA same as mature larva but a little darker brown. **5th-STAGE AND MATURE LARVA** (Fort Morgan) from far away looks striped with orangish-tan and dark-brown bands and cream lines and blackish head: the detailed pattern starts with a dark-brown heart-band that includes BD1 scoli, an orange-brown (sometimes brownish-orange) crescent clasps side of each BD1 scoli and rests in a narrow tan (the tan has a slight grayish--almost sickly-pale-greenish--tint) stripe, a brown band is above BD2 scoli, a subdorsal strong uninterrupted tanish-cream band includes the BD2 scoli and becomes light-orange in front of and behind each BD2 scoli, a broad dark-brown band encloses the BSD scoli on its lower edge, a tiny orangish-brown (sometimes brownish-orange) spot or crescent rests on anteroventral or entire ventral edge of BSD scoli, a tan-cream (with a slight grayish--almost sickly-pale-greenish-tint) band just below BSD scoli, a wider orangish-brown band touches top of the BL1 scoli, a brownish-orange ring all around each BL1 scoli, a tanish-cream lateral band encloses most of each BL1 scoli, a dark-brown line is below that, underside light-brown, all scoli cream-tan. Collar narrow and blackish with large pale seta bases. Other pattern details as in Scott (1994). **Head** blackish-brown, taller than *tharos*-group, a long cream (or tan ventrally and cream dorsally) vertex stripe (not constricted to form satellite spot) on top of head extends posteriorly to neck (this vertex stripe sometimes prominent, but often dark [brownish] and sometimes nearly absent), coronal sulcus/cleavage line cream from neck to adfrontal

sulci, frontoclypeus **brown** (except a tiny creamier dot is at top of frontoclypeus) including brown across bottom and lower corners on the "clypeus", adfrontal areas **brown**, a cream line runs along adfrontal cleavage line, cream or tan extends from lower corner of frontoclypeus on lower face (gena) to a cream or tan ring all around eyes (the eyes rest in a brown patch and the 4 adjacent eyes are on the border of the brown patch) (this cream area surrounding the eyes is sometimes prominent but is often dark [brownish] and sometimes is nearly absent), this cream or tan area extends posteroventrally from eye ring to rear mandible articulation (head narrowly brown just above front and rear mandible articulation), a small cream or tan spike angles upward from top of pale eye ring, a broad cream band mottled with brown extends rearward from cream eye ring to rear of head, membranous area above labrum cream, labrum brown. The frontoclypeus is **brown** (not cream as stated in *Papilio* #7 based on pickled larvae), as are the adjacent adfrontal areas, the whole brown area surrounded by a cream line along the adfrontal cleavage line; the cream coronal sulcus and adfrontal sulci form a **cream inverted-Y that readily identifies *P. picta***.

PUPA (Fort Morgan, Colorado). Very young pupae (an hour or two old) have abdominal pattern like the larva (the same tan and brown and cream bands), but wing cases/head/front of thorax are translucent dark-bluish-green; then the abdomen lightens somewhat and the wing cases etc. turn green. Overall color of older pupae variable: most are tan, but some are creamy-tan, some are tan-brown (many of these are slightly-orangish-light-brown), a few pupae are brown, rarely dark-brown. Wing mottling mostly weak (only the discal cell spot really noticeable), though the darker pupae have a dark streak from discal cell to margin and a small tornus spot and a darker anal (dorsal) margin; the base of hindwing is also dark on the darker pupae, as is T2-3 adjacent to the wing bases. All pupae have a slightly-creamier subdorsal abdominal band. The proboscis and sustensor ridges (of cremaster base) are darker distally (orange-brown on pale pupae, blackish on dark pupae) and the proboscis tip is always blackish. The usual rows of tiny brown abdominal dots occur. The head lacks pattern on the pale pupae but has the usual pattern on the brown pupae. Ridges and cones are so weak as to be nearly absent. Further pattern details as in Scott (1994).

10A. *PHYCIODES PHAON PHAON* (EDWARDS) 1864
 (=“orange-band variety”)
 (Figs. 38-39)

DIAGNOSIS. The type locality of *phaon* is St. Simons Is., Glynn County Georgia. Series of specimens that I have examined recently (since Scott 1994) from southern South Carolina and southern Florida have the pale upf median band orangish-yellow. Therefore *phaon* is characterized by this orangish-yellow band, in contrast to the whiter band of specimens from Arizona-Mexico, so Florida specimens should not be called the “orange-band variety” as Scott (1994) labeled them; instead the western subspecies is named below. I have not seen specimens from the intervening area (Ala.-Miss.-La.). The median uph band is orange, not ochre, and this uph band is fused with the postmedian uph orange band in about a third of adults.

