

INTER-SPECIFIC HYBRIDIZATION BETWEEN LIMENITIS  
ARTHEMIS ASTYANAX AND L. ARCHIPPUS (NYMPHALIDAE)

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The Nearctic genus *Limenitis* (Nymphalidae) contains five common, geographically widespread forms, all of which are polytypic, and exhibit tendencies toward hybridization (Edwards, 1879; Scudder, 1889; Field, 1904; Gunder, 1934; Remington, 1958, 1968; Gage, 1970). Four of the forms are mainly allopatric in their distributions, occupying adjacent regions, and coming in contact only along certain margins of their ranges (Hovanitz, 1949). Included among these are two conspecific eastern forms: the banded purple (*L. arthemis arthemis* Drury) and the red-spotted purple (*L. arthemis astyanax* Fabricius), an unbanded mimic of the blue swallowtail (*Battus philenor* L.). In addition, there are two western disruptively banded species: Weidemeyer's admiral (*L. weidemeyeri* Edwards) and Lorquin's admiral (*L. lorquini* Boisduval).

These four forms are closely allied, and conform well to Mayr's (1963) definition of a "super-species." The two subspecific eastern butterflies exhibit "free-interbreeding" and complete intergradation within the northeastern United States and southern Ontario (Edwards, 1877; Field, 1910; Hovanitz, 1949; Platt and Brower, 1968; Remington, 1968; Platt, Frearson, and Graves, 1970), whereas, the two western species exhibit "suturing" and "intense" interbreeding in certain restricted localities, often associated with mountain passes (Brown, 1934; Perkins and Perkins, 1966; Perkins and Perkins, 1967; Remington, 1968).

The fifth form is the predominantly orange-colored Viceroy (*L. archippus* Cramer). It is broadly sympatric with all four of the others and represents a distinct species having: a) evolved a mimetic color-pattern closely resembling the unpalatable monarch (*Danaus plexippus* L.), b) possessing highly modified male claspers (Scudder, 1889; Nakahara, 1924; Chermock, 1950; Platt, Frearson, and Graves, 1970), and c) being, in part, at least, ecologically isolated from the others, preferring open marshy meadows to woods-meadow ecotones and woodland glades.

The purposes of this report are: first, to document the occurrence of a recently collected wild hybrid between the two mimetic species, *L. a. astyanax* and *L. archippus*; second, to review previously known records of such inter-specific wild hybrids in order to verify the scarcity and wide geographic distribution of such specimens; and, third, to present a pre-

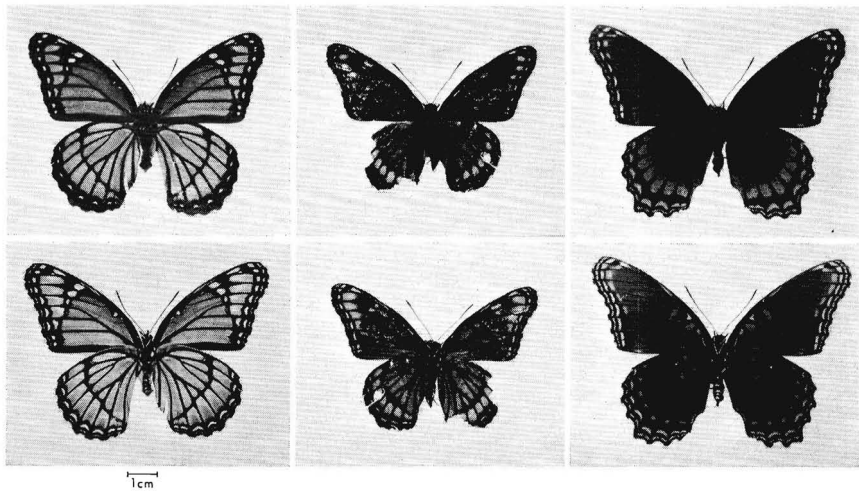


Fig. 1. Wild-caught hybrid male (form *rubidus* Strecker) from Durham, N. C. with parental species; top row dorsal, bottom row ventral. Left, *Limenitis archippus*; middle, hybrid form *rubidus*; right, *Limenitis arthemis astyanax*.

liminary report of recent laboratory crosses which confirm the hybrid nature of these intermediate "suspected" wild hybrids.

