INTER-SPECIFIC HYBRIDIZATION INVOLVING *LIMENITIS*ARCHIPPUS AND ITS CONGENERIC SPECIES (NYMPHALIDAE)

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ABSTRACT. The occurrence of 43 natural hybrids involving *Limenitis archippus* and its congeneric species (*L. arthemis-astyanax*, *L. lorquini*, and *L. weidemeyerii*) is reviewed. Nine of these hybrid records are reported for the first time. Data based on laboratory crosses are given in order to document the purported wild hybrid specimens. Reasons underlying the observed natural hybridization are suggested and their evolutionary implications are discussed.

Species of the North American genus Limenitis readily undergo interspecific hybridization both in nature and in the laboratory (Edwards, 1882; Scudder, 1889; Field, 1904, 1914; Newcomb, 1907; Gunder, 1934; Remington, 1958, 1968; Platt, 1975). The occurrence of 22 natural hybrids and the laboratory documentation of them in crosses involving either 1) L. arthemis arthemis Drury or 2) L. arthemis astyanax Fabricius × L. archippus Cramer have been reviewed and discussed by Monroe (1953); Grey (1968); Shapiro and Biggs (1968); Platt and Greenfield (1971), and Greenfield and Platt (1974). Since then, Johnson (1974) and Arbogast (1976) have reported two other wild-collected L. arthemis astyanax \times L. archippus hybrid specimens. Likewise, the natural occurrence of four L. lorquini Boisduval × L. archippus hybrids (Gage, 1970; Perkins and Gage, 1970) and five L. weidemeyerii Edwards × L. archippus hybrids (Cross, 1936, 1937; Simpson and Pettus, 1976) have also been recorded. Lab-bred equivalents of these wild hybrids are shown in Fig. 1.

In this paper we shall review these past records and will report records of nine other naturally occurring *Limenitis* hybrids involving *L. archippus*, a species broadly sympatric with other members of the genus. We will also present new information obtained from laboratory

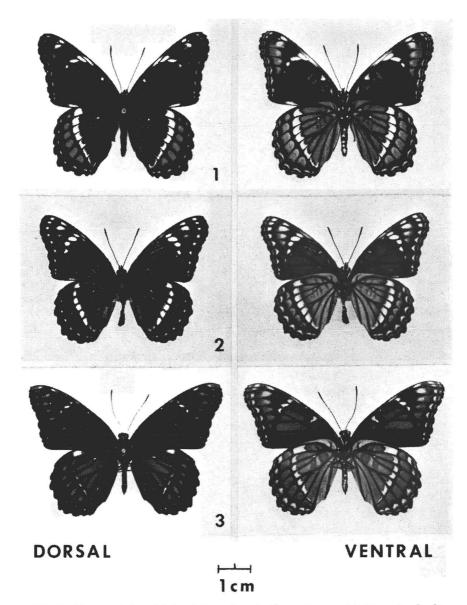


Fig. 1. Representative lab-bred F₁ male hybrid specimens. 1) Form "arthechippus," brood 893, No. 17, May 7, 1977; 2) form "weidechippus," brood 576, No. 7, Sept. 4, 1971; 3) lorquini $9 \times archippus$ § (unnamed hybrid), brood 987, No. 1, Sept. 8, 1978. These, and all other lab-bred specimens, were reared on either Salix babylonica L. or Prunus serotina Ehrh.

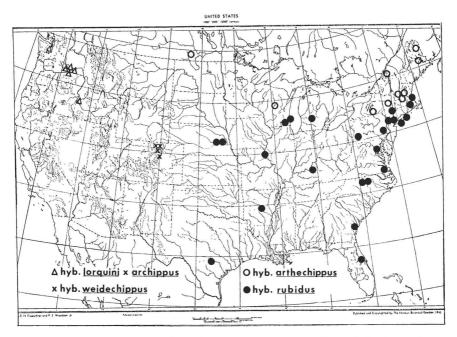


Fig. 2. Distribution map of 43 known wild, inter-specific F_1 hybrids involving cross-breeding with L. archippus collected from "prior to 1872" through 1976. All records for which the sex is known are males. These hybrids are widely distributed geographically. Touching symbols represent two (or more) specimens from the same locality. Most hybrids have been collected late in the season (August–November). Complete data for these hybrids are given in Tables 1, 1A, and 2. (Map reproduced with the permission of the Missouri Botanical Garden, St. Louis, Mo.).

crosses recently made by Platt, followed by a brief discussion of the relationships between *L. archippus* and its close relatives.