10B. *PHYCIODES PHAON JALAPENO* SCOTT 1998,
NEW SUBSPECIES
 (Figs. 40-41)

DIAGNOSIS. The pale upf median band is cream-colored, whereas it is orangish-yellow in South Carolina-Georgia-Florida subspecies *phaon* as noted above. In addition, the uph median band is usually a little paler (ochre) whereas it is just as orangish as the postmedian uph band in subspecies *phaon*. Also, the uph median and postmedian bands are nearly always separated by a strong black line in *jalapeno*, whereas this line is absent (thus the two bands fuse) in a third of subspecies *phaon* adults. **NAME.** This subspecies occurs in the ancestral land of chiles, in a hot climate, and is small, so I give it the name of a hot little chile. The spelling is required by ICZN to lack the spanish , but the name should be pronounced “hallapainyo” as if the were present. **TYPES:** Mesa, Maricopa County Arizona, holotype male and allotype female (both BMNH) and 3 male 1 female paratypes Aug. 4, 1962, 2 female paratypes Aug. 5, 1962, all collected by R. Arbogast. **RANGE.** Texas, New Mexico, Arizona, California, and all of Mexico (I have seen adults from Sinaloa, Tamaulipas, Nuevo Leon, and Quintana Roo). Riley’s (1975) fig. of a Cayman Is. male had a pale-yellow upf band, so this subspecies may occur there also.

10C? *PHYCIODES PHAON ?MAYA* HALL 1928

The type male of *maya* Hall from Guatemala is very dark according to Gerardo Lamas Müller, so *maya* may apply to a distinct subspecies. But obviously, more specimens will have to be examined to confirm this, because I have seen a specimen of ordinary *phaon jalapeno* from Quintana Roo just NE of Guatemala.

DISCUSSION

Variable characters and Evolution. Recent research on *Phyciodes* continues to demonstrate the basic problem humans have with this genus, in particular the *tharos*-group: many taxa appear very similar to each other, causing great problems in classification and identification. A contributing factor to the difficulty of identification is that almost every taxon--and almost every population--is quite variable in nearly every trait, including the traits we use for identification. Research continues to show that nearly all characters in *Phyciodes* are variable, except some of the characters separating very distinct species, such as the extreme wing pattern of *P. phaon*. In the *tharos*-group, the length of the gnathos hook varies individually (it is short in *pulchella* but is occasionally long, for instance), nearly all wing pattern traits vary, the antenna color varies somewhat in many taxa, the amount of silk web made by young larvae varies in some taxa, larval color varies, the amount of orange varies around the larval scoli, the larval cream bands vary in strength, scoli color and scoli tips vary from pale to dark in many taxa, the frontoclypeus varies slightly to greatly in color, pupal color varies, the height of pupal cones and ridges varies, etc. etc.

Great differences also occur between families (offspring) reared from single females, differences not much less than the differences between the most different individuals. Because of the great differences between families, it seems obvious that most characters in *Phyciodes* are genetic, that most of these characters seem to be inherited multifactorially (polygenically), and that most or all populations seem to have a large amount of genetic variation.

Evolution within *Phyciodes* seems to involve mostly just a shift of the average expression of these characters due to adjustment of the frequency of the multiple genes, so different taxa merely differ by their average characteristics, with the result that extremes of variation in one taxon can look identical to the extremes of another taxon, causing problems in identification. Clear-cut differences that make for easy identification are hard to find in *Phyciodes*, perhaps because this is a successful genus that has not suffered much extinction of the confusing intermediate taxa.

Yet careful study, especially rearing the offspring of individual females, shows that there are real species that evidently do not intergrade in nature, even though many of the species and individuals are difficult to identify.

The Secret of *Phyciodes* Speciation. Evidently, the secret of *Phyciodes* is that each species has some unique pheromone(s) that allow reproductive isolation. This must be true because I already proved (Scott 1986, 1994) that courtship movements (wing and body movements) are the same in all species, and the eyes of insects are not capable of discerning fine pattern details that would allow the butterflies to identify themselves by sight alone; therefore any prezygotic reproductive isolation that occurs must involve pheromones (additional senses such as hearing are evidently absent). Thus, one species evolves into two when a population of the first species changes pheromones, creating two species where there was one, while both taxa retain all the variable characters involving wing pattern and larval and pupal pattern etc. that they had before the split. Then there are two species, which will be very similar to each other in the characters humans can see (causing our problems in identification), unless the second species evolved from some allopatric population that had sufficient time to become different before its pheromones changed.

Convergence. Numerous examples of convergence have been found. Since pheromones seem to be important in speciation rather than the color pattern and shape of adults/larvae/pupae, the non-pheromone characters--or other characters that are genetically linked with them--can adapt to local conditions, creating convergence when sympatric species adapt to the same local conditions. Convergence in regions of sympatry was found in the two-toned ups of California Coast range *pulchella pulchella* and *oriseis oriseis*, and between most characters of adults/larvae/pupae of *cocyta selenis* and *batesii anasazi*.

Convergence is also frequent between allopatric taxa. The unh brown patch has been lost by *batesii batesii* of the Appalachians/eastern Canada, by *pulchella shoshoni* from northern Nevada, and by *pulchella montana* and *oriseis herlani* from the Sierra Nevada. The antenna club nudum has become orange in some taxa of three species that also have black-club taxa, including *tharos orantain*, *batesii apsaalooke*, *batesii anasazi*, *pulchella owimba*, and *pulchella tutchone*. A narrow valva tip was evolved by *oriseis* and *mylitta thebais*. Smaller gnathos hooks were evolved by *pulchella* and *pallida*. The ups became blackish in *oriseis oriseis* and *mylitta thebais* and *pulchella pulchella*. Batesian mimicry with *Euphydryas chalcedona* models has evidently caused the evolution of oranger wing color in the unrelated *oriseis herlani* and *pulchella montana* in California, and in *batesii anasazi* in the Rocky Mts. The ups also became oranger in *pulchella deltarufa* and *pallida* and *mylitta*.