The new hybrid specimen (Figure 1) is a male, collected on Highway 751, eight miles south of Durham, Durham County, North Carolina, on October 10, 1970 by J. C. Greenfield, Jr.<sup>1</sup> It can be referred to hybrid form *rubidus* Strecker, in that its basic ground color is orange like that of *archippus* but the dorsal surfaces of the forewings are darkly pigmented, whereas, the hind wings possess large red-orange marginal spots. Ventrally, both the proximal and marginal red-orange spotting and remnants of the double row of marginal iridescent lunules characteristic of *astyanax* are present. Both parental species fly commonly in the fields and woods surrounding the vicinity where the specimen was secured.

Other known records of wild hybrids between butterflies of the *L. a. arthemis-astyanax* complex and *L. archippus* are given in Table 1. By reviewing the literature, and corresponding with museum curators and Society members, a total of eight records of wild *arthemis* × *archippus* hybrids (form *arthechippus* Scudder), and 12 previous reports of wild-caught *rubidus* have been found. The wild specimens are widely distributed, but exceedingly rare, those reported in Table 1 having been collected from 1872–1970. Insofar as is known, all wild specimens collected to date have been males.

<sup>1</sup> This specimen has been donated to the collection of the American Museum of Natural History in New York.

TABLE 1. Records of 20 previous wild-caught *Limnitis arthemis astyanax* × *L. archippus* hybrids. Dashes indicate that information was not available.

LOCALITY			Date	No. and Sex <sup>1</sup>	Collector or Collection	Source
State or province	County	Township				
<i>L. a. arthemis</i> × <i>L. archippus</i> ( <i>arthechippus</i> Scudder) <sup>2</sup>						
Quebec	—	Chateauguay Basin	1879	1 ♂	J. G. Jack	Edwards (1882)
Maine	Penobscot	Vic. Montreal Passadumkeag	"many yrs. ago" (2nd brood)	1	L. P. Grey	Grey (1968)
New Hampshire	Cheshire	Alstead	1895, 1896, 1902 (seen)	3 ♂ ♂	W. L. W. Field	Field (1904)
Manitoba	—	Beulah	VI.29.1904	1 ♂	A. J. Dennis	Gunder (1934)
New York	Tompkins	Dryden	VIII.6.1967	1 ♂	A. M. Shapiro	Shapiro and Biggs (1970)
New York	Albany	East Berne	VIII.8.1938	1 ♂	E. Statsinger	F. H. Rindge
Total				8		
<i>L. a. astyanax</i> × <i>L. archippus</i> ( <i>rubidus</i> Strecker) <sup>3</sup>						
Pennsylvania	Berks	—	Prior to 1872	1 ♂	T. L. Mead	Gunder (1934)
Pennsylvania	Westmoreland	Jeanette	—	1	Barnes Coll.	" "
Massachusetts	Norfolk	Wellesley	—	1 ♂	A.M.N.H. Coll.	" "
Massachusetts	Middlesex	Sherborn	VIII.1896	1 ♂	A. L. Bablock	" "
New York	—	Brooklyn	IX.9.1913	1	Barnes Coll.	" "
New York	"Eastern" (Catskills?)	—	—	1	—	Shapiro and Biggs (1970)
New York	—	Long Island	—	1 ♂	Jacob Doll	Field (1904)
Kentucky	Jefferson	Louisville	IX.1948	1	R. Steilberg & J. Smith	Monroe (1953)
Arkansas	Pulaski	Rose City	IX.1.1933	1 ♂	A.M.N.H. Coll.	F. H. Rindge
Nebraska	Platte	Columbus	IX.4.1963	2 ♂ ♂	E. A. Froemel	K. Johnson
Texas	Bexar	San Antonio	IX.22.1970	1 ♂	J. F. Doyle III	J. F. Doyle III
Total				12		

<sup>1</sup> Insofar as is known, all specimens collected to date have been males.

