JOURNAL OF
THE LEPIDOPTERISTS' SOCIETY

Volume 29 1975 Number 2

PAPILIO "GOTHICA" AND THE PHENOTYPIC PLASTICITY OF *P. ZELICAON* (PAPILIONIDAE)

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Since the description of *Papilio gothica* Remington (Remington, 1968), its taxonomic status and the nature of its relationship with *P. zelicaon* Lucas have remained unclear (Clarke & Sheppard, 1970). *Papilio gothica* (type locality Gothic, Gunnison Co., Colorado) was proposed to apply to univoltine, montane populations from the Rocky Mountains and adjacent areas, showing an alleged host preference for (or restriction to) *Pseudocymopterus montanus* (Gray) Coulter & Rose (Umbelliferae), and differentiable from lowland California *P. zelicaon* in the phenotypes of their F_1 hybrids with *P. polyxenes* Fabricius and *P. bairdii* Edwards. Actual or potential reproductive isolation from *P. zelicaon* was not demonstrated. Remington was unable to find any "all or none characters . . . by which every dead specimen would be infallibly recognized," but he did provide a list of 11 characters whereby "most *gothica* differ from most *zelicaon*. . . ." He cited four of these as "the most reliable for distinguishing adults of montane Colorado *gothica* from lowland coastal Californian *zelicaon*." In his discussion of the geographical distributions of *zelicaon* and *gothica* he tentatively assigns genetically unknown populations to one or the other name, based on these pattern characters.

In many species of butterflies lowland, multivoltine populations produce vernal (or vernal/autumnal) phenotypes which are very similar to—if not indistinguishable from—those emerging in the single annual brood at high elevations or latitudes. Klots (1951) refers to this situation in *Papilio glaucus* L. ("*canadensis*" phenotype) and *Lycaenopsis pseudargiolus* Bdv. and LeC. ("*lucia*"). In California, it occurs in *Polites sabuleti* Bdv. ("*tecumseh*" phenotype) and *Pieris occidentalis* Reak. ("*calyce*"), to name two species under study in my laboratory. *Papilio* *zelicaon* is continuously brooded in the Sacramento Valley of California, flying from March–October or November, with four to five broods. Since virtually every multivoltine butterfly studied (even the dull, dark species of *Erynnis*; Burns, 1964) shows seasonal phenotypic changes, it is scarcely surprising that *P. zelicaon* does so. The *gestalt* of the spring phenotype is immediately recognizable, but it has never been described in detail, or quantified as frequencies and correlations of individual character states. I propose that the seasonal phenotypic variability of *P. zelicaon* has a bearing on the validity of Remington's characterization of *P. gothica.*

When Remington's set of 11 *gothica* characters is examined in large samples of lowland California *zelicaon*, it becomes evident that spring *zelicaon* differ from their summer counterparts in precisely the same ways that *gothica* is alleged to differ from *zelicaon.* I have examined 320 *zelicaon* collected below 500′ in six central California counties in 1972, 1973, and 1974, mostly as singletons or in series of ten or fewer. There are, however, two large series collected at single localities on single days: 12♂, 16♀ from Suisun City, Solano Co., 20 March 1974, and 35♂, 4♀ from the American River Parkway, Sacramento Co., 2 June 1973. These represent the first and second generations in their respective localities and years. Suisun City (elevation ca. 10′) and the American River (ca. 15′) are approximately 50 air miles apart, and potentially isolated from each other by the Inner Coast Ranges, which rise from a low pass at Vacaville, eight miles east of Suisun, to a crest of 2800′ a few miles to the north. However, hilltopping *P. zelicaon* have been taken along the crest, and breeding populations exist in and on both sides of the pass, along Interstate Highway 80. Suisun City has a distinctly more maritime climate than the American River; it is exposed to afternoon sea breezes and occasional summer fog entering through the Carquinez straits. Both populations feed on the introduced umbelliferous weed, *Foeniculum vulgare* Mill., to the apparent exclusion of all other (native and introduced) umbellifers.

The four "most reliable" *gothica* characters (Remington's characters 2–5) are:

(2) Forewing below, in postmedian broad yellow band, with the anterior spot having an outer edge strongly offset from a line drawn through the outer edges of spots 2–9.