More "missing links" have been discovered. Thus *tharos orantain* is somewhat intermediate between *tharos tharos* and *cocyta*, and *pulchella owimba* is somewhat intermediate between *pulchella pulchella* and *pulchella tutchone*. Major step-clines occur in the *tharos*-group, so the taxa can be arranged in a linear sequence (the sequence shown on the tables) and many or most characters change in that sequence.

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Paul Catling kindly sent specimens and information on eastern North American *Phyciodes*, and reviewed the mss. John Rawlins of Carnegie Museum provided a slide of the type of *Phyciodes mylitta arida*. Ronald Gatrell, Andrew Warren, and Ray Stanford provided records and specimens for examination. Kenneth Hansen sent immatures and reared adults. Gerardo Lamas Müller provided information on nomenclature. Arthur M. Shapiro provided information on California taxa. Paul A. Opler reviewed the manuscript. Stephen M. Spomer and Jim Reiser provided information on antenna color of *P. tharos*. Clyde Gillette provided Utah hostplant information. Jonathan Pelham provided information on life histories of Wash. species.

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Table 1. Older Larvae of *Phyciodes tharos*-group.

Taxon	Fronto-clypeus Patch (Triangle When Large)	Overall Ground Color	Color Above Vs. Below Subdorsal Cream Band	Subdorsal Cream Band Color	Dorsal Scolus Tip Color	Lateral (BL1) Scolus Base	Color of Ring around BL1 Scolus
<i>riocol-orado</i>	large & cream	brown	dark to paler	strong	pale	ochre-tan or tan	orange
<i>tharos</i> (Minn.)	large & cream, seldom small & brown	brownish-black	dark in one family	strong, but 30% nearly absent	pale	light-brown or creamy-tan or orangish-tan	brownish-orange below BL1 scolus, brown-black above
<i>orantain</i>	mostly large & cream, seldom small & orange-brown	brown (few blackish-brown, few orange, few creamy-frosted)	paler, few dark (dark in some Neb. families)	strong (seldom moderately interrupted)	pale	ochre-tan, some creamy-tan, some orangish-tan, seldom creamy, rarely light-brown	brownish-orange or orange, some orange-brown
<i>cocyta selenis</i>	mostly large & cream, seldom 1-3 small brown spots	brown (fewer cream dots on average)	dark, some slightly paler	strong (slightly interrupted on many)	pale	orangish or orangish-tan, some orangish-brown	brownish-orange, some orange, some orange-brown (brown in some Ont. larvae)
<i>diminutor</i>	large and cream, seldom dark-brown	brown to blackish brown	dark	strong (slightly interrupted on some)	most pale	orangish-tan, some light-brown	orange-brown, many brownish-orange
<i>batesii</i>	large & cream	brown	dark	strong to moderate	dark	dull orangish-red	reddish-brown to brown
<i>lakota</i>	variable: usually black, rarely large and cream	dark-brown, some brown, many black	dark (rarely slightly paler)	strong to absent	black, some tan	usually slightly reddish-orange, some orange-tan, rarely orange-red or brown or sl.-orangish-black	orange to brown, a few reddish-orange, rarely orangish-black or brownish-black
<i>apsaa-looke</i>	80% black, some ochre, tan, or cream	blackish-brown, some dark-brown, some black	dark (few paler)	strong, many partial, few absent	dark, few pale	usually orangish-tan, some brown, rarely black	brownish-orange, often orange-brown, rarely orange, brown, or dark-brown
<i>anasazi</i>	often (~33%) black, often small orangish, some cream	blackish to dark-brown, some black, rarely somewhat orangish-brown	dark, few paler	strong, few mod. interrupted (rarely orangish)	blackish to cream	most tan or orangish-tan, rarely brown, creamy, or orange	orange-brown, brownish-orange, seldom orange or brown
<i>camillus</i>	black, very rarely a brown spot	dark-brown, some blackish	dark, some paler	complete to moderately interrupted	dark	orangish-tan, some ochre-tan	brown-orange or brownish-orange
near <i>camillus</i> (Bighorns)	black	dark-brown, some very dark, some moderately orange-brown	dark, few slightly paler	strong to often nearly absent	dark	orangish, orangish-tan, brown, or sl.-reddish-orange-brown	brownish-orange, some orange-brown, rarely brown
<i>pulchella</i>	black	dark-brown	dark, some paler	strong	dark	orange-tan or brownish-orange	brownish-orange
<i>montana</i>	----	dark-reddish-brown	----	----	dark	----	----

Table 2. Larvae and Pupae of *Phyciodes tharos*-group. (*The 1st-stage larva always has a brownish subdorsal band when molting to 2nd-stage.)