<sup>2</sup> Eight male *arthechippus* were reared by Field (1914) from an *L. archippus* ♀ × *L. a. arthemis* ♂ cross. Other reciprocal crosses have been made recently by Platt.

<sup>3</sup> A ♀ *L. a. astyanax* × ♂ *L. archippus* were collected in copula VIII. 26. 1957 in a barnyard by Mrs. H. E. Hanna at El Dorado, Union Co., Arkansas. The two specimens are in the AMNH (Dr. F. H. Rindge pers. comm.).

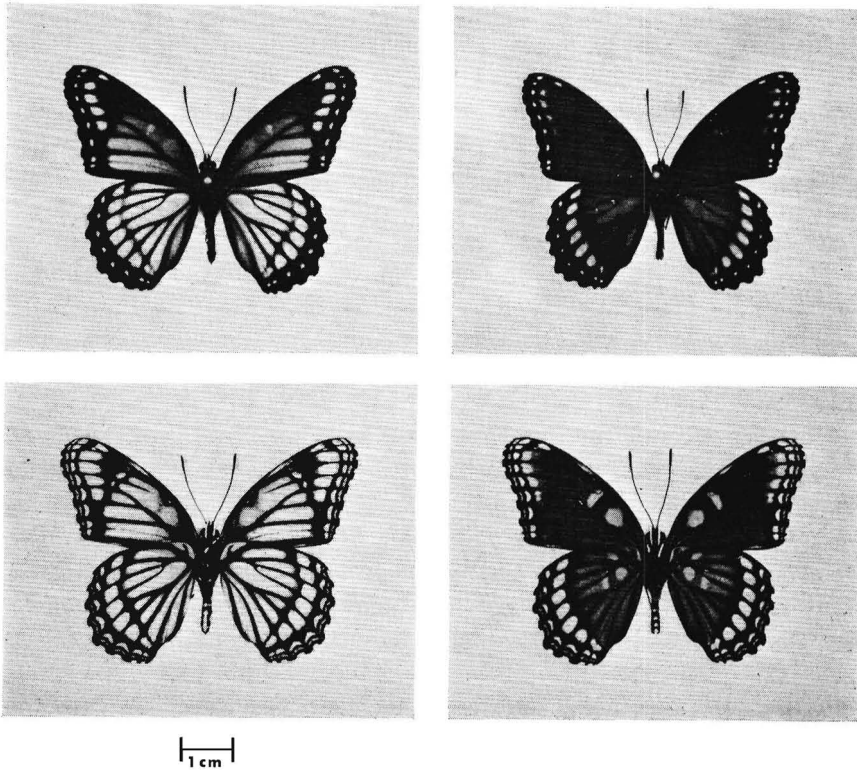


Fig. 2. Lab-bred  $F_1$  *L. arthemis astyanax*  $\times$  *L. archippus* hybrids; top row dorsal, bottom row ventral. Left, light (*archippus*-like) form; right, dark (*astyanax*-like) form. Specimens bred from Maryland stocks in January, 1970.

Proof of the hybrid nature of *rubidus* requires experimental crosses between the two parental species. As noted in Table 1, there is at least one record of *astyanax* and *archippus* having been collected *in copula* in the natural environment. Such hybrid crosses recently have been made by Platt (Figure 2) by hand-pairing the insects (Platt, 1969), and earlier ones are known to have been done at Yale University (C. L. Remington and R. W. Pease Jr. personal communication). To date, seven fertile crosses have been obtained by Platt. Since these data will be reported in greater detail later, only a brief report of the findings will be included here.