(3) Forewing below with postmedian spot 2 tending to have its outer edge forming an angle with its caudal edge only slightly greater than 90°. (In *zelicaon* this is described as "much greater than 90°.")

(4) Forewing above, near coastal edge, usually with 2 fine yellow lines opposite end of cell, one anterad and one posterad of the closely parallel veins Sc and R_1.

(5) Hindwing above has cell Cu_2, near the anal margin, with basal dark

TABLE 1. Distribution of character states in two samples of lowland California *Papilio zelicaon.* The characters are described in the text (G = *gothica* state; Z = *zelicaon* state).

Remington's numbered characters		2	3	4	5
Suisun City, 20 March 74	12 ♂♂	8G: 4Z	4G: 8Z	6G: 6Z	7G: 5Z
(1st generation)	16 ♀♀	10G: 6Z	11G: 5Z	13G: 3Z	8G: 8Z
	28	18G:10Z	15G:13Z	19G: 9Z	15G:13Z
American River, 2 June 73	35 ♂♂	6G:29Z	6G:29Z	4G:31Z	7G:28Z
(2nd generation)	4 ♀♀	2G: 2Z	1G: 3Z	0G: 4Z	3G: 1Z
	39	8G:31Z	7G:32Z	4G:35Z	10G:29Z
χ_1^2 within characters	χ^2	12.65	9.9	21.93	6.6
	p:	$<< .005$	$< .005$	$<< .005$	$\sim .010$

color usually extending far distad of origin of vein Cu_2 from cell. (Described as greatly reduced in *zelicaon* males.)

For each specimen in the two long one-day series, each of these characters was scored as being in the *gothica* (G) or *zelicaon* (Z) state. The results are summarized in Table 1, along with the chi-square test for homogeneity of the two samples in each character; for all four characters the distributions of states in the two samples differ at a high level of significance. As may be seen from Table 2, the frequency of *gothica* character states deviates significantly from a random (Poisson) pattern in the spring, but not the summer sample. Point correlation coefficients (Poole, 1974) were calculated within each sample between all possible pairs of characters to test for association among character states (Table 3). Characters 3 and 4 have the strongest association in both samples, while 3 and 5 are essentially independent of each other. It is clear that the spring phenotype is not produced *in toto*, by the action of a major "switch-gene."

Remington suggests that *gothica-zelicaon* sympatry should be sought "at mountain-lowland contacts in central and eastern California." Can the distribution of *gothica* characters in these samples be explained in terms of introgressive hybridization? The American River Parkway sits at the base of one of the major canyons of the west slope of the Sierra Nevada, precisely where Remington predicts contact between *zelicaon* and *gothica*, but the June sample from there shows essentially no *gothica* tendencies. Suisun City is very nearly on the coast and is within easy flying range of the large vacant-lot populations in Oakland and Richmond. The March sample from Suisun City is phenotypically strongly reminiscent of the picture Remington portrays of *gothica.* These ob-

TABLE 2. Distribution of *gothica* (G) and *zelicaon* (Z) character states among numbers of characters, and their fit to a Poisson distribution (assumed independence among the characters).

Number of characters in G state	Number of Individuals Observed (O)	Number Expected from Poisson (E)	$\frac{(O-E)^2}{E}$
Suisun City, 20 March 74			
0	0	7.84	7.84
1	4	9.80	3.43
2	11	6.44	3.23
3	11	4.08	2.77
4	2	0.84	1.60
			$\chi^2 = 18.87$,
			$p << .005$
American River, 2 June 73			
0	19	11.65	4.64
1	12	14.04	0.29
2	6	9.36	1.21
3	2	1.56	0.12
4	0	0.39	0.39
			$\chi^2 = 6.65$
			$.10 > p > .05$

servations make no sense biogeographically, but they do seasonally. I have 45 summer *zelicaon* (collected on 16 different days) from Suisun and 20 spring *zelicaon* (6 days) from the American River, and their phenotypes confirm the seasonal pattern. (For example, of six taken on 19 March 1974 at the American River, one has 1, four have 2, and one has all 4 of its characters in the *gothica* state.) The only alternative hypothesis, that *gothica* and *zelicaon* are sympatric in lowland California with the former being spring-univoltine and the latter summer-multivoltine, is not only not parsimonious; it is demonstrably incorrect from my breeding experiments at Davis.