Taxon	Larva 1 st -Stage Pattern*	Larva Silk Web Stages 1-2	Pupa Overall Color	Pupa Dark Wing Streaks	Pupa Cremaster Wings	Pupa Cremaster Roughness
<i>rio-colorado</i>	none	absent or weak	most orange-brown, 20% creamy-orangish-brn.	moderate	95% tapered, 5% winged	weakly to moderately rugose
<i>tharos</i> (Minn.)	none	absent	orange-brown, some brown-orange	weak, with moderate discal cell spot	almost all winged	moderately to strongly rugose
<i>orantain</i>	none	absent, sometimes present	orangish-brown (rarely sl. reddish) or creamier-brn., few creamy, few brown	weak to fairly strong	95% winged, 5% tapered	moderately rugose
<i>cocyta selenis</i>	none or weak, sometimes fairly strong	absent or present	50% quite cream, some light-orange-brown, few dark-brown	strong or moderate, few weak	most winged, ~30-40% tapered	moderately (some very) rugose
<i>diminutor</i>	none or weak	absent or weak	orangish-tan, many cream-tan, some creamy, few brown or gray	moderate, some weak, few strong	most winged, ~20% tapered	moderately rugose
<i>batesii</i>	none (McDunnough)	present	creamy-brn, some orangish-brown	moderate to fairly strong	wide wings	very rugose
<i>lakota</i>	absent or weak	always present	orangish-brn. (a few slightly reddish), often creamy-brown, few creamy, few brown	fairly weak, sometimes strong	wide wings	very rugose
<i>apsaa-looke</i>	absent or weak	always present	creamy-tan or creamy-brown, often grayish or orange-tan or brown, few orange-brown or dark-blackish-brown or blackish	moderate to strong, some weak	wide wings	very rugose
<i>anasazi</i>	absent or weak	always present	orangish-tan, cream-tan, rarely orange-brown, gray, brown, or black	weak to moderate, some strong	wide wings	very (some moderately) rugose
<i>camillus</i>	banded with brown even when young	present	medium-orangish-brown, many brown, some orangish-light-brown or creamy-brown	weak (some moderate)	wide wings	very rugose
near <i>camillus</i> (Bighorn Mts.)	at least dorsolateral band present	little	orangish-brown, few dark-brown, few creamy-orangish-brown	weak (rarely moderate)	wide wings	very rugose
<i>pulchella</i>	weak	weak in one family	light-brown	weak (more or less)	90% winged, 10% tapered	very rugose

Table 3. Pupa and Antenna of *Phyciodes tharos*-group.