Five crosses between *astyanax* females and *archippus* males have produced a total of 52  $F_1$  male progeny. Two crosses between *archippus* females and *astyanax* males have yielded 78  $F_1$  males, for a combined total of 130  $F_1$  males. As shown in Figure 2, the inter-specific hybrids occur in both light (more *archippus*-like) and dark (more *astyanax*-like) morphs,

the wild-caught specimen described above being of the darker variety (Figure 1). In contrast to *arthechippus* hybrids, all *rubidus* entirely lack the partial white band markings on their dorsal surfaces. However, some, but not all, have traces of the white band persisting in the costal regions of the forewing, as does the recent wild-caught specimen. Such white markings are more fully expressed in *archippus*, but similar markings also are found in certain individuals of *astyanax* (Clark and Clark, 1951; Platt and Brower, 1968).

The complete documentation of *rubidus* as an interspecific hybrid is shown by the fact that all bred  $F_1$  specimens obtained to date are males. Complete heterogametic (female) inviability is encountered when the two full species are hybridized, in accordance with Haldane's Rule (Stebbins, 1958; Bowden, 1966).

However, recently the *rubidus* hybrids have been backcrossed successfully to both *astyanax* and *arthemis* females, and to *archippus* females, as well, yielding four viable broods having a total of 34 male and 12 female progeny (46 in all). Recovery of some of the females is noteworthy, although the sex ratios are still biased in favor of males ( $X^2_1 = 10.52$ ,  $P < 0.1$ ). Only three males have been obtained so far in two backcrosses to *archippus* females, and breeding experiments are continuing.

Nevertheless, these preliminary broods demonstrate that the  $F_1$  male hybrids are fertile in backcrosses to the parent females. Genetic and phenotypic segregation also is apparent in these crosses, all combinations of which have yielded "parent-like" and "hybrid-like" individuals.

Environmental selection probably is operating against the rare naturally occurring hybrids. Since the two parental species are considered to be Batesian mimics of two totally different unpalatable models, such intermediate morphs become exceedingly poor mimics of either one. The total female inviability encountered in  $F_1$  crosses means that the wild males must have to breed with parental females, if at all. Platt, Frearson, and Graves (1970) have shown that *arthechippus* males possess valvae intermediate in shape between those of the two parent species; the same also undoubtedly is true of *rubidus* males. Consequently, sexual selection and mate choice, in which coloration and courtship behavior likewise are important, would not seem to be favoring the male hybrids.

In conclusion, the rare wild hybrid form *rubidus* Strecker represents a true inter-specific  $F_1$  hybrid arising from "stray" matings between two closely related, but distinct mimetic species, *L. a. astyanax* and *L. archippus*. As such, it illustrates well the breakdown of Batesian mimicry in the natural environment, and the selective elimination of an unfit phenotype.

## Acknowledgments

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IDENTITY OF *PHANETA REFUSANA* (WALKER) WITH  
DESCRIPTION OF A NEW SPECIES (TORTRICIDAE)

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The name *Phaneta refusana* (Walker) is currently used for moths matching Heinrich's (1923) idea of Walker's species. Although Heinrich's interpretation is the most explicit available, Heinrich never saw the Walker type. He perpetuated Kearfott's (1905a) identification which was based mainly on Walsingham's (1879) description and lithograph figure. Photographs of the holotype taken by N. S. Obraztsov at the British Museum (Natural History), and made available by the American Museum of Natural History, show that true *refusana* is actually different from the *refusana* of Heinrich. I confirmed this finding by examining the type itself at the British Museum. The misidentified moths have no valid name and I here propose a new one for them.

The letter *n* in this paper signifies the number of specimens observed for a particular statement. Values of *n* differ from the total number studied because all specimens were not satisfactory for all purposes. Forewing lengths (one wing) are given to the nearest 0.5 mm including fringe and excluding patagium. The generic name *Phaneta* is used as suggested by Obraztsov (1952).

*Phaneta refusana* (Walker), new combination

*Grapholita refusana* Walker, 1863.

*Semasia refusana*; Walsingham, 1879.