A survey of valvae of Euphydryas chalcedona,

E. c. colon, and E. c. anicia

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Abstract.—A survey of male valvae of almost 500 Euphydryas chalcedona, E. c. colon, and E. c. anicia in western North America demonstrates that very many populations are intermediate between these entities. Six intergrading valval types are recognized, and populatons exist having each of these types as the mode. Male valvae therefore do not support treating these three as distinct species. Because wing pattern shows complex patterns, with many intermediate populations, these three entities should be treated as subspecies of chalcedona.

Introduction

Before 1927 the Euphydryas of North America, except for E. phaeton (Drury) and gillettii (Barnes) were in chaos with about 30 "species." Then McDunnough (1927) and Gunder (1929) used male genitalia to reduce the number of species to five. They include in E. editha (Boisduval) populations with a distinctive valva and reduced uncas with two short blunt projections. They treated chalcedona (Doubleday), colon (Edwards), and anicia (Doubleday) as two species, chalcedona (with colon) and anicia, which all have a bifid uncas with two curved claw-like hooks. E. chalcedona and colon were found to have the same short dorsal valval process, whereas anicia was found to have a longer process. Their treatment has been followed more or less unchanged until now, although Bauer (1975) treats colon as a distinct species.

I recently collected populations with male valvae intermediate between *chalcedona-colon* and *anicia*. This paper is a detailed survey of male valvae, concentrating on areas where intermediates in valvae or wing pattern occur. It proves the existence of numerous populations over a large area that are intermediate in valvae. This, together with other published evidence, leads me to conclude that *colon* and *anicia* both belong to the highly polytypic polymorphic species *chalcedona*.

Methods

Males of each population were examined and tabulated in Table 1 according to best resemblence to the drawings in Fig. 1. The dorsal wing pattern was rated in Table 1 according to whether the overall appearance is blackish, whitish, or reddish. There are numerous other

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wing characters involved (Hovanitz & Le Gare 1951) which this paper does not consider.

Results and Discussion

The samples fall into three arbitrary categories: chalcedona-colon (mostly a or b of Fig. 1), anicia (mostly e or f), and intermediates between the two (c or d). Some samples have a the usual form, others hav b, c, d, e, or f (Table 1). There are clearly many intermediate populations. These occur almost everywhere between the ranges of chalcedona-colon and anicia, including California, Arizona, Nevada, Washington and Montana. They are probably found in Idaho, Oregon, and British Columbia also (intermediate populations are reported for the Wallowa Mts. Oregon.) McDunnough's paradoxa from B.C. has somewhat intermediate genitalia (McDunnough 1927). In wing pattern the chalcedona and colon samples are very similar, black with cream spots. The anicia samples are usually some shade of reddish or creamcolored, rarely blackish. The intermediate genitalia samples have every type of wing pattern, and many of the populations are polymorphic in wing pattern, as are some of the anicia samples. The large number of samples intermediate in valvae proves conclusively that valvae cannot be used as the basis for dividing the populations into separate species.

Turner et al. (1961) show that genitalia differences do not necessarily inicate separate species are involved. They showed that the phenotype of *Papilio dardanus* Brown with a long process on the valva is due to a dominant gene, whereas the phenotype with a short process is due to its homozygous recessive allele.

A character mentioned by Bauer (1961), the minute spines on the upper process, is not useful. All samples have the dorso-posterior rim of the upper process with minute teeth. The teeth are dense on short processes and less dense on longer processes as if the same number of teeth are spread over a larger area. Associated with a long upper process is a slightly longer lower process having a reduced anterior bump. This bump sometimes is formed into a separate lobe making a bifurcate lower process, frequent in ssp. quino (Behr).

Gradual clinal changes in the proportions of valval forms seem to occur in some geographic areas, whereas more abrupt changes seem to occur in other areas. This is also true of the wing pattern, which is almost hopelessly complex, making the use of subspecies very dubious. Jewett (1959) accordingly suggested that further naming of subspecies be stopped.

The most reasonable interpretation of the genitalic intermediates is that of only one polytypic polymorphic species, *chalcedona*. The name *chalcedona* has page priority over *anicia*, being named on Fig. 1 versus Fig. 2 for *anicia* in the same paper.