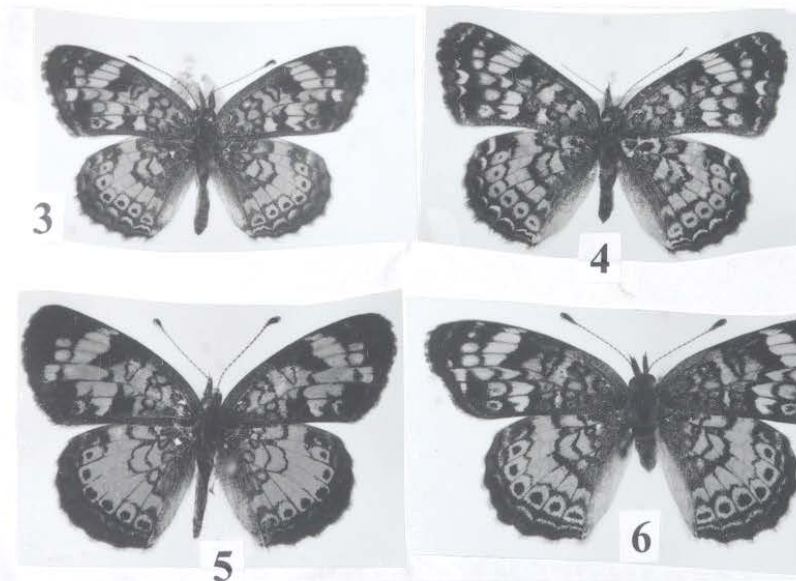
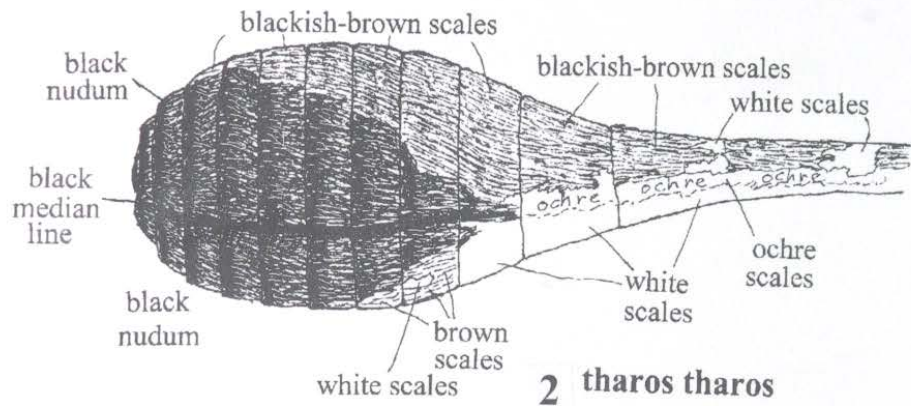
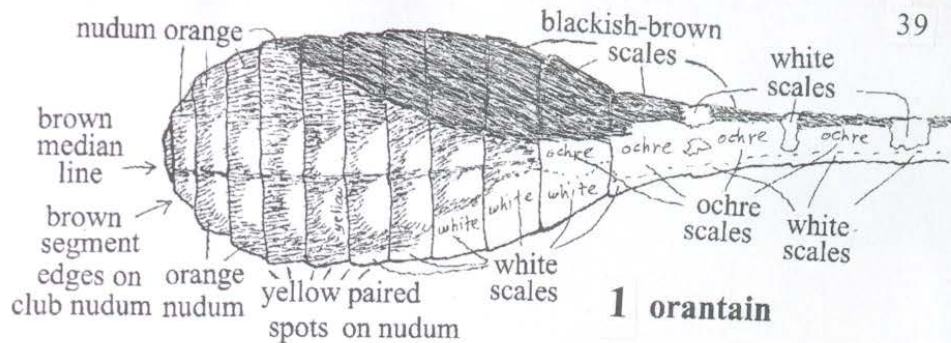
Taxon	Pupa Cremaster Width	Pupa Transverse Ridges A4-7	Pupa Weak Middorsal Crest A2-4	Pupa Cones	Pupa Subspir. A4 Cone	Antenna Club Nudum Color	Antenna Club Usual Shape
<i>rio-colorado</i>	.83 mm	large	absent	large	moderate	blackish (some && orangish tip)	oval
<i>tharos</i> (Minn.)	(1.05 mm in one family)	large	seldom present	large	moderate	blackish (some && orangish tip)	oval throughout range
<i>orantain</i>	.87 mm (1.0 lot #M)	large (sometimes rather small)	5-<10% present	large	moderate	orangish (some && blackish)	ellipse
<i>cocyta</i> and <i>selenis</i>	.94 mm (to 1.12 mm)	large/moderate, some rather small	25% present	large	moderate	orange (some && brown)	ellipse, some more elongate
<i>diminutor</i>	.99 mm S Minn.	large, many moderate, some rather small	few (~5%)	large	moderate	orange (some && brown)	ellipse, some more elongate
<i>batesii</i>	.95 mm	moderate	~75% present	smaller	smaller	brown-black	ellipse
<i>lakota</i>	1.02 mm (.94 lot W7)	moderate (weak near wing)	~80% present	smaller	smaller	brown-black	ellipse
<i>apsaa-looke</i>	1.00 lot F 1.15 lot D	moderate, some larger, rarely large (weak near wing)	~65-70% present	smaller, rarely large	smaller	orange (&& rarely black)	ellipse
<i>anasazi</i>	1.03 mm	small or moderate, few large (weak near wing)	~80% present	smaller, rarely large	smaller	orange (&& seldom brown)	ellipse
<i>camillus</i>	1.01 mm	quite small	~65-70% (Moffat Co. ~5%) present	quite small	quite small	blackish	ellipse
near <i>camillus</i>	1.05 mm	quite small	~65-70% present	quite small	quite small	blackish	ellipse
<i>shoshoni</i>	----	----	----	----	----	blackish	ellipse
<i>pulchella</i>	.78 mm in one family	quite small	~33% present	quite small	quite small	dark (some && orange- brown)	ellipse
<i>delta-rufa</i>	----	----	----	----	----	dark (some orangish esp. &&)	ellipse
<i>montana</i>	----	quite small	----	quite small	quite small	brown (&& dark-orange/ orange-brown)	ellipse
<i>owimba</i>	----	----	----	----	----	orange	ellipse
<i>tutchone</i>	----	----	----	----	----	orange	ellipse

Table 4. Voltinism, Size, and Upperside Wing Pattern of *Phyciodes tharos*-group.