Tables 1, 1A and 2 summarize the collection data for all 43 records of wild hybrids involving *L. archippus* and its congeneric species. The geographic distributions of the various hybrid forms have been plotted in Fig. 2. The new hybrid locality records given in Table 1 are those from Maine (hyb. form "arthechippus" Scudder), Wisconsin, Illinois, Michigan, New Jersey, Virginia, and Florida (hyb. form "rubidus" Strecker). The specimens from Idaho, Illinois, Michigan, New Jersey, Virginia, and Florida probably represent state records for these hybrids.

The Florida record represents the first report of a natural hybrid between L. a. astyanax Fabricius and the sub-species L. archippus floridensis Strecker. The live specimen was observed circling a shrub willow along the edge of Mud Lake by G.W.R. while he was lunching

Table 1. Fourteen records of naturally occurring inter-specific hybrids between the *limenitis arthemis-astyanax* complex \times *L. archippus* (See Table 1A for previous records).

	State	County	Locality or Township	Date	No. & Sex	Collector &/or collection	Source and notes
$1)^{2}$	Maine	Aroostook	$L.~a.~arthemis \times L.$ So. of Castle Hill	archippus ("arthec Sept. 8, 1971	hippus" 1 ♂	'Scudder) J. D. Zeligs; pers. coll.	J. D. Z., pers. comm.
	Wisconsin	Portage	Stevens Point	July 6, 1961	18	J. M. Malick; Milw. Co. Mus.	Johnson (1974)
			T a actuanar V	L. archippus ("rub	idue" Si	rocker)	
2)	Wisconsin	Milwaukee	RR tracks vic. Estabrook Park	Aug. 9, 1971	1 8	R. Borth; pers. coll.	G. Balogh
3)	Wisconsin	Walworth	Troy, W. of Lulu Lake	Aug. 8, 1976	18	G. Balogh; pers. coll.	G. Balogh
4)	Illinois	Adams	Quincy, nr. Electric Wheel Plant	Sept. 29, 1960	18	A. Hunter; E. C. Tryon coll.	D. Hess & E. C. Tryon, pers. comm.
5)	Michigan	Clinton	_	Aug. 20, 1974	1 8	J. R. Johnson; Entomol. Mus., Mich. St. Univ.	M. C. Nielsen, pers. comm.
6–7)	New Jersey	Hudson	Kearny	June 21, Aug. 14 (yrs. not given; circa 1880–1910)	2 3 3	C. Leonhardt; U.S.N.M.	U.S.N.M. coll.: both bear Brooklyn Mus. labels; one has Barnes Coll. and Accen- sion 11782 labels, as well
		_	Washington, D.C.	Not known	1 8	E. Shoemaker; Acad. Arts & Sci., Brooklyn, N.Y.	Newcomb (1907)

Table 1. Continued.

State		County	Locality or Township	Date	No. & Sex	Collector &/or collection	Source and notes
8)	Virginia	Suffolk	Washington Ditch Great Dismal Swamp	Sept. 3, 1976	18	B. N. Hartgroves; U.S.N.M.	B. N. Hartgroves, pers. comm.
	No. Carolina	Durham	So. of Durham	Oct. 10, 1970; Oct. 15, 1972	288	J. C. Greenfield, Jr., A.M.N.H., A.P. Platt coll., respectively	Platt & Greenfield (1971 Greenfield & Platt (1974)
	Georgia	Chatham	Savannah	Sept. 22, 1974	18	R. T. Arbogast; pers. coll.	Arbogast (1976)
9)	Florida	Volusia	Lake Woodruff Wildl. Refuge, vic. Mud Lake	Nov. 22, 1974	18	G. W. Rawson; U.S.N.M.	G. W. Rawson

¹ This table excludes 20 records previously listed by Platt and Greenfield (1971).

² Numbered records have not been previously reported by Newcomb (1907), Platt and Greenfield (1971), Greenfield and Platt (1974), Johnson (1974), or Arbogast (1976).

Table 1A. Records of 20 previously wild-caught *Limenitis arthemis-astyanax* hybrids, modified from Platt and Greenfield, 1971: 280. Dashes indicate that information was not available. (Reproduced by permission of the authors.)