Bauer (1975) states that in several places *colon* is sympatric with *chalcedona* and *anicia*, although these places are not stated or the statements documented. However, I cannot distinguish genitalia of *chalcedona* from *colon* and suspect that apparent cases of sympatry really are polymorphisms. Certainly such cases, if they exist, should be fully investigated and the results published. Populations only a few hundred meters from each other may exchange very few individuals and fluctuate in population size independently (Ehrlich et al. 1975), so the occurrence of two forms in the same region does not necessarily prove that they are distinct species.

The larval web character of colon cited by Bauer (1975) is not diagnostic because chalcedona and anicia also have webs. E. c. capella (Barnes) webs its Penstemon hostplant so extensively that defoliated plants look as if a nylon stocking had been placed over them. Dammers (1940) and Bauer (1975) state that colon has whiter larvae than chalcedona although Bauer states that colon colon has less white on the body than some other populations.

The one-species interpretation has also been suggested by previous work. Lionel Higgins (pers. comm.), in an unpublished study done many years ago, was not able to define the species to his satisfaction using genitalic characters. McDunnough (1927) showed that his "colon" paradoxa McDunnough has a longer dorsal valval process than does "colon" perdiccas (Edwards) and has redder wings, both traits tending toward anicia; wing pattern of paradoxa, and of anicia from Keremeos B. C., is identical. The original description of wallacensis Gunder (Gunder 1928a), previously placed in colon by Bauer (1975), states "genitalia of this race approach the anicia group" and "this race probably represents a connecting link as Dr. McDunnough has suggested." The holotype of irelandi Gunder has intermediate genitalia and was placed in anicia by Gunder (1929) and dos Passos (1964), in chalcedona by Bauer (1975). Gunder (1928b) described red versus white or black forms connected by intergrades for two populations [mcglashanii (Rivers) black, truckeensis Gunder red; olancha (Wright) whitish, georgei Gunder red]. The genitalia figure of georgei by Gunder (1929) is intermediate. Dammers (1940) successfully hybridized and backcrossed chalcedona and kingstonensis Emmel and Emmel which are very different in appearance. E. c. hermosa (Wright)

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was placed in anicia by Gunder (1929) and Bauer (1975), but in chalcedona by dos Passos (1964) and Emmel and Emmel (1972); kingstonensis, klotsi dos Passos, hermosa, and morandi Gunder all have very similar wing pattern, yet have been placed in several "species." Bauer's (1975) subspecies of "colon" from Elko Co. Nevada is stated to have white, red, and black forms. Red populations from California (sierra [Wright]) and Arizona (klotsi) have been included among the west coast black populations in the same species chalcedona by Gunder (1929), dos Passos (1964), and Bauer (1975). Finally, dos Possos (1964), McDunnough (1927), and Gunder (1929) treated colon and chalcedona as conspecific.

In many places in the intergradation zone in western U.S. the male valvae change from one form to another at a different place than the wing pattern. Wing patterns change in regions where valvae do not (many places), and valvae change in regions where wing patterns do not (such as in British Columbia, Arizona, and Nevada). This phenomenon of non-concordance of characters is typical of many polytypic species, such as for wing characters of *Speyeria callippe* (Boisduval) (Hovanitz 1943). When separate species are involved most characters usually change at the same place.

Higgins (1978) has split the genus *Euphydryas* into four separate genera, placing *editha*, *chalcedona*, *c. colon*, and *c. anicia* into *Occidryas* Higgins; I prefer to treat these names as subgenera to avoid the awful fate of the birds, in which each species is in its own genus.

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TABLE I

Number of individuals of each valval type (a to f of Fig. 1),
and predominant wing color and subspecies, for each locality.