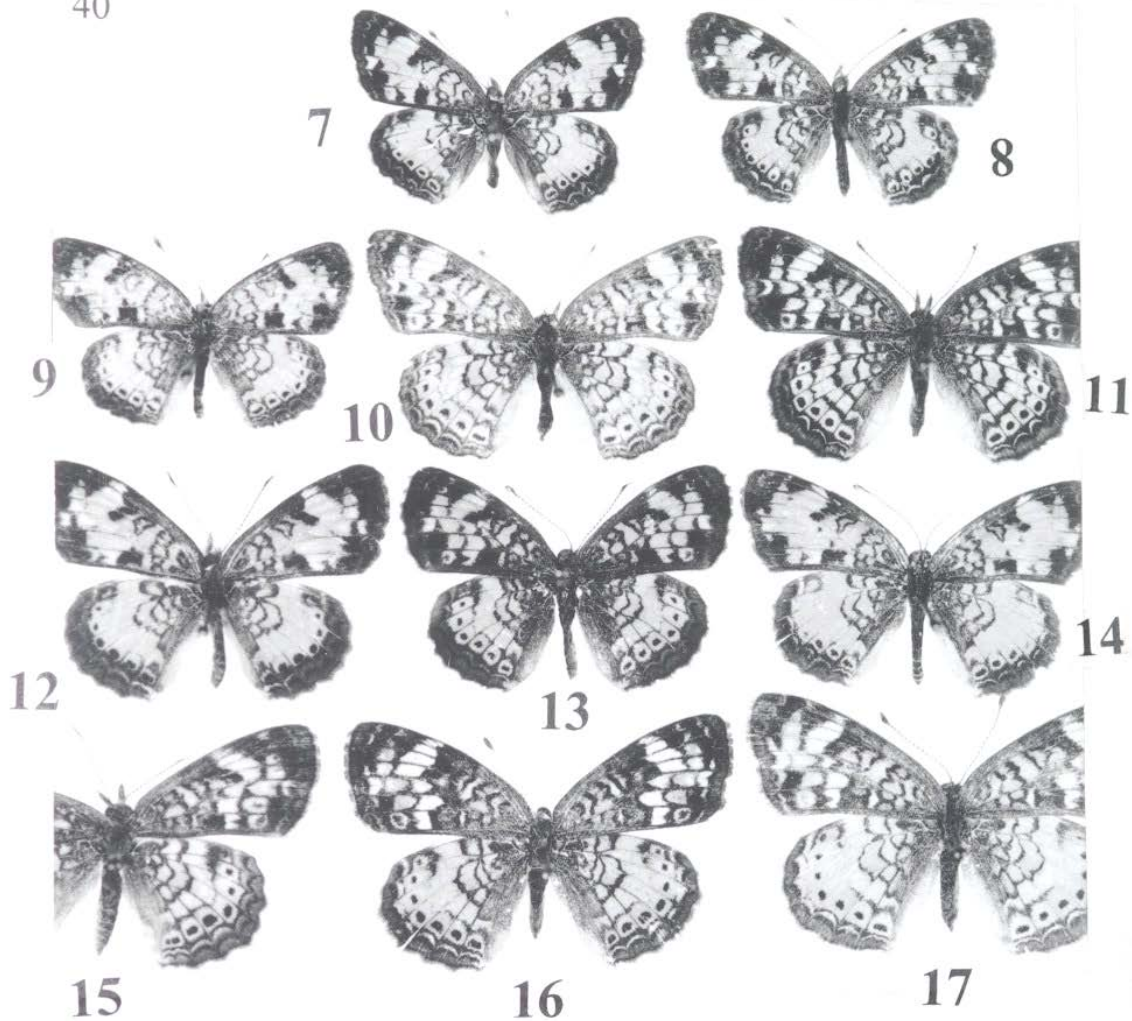
Taxon	Yearly Flights	Forewing Length (mm)	upf median band	upf base color	Dark-Upf &&	uph/upf orange center	Uph Pale Submarg. Line
<i>rio-colorado</i>	3	% 14-16 & 15-17	orange	pale orange	absent	divided && & most %%	moderate
<i>tharos</i>	2-6	% 13-16 & 15-18	orange (some && paler)	orange	rare	divided && & most %%	moderate
<i>orantain</i>	2-3	% 14-16 & 16-18	orange (some && paler)	orange	sometimes	divided && & most %%	moderate
<i>coccyta</i> and <i>selenis</i>	1 (2 sometimes Wash.-Ore.)	% 16-18 & 17-20 (Nfld. & 15-16 & 16-18)	usually orange (many or most && paler)	orange	often	very large, undivided (except some &&)	weaker (strong to rarely absent)
<i>diminutor</i>	2, perhaps 3	% 16-18 & 17-20 (3 rd -gen. & 15-17 & 16-19)	orange (rarely paler), (most && paler)	orange	some	very large, undivided (except many &&)	weaker (strong to absent)
<i>batesii</i>	1	% (14) 15-18, & (16) 17-20	paler	dark or oranger	always	usually divided (some %% large)	weak, seldom moderate
<i>lakota</i>	1	% (14) 16-18 & (16) 17-19	paler	dark or oranger	usually	usually divided	weak, rarely strong
<i>apsaa-looke</i>	1	% 15-18 & 16-20	paler	dark, often oranger	usually	usually divided	weak
<i>anasazi</i>	1	% 16-18 & 18-20	paler usually	very orange	very few	very large, rarely divided except some &&	weak or absent
<i>camillus</i>	2 (1 in Bighorn Mts.)	% 15-16 & 16-19	paler	dark, few oranger	most	divided	moderate to strong
<i>shoshoni</i>	2	% 14-16 & 16-18	paler	dark, some oranger	most	divided	strong, few moderate
<i>pulchella</i>	3-4 (1 N & high Sierras)	% 16-19 & (18)-20	paler	dark	always	divided	absent to moderate
<i>delta-rufa</i>	3	% 15-17 (14) & 17-19	paler	orange, some dark	some	most divided	most strong
<i>montana</i>	1	% 16-17 & 17-18	paler or orange	orange	rare	usually divided	strong
<i>owimba</i>	1 (2)	% 16-17 & 17-18	paler, few orange	mostly dark	most	divided	absent to moderate
<i>tutchone</i>	1	% 14-16 & 17	paler (often orange)	rather orangish	most?	divided	weak to moderate

Table 5. Underside Wing Pattern of *Phyciodes tharos*-group.