Province or State	County	Locality or Township	Date	No. & Sex ¹	Collector &/or collection	Source and notes
	1	L. a. arthemis $ imes$ L. arch	hippus ("arthechipp	us" Scu	idder)²	
Quebec	_	Chateauguay Basin vic. Montreal	Sept., 1879	1 8	J. G. Jack	Edwards (1882); Scudder (1889)
Maine	Penobscot	Passadumkeag	"many years ago" (2nd brood)	1	L. P. Grey	Grey (1968)
New Hampshire	Cheshire	Alstead	1895, 1896, 1902 (seen)	3 8 8	W. L. W. Field	Field (1904)
Manitoba		Beulah	June 29, 1904	1 8	A. J. Dennis	Gunder (1934)
New York	Tompkins	Dryden	Aug. 6, 1967	1 3	A. M. Shapiro	Shapiro and Biggs (1968)
New York Total	Albany	East Berne	Aug. 8, 1938	1 8 8	E. Statsinger	F. H. Rindge
		L. a. astyanax $ imes$ 1	L. archippus ("rubic	<i>lus</i> " Str	ecker)³	
Pennsylvania	Berks	_	Prior to 1872	18	T. L. Mead, F.M.N.H. Coll.	Gunder (1934)
Pennsylvania	Westmoreland	Jeanette		18	Barnes coll., U.S.N.M.	Gunder (1934)
Massachusetts	Norfolk	Wellesley		1 8	A.M.N.H. coll.	Gunder (1934)
Massachusetts	Middlesex	Sherborn	Aug., 1896	1 8	A. L. Bablock	Gunder (1934)
New York	_	Brooklyn	Sept. 9, 1913	18	Barnes coll., U.S.N.M.	Gunder (1934)
New York	"Eastern" (Catskills?)	_	_	1	_	Shapiro and Biggs (1968)

TABLE 1A. Continued.

Province or State	County	Locality or Township	Date	No. & Sex ¹	Collector &/or collection	Source and notes
New York		Long Island		1 &	Jacob Doll	Field (1904)
Kentucky	Jefferson	Louisville	Sept., 1948	1 &	R. Steilberg & J. Smith	Monroe (1953)
Arkansas	Pulaski	Rose City	Sept. 1, 1933	1 3	A.M.N.H. coll.	F. H. Rindge
Nebraska	Platte	Columbus	Sept. 4, 1963	2 8 8	E. A. Froemel	K. Johnson
Texas	Bexar	San Antonio	Sept. 22, 1970	1 8	J. F. Doyle III	J. F. Doyle III
Total				12		

¹ Insofar as is known, all specimens collected to date have been males. ² Eight male arthechippus were reared by Field (1914) from an L. archippus $\mathcal{Q} \times L$. a. arthemis \mathcal{C} cross. Other reciprocal crosses have been made re-

The trace and the control by Platt.

3 A \(\beta \) L. a. astyanax \(\times \) d. L. archippus were collected in copula Aug. 26, 1957 in a barnyard by Mrs. H. E. Hanna at El Dorado, Union Co., Arkansas. The two specimens are in the A.M.N.H. (Klots, 1959; Dr. F. H. Rindge, pers. comm.).

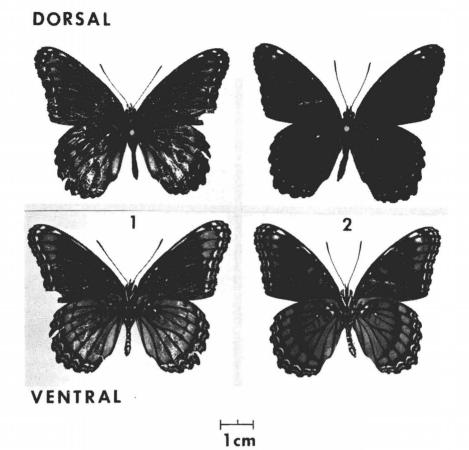


Fig. 3. 1) Wild-caught and 2) lab-bred male specimens of L. arthemis astyanax \times L. archippus floridensis F_1 hybrids (form "rubidus"). Data for the lab-bred specimen are brood 986, No. 1, Sept. 19, 1977 (Data for wild-caught specimen are given in Table 1).

with members of the Florida Audubon Society in the northeastern portion of the Ocala National Forest. He recognized the specimen as an "off-color" Limenitis and investigated it further. The insect then settled on the willow shrub. Since he had no net, George made a "desperate strike" at it with his cap, knocking the butterfly to the ground and collecting it. The specimen is illustrated in Fig. 3, along with a similar, single specimen recently reared by A.P.P. in the laboratory from a hand-paired cross between a Maryland $astyanax \ ^{\circ}\times a\ floridensis$ δ (from a stock obtained just east of the Everglades [near Home-