Locality	a	b	c	d	e	f	Main Color	Subspecies
Jerseydale, Mariposa Co. Calif.	-	-	1	-		-	black, cream	chalcedona
Indian Flat, Mariposa Co. Cal.		2	-	-		-	black, cream	chalcedona
El Portal, Mariposa Co. Cal.	1	-	-	-	-		black, cream	chalcedona
Lang Crossing, Nevada Co. Ca.	2	1	-	-		-	black, cream, red	chalcedona
Foote Crossing, Sierra Co. Ca.	1	2	-	-	•	-	black, cream	chalcedona
Blue Ravine, Sierra Co. Ca.	-	-	1	-	-	-	black, cream, red	chalcedona
Fiddle Crk., Sierra Co. Ca.	-	1	1	-		-	black, cream	chalcedona
Whiskeytown Res., Shasta Co.	5	4	1	•	-	-	black, cream	chalcedona?
Calif.								
Cedar Pass, Modoc Co. Ca.	-	1	-	-	-	-	black	colon
SE Copper, Siskiyou Co. Ca.	3	4	1	1	-	-	black, cream	colon?
Kinney Crk., Jackson Co. Ore.		2	-	-		-	black, cream	colon?
French Gulch,	1	1	-	-		-	black, cream	colon?
Jackson Co. Ore.								
Illinois R. rd.,		1	-	-		-	black, cream	colon?
Josephine Co. Ore.								
Wolf Creek, Josephine Co. Ore.	1	2	-	-	-	-	black, cream	colon?
Bly Mtn., Klamath Co. Ore.	4	4	1	-		-	black, cream, red	colon-dwinellei Hy. Edw.
S. La Pine, Klamath Co. Ore.	1	-	-			-	black, cream	colon-dwinellei
Odell L., Klamath Co. Ore.	2	1	-			-	black, cream	colon?
Hart L., Linn Co. Ore.	1		-	-		-	black, cream	colon
Monument Pk, rd. Linn Co. Ore.	1	1	•	•		-	back, cream	colon

Cascadia, Linn Co. Ore.	1	-	-	-		-	black, cream colon
Cascadia S. Park,	1	-	-	-	-	-	black, cream colon
Linn Co. Ore.							
nr. Halfway, Baker Co. Ore.	-	3	1	-	-	-	black, cream wallacens
Lost Prairie, Linn Co. Ore.	-	1		-	-	-	black, cream colon
SE Drew, Douglas Co. Ore.	-	1	-	-	-	-	black, cream colon
McDonald Forest,	1	-	-		-	-	black, cream colon
Benton Co. Ore.							

Locality	a l	b	c	1	e	f	Main Color	Subspecies
Siskiyou Summit, Jackson Co. Ore.	2	1			•	•	black, cream	colon
Satus Pass, Yakima Co. Wash.	- 1	1			-	-	black, cream, some red	paradoxa?
Hurricane Ridge Clallam Co. Wash.	8 3	3			-	-	black, cream	perdiccas
Tucannon R., Columbia Co. Wash.	1	-				•	black, cream	wallacensis
Horse Crk., Wallowa Co. Ore.	1 .	-			-	-	black, cream	wallacensis
Camas Prairie,	- 2	2 -	-				black, cream,	wallacensis
Sanders Co. Mont.							some red	
Gilbreth Spgs., Columbia Co. Wash.		- :	1 -		-	-	black, cream	wallacensis
9-mile Crk., Missoula Co. Mont.	-	- 5	2 -		•	•	black, cream	wallacensis
Pattee Can., Missoula Co. Mont.	•	- 5	2 4	1	-	•	black, cream	wallacensis
Miller Crk.,	- :	1 1	01	7	8	-	black, cream	wallacensis
Missoula Co. Mont.								
Warm Spgs. Cgd., Ravalli Co. Mont.	•	-	-]	1		-	black, cream, red	howlandi S. & T.?
Ronan, Lake Co. Mont.			. 1	L	-	-	cream, black	bernadetta?
SE Easton, Yakima Co. Wash.	- :	1	1 2	2	-	•	some black, some red-cream	hopfingeri Gunder
Peoh Peak, Kittitas Co. Wash.	1	1	- 4	1	-	-	black, cream	paradoxa?
Rush Creek, Washoe Co. Nev.	•	•	- 1	2	8	1	cream, black, some red	veazieae F. & J.
N. Hallelujah Jct. Lassen Co. Cal.	2	5	3 1	1	1	-	black, cream, some red	veazieae-sierra?
Bartle, Siskiyou Co. Cal.	- !	2	2	-		•	black, forewing reddish	dwinellei
Kin Can., Ormsby Co. Nev.	-	4	3	1		-	cream, black, sl. red	olancha-sierra?
Loon Lake, El Dorado Co. Ca.	- 1	14	8 3	3	•	-	red to black, sl. cream	sierra
Sonora Pass, Tuolumne Co. Calif.	-		- 1	1	2	2	black-cream-red	sierra-olancha
Ebbets Pass, Alpine Co. Ca.			- 1	1		-	red	sierra
Hermit Valley, Alpine Co. Calif.	-			_			red	sierra
Echo Lake, El Dorado Co. Ca.	1 :	2	1 2	2			red	sierra