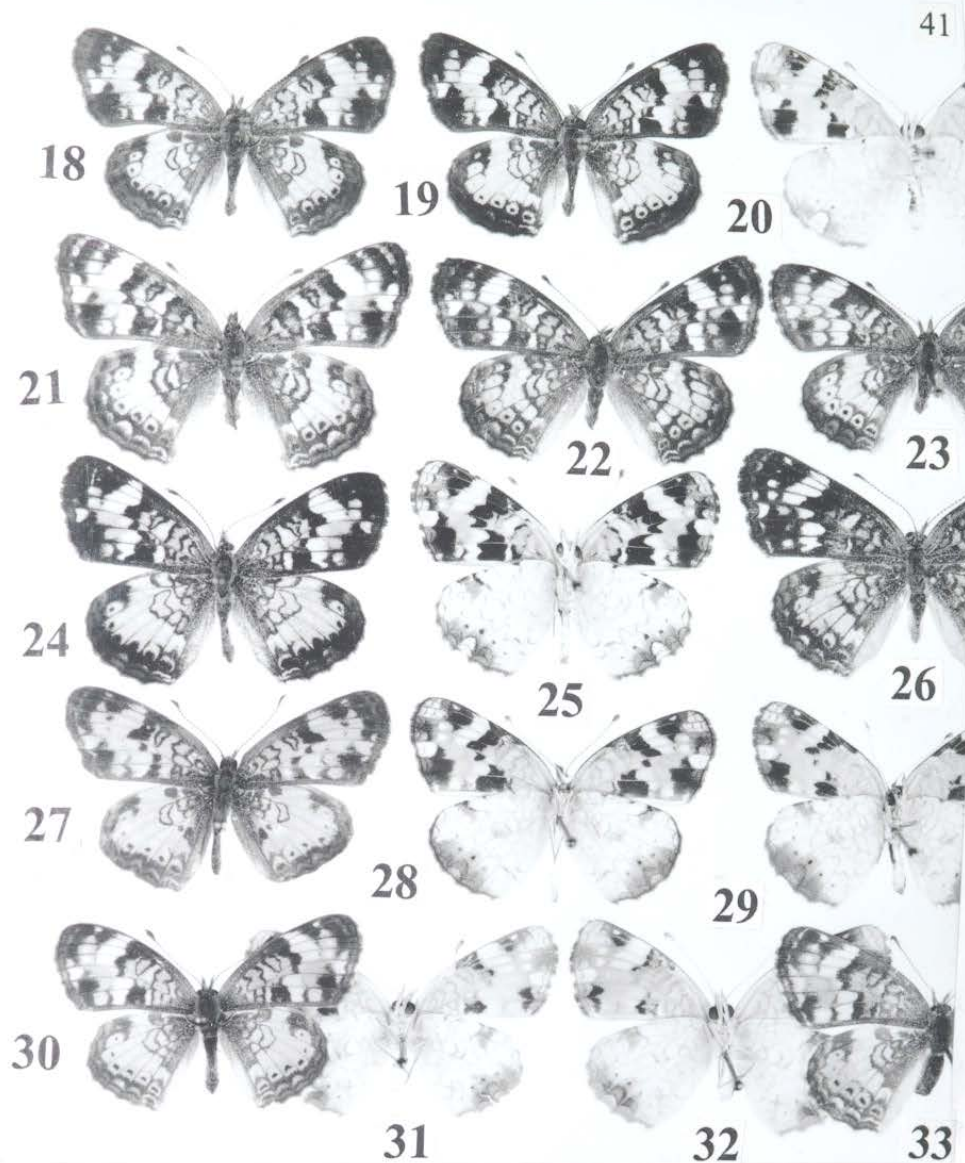
Taxon	unf black subapical costal patch	unf sub-marginal spot cells M1-2	unf black tornus spot (narrower in &)	unf posterior median black spot	unf yellow discal cell bar	unh brown marginal patch	% unh pale marginal crescent (in &&, usually cream) (whiter in form marcia)
<i>rio-colorado</i>	small	russet-brown	large	small or very small	absent	fairly strong	absent (some weak)
<i>tharos</i>	large	russet-brown & blackish	large	small, few large	absent	strong (darker-brown in east)	absent (some yellow, seldom cream)
<i>orantain</i>	large	russet-brown, some blackish	large, very rarely giant	small or large	absent	strong (rarely absent)	absent (some yellow, seldom cream)
<i>cocyta and selenis</i>	large	russet brown	large, some moderate	smaller or large	absent	strong, paler-brown	absent (few yellow or cream)
<i>diminutor</i>	large	russet brown	large, many moderate	smaller, some large	absent	strong, paler brown	absent (few yellow or cream)
<i>batesii</i>	small	orangish, with yellow streaks, rarely a little black	large, few giant	very large, some fairly small in &	absent, sometimes present	absent (some && weak); some tiny northward	yellow (56% lost in yellow background), but cream in many &&
<i>lakota</i>	small, seldom large	russet-brown or orange-brown, rarely blackish	large (some larger, seldom giant)	very large, sometimes fairly small	absent, often weak or present	strong (seldom weak)	2/3 present, but usually yellow
<i>apsaa-looke</i>	large	black or blackish	giant	very large, some fairly small	absent, often weak or present	strong	33% brown, 33% yellow, 33% cream
<i>anasazi</i>	large	brown, some black	medium, many giant, few small	very large or medium (some small)	absent, some present	strong (rarely weaker)	33% brown, 33% yellow, 33% cream
<i>camillus</i>	orange or brown (almost no black)	orangish M1, crescent M2	large	large	mostly yellow	strong	yellow (cream in spring)
<i>shoshoni</i>	orangish or tan (almost no black)	orangish or tan or yellow M1, yellowish M2	large	large, some small (small &&)	yellow	absent (some weak)	creamy or yellow
<i>pulchella</i>	orangish (no black)	orangish	narrow dash	small (varies)	most yellow	absent to strong	yellow
<i>delta-rufa</i>	orangish (no black)	orangish	narrow dash	small (varies)	yellow	absent, few moderate	yellow
<i>montana</i>	orangish (no black)	orangish	narrow dash	most absent	absent (orange)	absent, few weak	yellow
<i>owimba</i>	orangish (no black)	orangish	narrow dash	moderate (varies)	most yellow	strong, few gone	yellow
<i>tutchone</i>	orangish (no black)	orangish	narrow dash	most small	yellow or absent	strong (some weaker)	usually cream