The tendency for spring *zelicaon* to resemble *gothica* is not restricted to the four "most reliable" characters. In the Suisun and American River samples, nine of the eleven characters are significantly more like *gothica* in spring. The tenth, ground color of females, could not be evaluated because so few American River females were on hand. The eleventh, absence of yellow striping in the ventral forewing discal cell, was proposed as a trait distinguishing *zelicaon* and *gothica* from *P. brucei* Edwards.

TABLE 3. Point correlation coefficients (V) between all possible pairs of characters 2, 3, 4 and 5. The variances have been omitted.

Remington's numbered characters		3	4	5
Suisun City, 20 March 74	2	−.096	−.024	−.344
	3		+.126	0
	4			−.192
		3	4	5
American River, 2 June 73	2	+.258	+.247	+.105
	3		+.282	+.004
	4			−.212

None of this proves anything about the specific distinctness of *gothica.* If speciation is to be defined biologically, it can be "proven" only by the demonstration of reproductive isolation, a demonstration Remington has not made (Clarke & Sheppard, 1970). Decisions on species distinctness based entirely on statistical analysis of dead specimens, in the absence of biological data, can readily lead to absurd conclusions, e.g., the revision of *Pieris,* by Abbott et al. (1960) in which four very distinct (and widely sympatric) species group "*protodice*" species are synonymized. On the other hand, there is no doubt that sibling species exist which are indistinguishable to the museum taxonomist but meet all the biological criteria of speciation. Ayala (1973) described two partially isolated subspecies of the *Drosophila willistoni* group which are "nameable" only statistically, by the frequency pattern of isozymes when they are subjected to starch gel electrophoresis! If *Papilio gothica* proves to be a valid species, it will be "nameable" only by the locality label. Remington's characters are clearly useless for discriminating individual *gothica* from individual spring specimens of multivoltine *zelicaon.* (Since he did not quantify his diagnosis, we do not even know whether series of Colorado *gothica* and spring California *zelicaon* are statistically separable.) The only readily recognizable entity is summer, lowland *zelicaon.* The adaptive significance of these characters is unknown (the blackening in cell Cu_2 is likely to function in thermoregulation), but since they seem to be associated with diapause in both uni- and multivoltine populations, there is no reason to predict any correlation with the *gothica* × *polyxenes* (or *bairdii*) hybrid phenotype—on which the name *gothica* now wholly depends.

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CORRECTIONS TO TWO ARTICLES ON ABERRANT *CYNTHIA* (NYMPHALIDAE)

Two recent articles on aberrant *Cynthia* have contained errors of identification which should be corrected to prevent perpetuation of inaccurate records. Phillips (1971, Great Basin Natural. 31: 256–260) reported the capture of *Cynthia cardui* ab. *elymi* Rambur from Salt Lake City, Utah. This aberration, illustrated in color, is clearly *C. annabella* ab. *letcheri* Grinnell, which is easily distinguished from *C. cardui* ab. *elymi* by the forewing discal cell marking which completely crosses the cell in *C. annabella* but remains a spot against the anterior cell margin in *C. cardui*, and by the forewing apex which is pointed at M_1 in *C. annabella* and more rounded in *C. cardui*. *C. cardui* ab. *elymi*, then, remains unrecorded for Utah.

Shapiro (1973, Pan-Pac. Entomol. 49: 289–293) described and illustrated aberrations of *C. annabella*. His Figs. 1 and 2 are indeed *C. annabella*, but Fig. 3 is *C. cardui* showing tendencies toward ab. *elymi*. The same characteristics used to separate *C. annabella* ab. *letcheri* and *C. cardui* ab. *elymi* in the previous article can be used to correctly determine this specimen.

When used with care the excellent color illustrations of aberrant *Cynthia* (= *Vanessa*) in Comstock's *Butterflies of California* (1927) should leave no doubt as to the correct species identifications of some aberrations. However, the above mistaken identifications show the difficulty of applying names to aberrations, which by their very nature can be quite variable.

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