Carson Pass, Alpine Co. Ca.	9 16 19 5 1 -	red to black, mixed	sierra?
Big Pine Mdw., Tulare Co. Calif.	3 9 3	cream, some red-black	olancha?
Oak Crk. Can., Coconino Co. Ariz.	- 1 2 5	ochre, some black- cream	klotsi
N. Canyon, Yavapai Co. Ariz.	3	ochre, some black- cream	klotsi
Yava, Yavapai Co. Ariz.	2	ochre, some black- cream	klotsi

Locality	abcdef	Main Color	Subspecies
Providence Mts.	- 2 10 1	ochre	kingstonensis
San Bern. Co. Calif.			
Rock Corral,	1 1 2	red	corralensis
San Bern. Co. Calif.			E. & E.
E. Jacumba, San Diego, Co.Ca.	- 1 3 1	cream, black	quino
W. Jacumba, San Diego Co. Ca.	- 2 2	cream, black	quino
E. Jacob Lake,	1 1	ochre	hermosa?
Coconino Co. Ariz.			
Peppersauce Can.,	2 1	ochre	hermosa
Pima Co. Ariz.			
Horseshoe Cienega,	23	ochre-red-black	magdalena
Apache Co. Ariz.		cream	B. & McD.
Mt. Wheeler Scenic Area,	2	red, cream	wheeleri
White Pine Co. Nev.			
Austin Summit,	1	red, cream	wheeleri
Lander Co. Nev.			
W. Durkee, Baker Co. Ore.	2 -	white, some red	bakeri S. & T.
Trout Crk. Rd.,	1 1	white, some red	macyi F. & J.
Harney Co. Ore.			
Wildhorse Crk.,	1	white, some red	macyi
Harney Co. Ore.			
Salmon Mdws.,	2 2	black, red, cream	hopfingeri
Okanogan Co. Wash.			
Humphrey, Clark Co. Idaho	1	black, red, cream	howlandi?
Swan L., Madison Co. Mont.	3	black, red, cream	howlandi?
S. Norris, Madison Co. Mont.	2 5	cream, black	bernadetta
			Leussler
4 Mile Crk.,	1 -	red, some black-	windi Gunder?
Sweet Grass Co. Mont.		cream	
5 mi. S. Wasa, B.C.	1 1	red, some black-	anicia
		cream	
Ft. Steele, S. Wasa, B.C.	2	red, some black-	anicia
		cream	
Elko, B.C.	2 3	red, some black-	anicia
		cream	
8 mi. W. Cranbrook B.C.	1	red, some black-	anicia
		cream	
Halfmoon Park,	1	cream, black	bernadetta
Sweet Grass Co. Mont.			

Swamp Crk.,	1	cream, black	bernadetta
Sweet Grass Co. Mont.			
McLeod, Sweet Grass Co.	3 5	cream, black,	howlandi?
Mont.		red	
Polaris, Beaverhead Co.	5 5	cream, black,	howlandi
Mont.		red	
Bozeman, Gallatin Co. Mont.	1 2 4	cream, black, red	howlandi
Gallatin Mts.,	16	cream, black,	bernadetta-
Gallatin Co. Mont.		red	howlandi
Bridger Can.,	1 1	cream, black, red	same
Carbon Co. Mont.			
Mile 154, Haines Jct., Yukon	3 1	red, black, cream	helvia Scudder

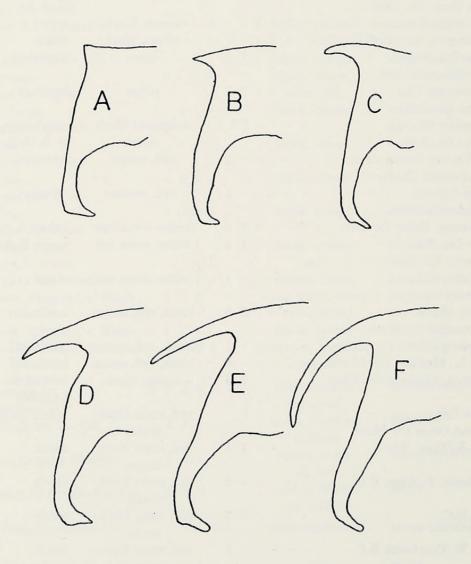


Figure 1. Six shapes of the valval process in *Euphydryas chalcedona*, *E. c. colon*, and *E. c. anicia* used in Table I.



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