Figures 1-6. 1-2, antenna clubs (ventral view showing nudum= scaleless area). 1, *P. tharos orantain* male holotype, Adams Co. Colo. 2, *P. tharos tharos* male, Monroe Co., Pennsylvania. 3-4, *P. tharos orantain*, below Barr Lake, Adams Co. Colo., egg cluster #1, emgd. Oct. 11, 1985: 3 holotype male, 4 allotype female. 5-6, *P. cocyta diminutor*, smaller Sept. form (photos larger in scale than Figs. 7-17), NE Conger, Freeborn Co. Minn., Sept. 12, 1994, eggs on *Aster simplex* Sept. 12, 1994 J. Scott: 5 holotype male emgd. Oct. 25; 6 allotype female emgd. Oct. 27.



Figs. 7-17, *P. cocyta diminutor* paratypes (7-11 smaller Sept. form, 12-17 larger June form), Freeborn Co. Minn., J. Scott: 7-9 males NE Alden Sept. 13, 1994; 10 female NE Alden Sept. 13, 1994; 11 female Hall of Humes Lake, Sept. 13, 1994; 12 male NE Alden June 23, 1991; 13 male (uph has slight postmedian line, but nudum is orange) NE Alden, June 10, 1993; 14 male NE Alden June 19, 1991; 15 female NE Alden June 10, 1993; 16 female NE Alden June 19, 1991; 17 female NE Alden June 23, 1991.



Figures 18-33. 18-23, *P. cocyta selenis*, *Aster foliaceus* populations: 18-22 E side Vail, Eagle Co. Colo., lot A, 18 male with uniformly-orange upf, emgd. Sept. 17, 19 the most two-toned-upf male in family, emgd. Sept. 17, 20 male emgd. Sept. 17, 21 female emgd. Sept. 19, 22 female emgd. Sept. 23; 23 N Dillon Res., Summit Co. Colo., lot H, female emgd. Sept. 23. 24-33, *P. batesii anasazi*: 24-26 Deep Creek, Eagle Co. Colo., 6500', lot B, July 17, 1996, a large-black-spotted family, 24-25 males emgd. Aug. 19, 26 female emgd. Aug. 24; 27-29 NE Radium, Grand Co. Colo., 7300', lot 98, a moderately-spotted family, 27 male (unusual in lacking two-toned upf) emgd. Aug. 22, 28-29 males emgd. Aug. 19; 30-33 Game Creek, Eagle Co. Colo., 8050', a weakly-black-spotted family, 30 male emgd. Oct 1, 31 male emgd. Oct. 2, 32 female emgd. Oct. 8, 33 female emgd. Oct. 6.



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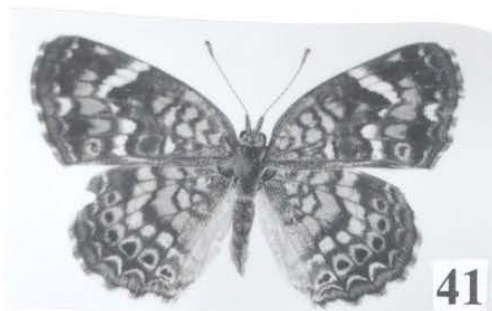
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Figures 34-41. 34-35, *P. pulchella deltarufa*, N of Davis, Yolo Co. Calif., Aug. 31, 1974 J. Scott: 34 holotype male, 35 allotype female. 36-37, *P. pulchella owimba*: 36 holotype male Pattee Can., Missoula Co. Mont., 3500', June 23, 1962 J. Scott; 37 paratype female Mt. Edith Cavell, Alta., July 1, 1962. 38-39, *P. phaon phaon*, Hunting Island, Beaufort Co. S.C., July 4, 1984 R. Gatrell: 38 male, 39 female. 40-41, *P. phaon jalapeno*, Mesa, Ariz., Aug. 4, 1962 R. Arbogast: 40 holotype male, 41 allotype female.