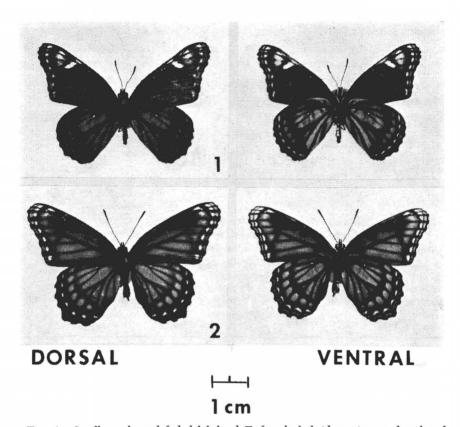
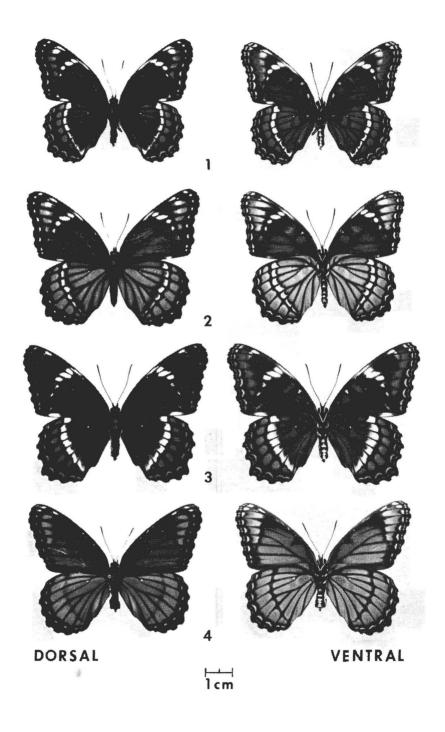


Fig. 4. Small, weak, and faded lab-bred F_1 female hybrid specimens, dorsal and ventral views. 1) Form "weidechippus," brood 576, No. 1, Aug. 28, 1971; 2) form "rubidus," brood 648, No. 4, July 26, 1973.

stead] in southern Florida). Astyanax evidently is relatively uncommon in central Florida. Near his home at New Smyrna Beach (Volusia Co.), G.W.R. has seen only two specimens of astyanax during the past 20 years. Also, F. Rutkowski (pers. comm.) recently collected a & astyanax 1.5 miles north of Shamrock (Dixie Co.) in Florida, and he mentioned other records from as far south as Dade Co. (Kimball, 1965). Possibly such scarcity of one (or both) species accounts in part for such interspecific hybridization (Simpson and Pettus, loc. cit.).

So far as is known, all of the wild hybrids thus far collected have been males, although five broods containing small, faded, weak (and often malformed) F_1 females (Fig. 4) were reared at UMBC in June and July, 1973 by crossing inter-specific strains having different geographic origins (Maryland *L. astyanax* \mathfrak{PP} × Vermont *L. archippus*



 $\delta \delta$). Among these broods, there were a total of 39 (27%) F_1 females among 143 hybrid "rubidus" progeny. Two of the larger broods, involving sibling female astyanax and the same male archippus parent, yielded 1:1 sex ratios.

Earlier crosses reported by Platt (1975) showed that such interspecific crosses, in which strains from the same (or closely adjacent) northeastern geographic origins were crossed, gave rise to complete adult heterogametic (female) inviability. However, robust females of the "arthechippus" and "rubidus" hybrid phenotypes (Fig. 5) also have been obtained by backcrossing F_1 hybrid males to females of the three parental forms (arthemis, astyanax, and archippus, respectively). Such backcrosses often have low viability, but sometimes yield relatively large numbers of progeny (Platt, loc. cit.). Although fertile crosses have been obtained in all possible reciprocal combinations, crosses using L. arthemis, astyanax, lorquini, or weidemeyerii $9.9 \times L$. archippus 3.5×10^{-10} have been the easiest to effect in the laboratory using hand-pairing. The fact that such a pairing also has been seen in the wild (Klots, 1959; Table 1A) suggests that these inter-specific hybrid crosses may occur most often in this direction in nature, as well.

Table 1 indicates that eight of the nine previously unreported arthemis $astyanax \times archippus$ hybrids, like most of those reported earlier, were collected during the late summer and fall months (August–November). Only one (from New Jersey) was collected in June, a time suggesting that it most likely arose from an over-wintering larva. Thus, these new records, as well as the previous ones, support the contention that the ecological and behavioral barriers normally preventing inter-specific hybridization in Limenitis tend to break down later in the season (Greenfield and Platt, loc. cit.). This break down may well be correlated with the onset of facultative larval diapause in Limenitis which occurs during the third instar. Thus, it seems as if those individuals most often selecting mates of the wrong species are the very ones which seem to be "genetically mal-adapted" to their environment (that is, they are the ones which are not diapausing at that time of year when they are

Fig. 5. Representative robust, lab-bred hybrid-type backcross females. 1) L. arthemis $\mathcal{Q} \times F_1$ hybrid "arthechippus" \mathcal{E} ("arthechippus-like" morph), brood 63c, No. 4, July 30, 1968; 2) L. archippus $\mathcal{Q} \times F_1$ hybrid "arthechippus" \mathcal{E} ("arthechippus-like" morph), brood 915, No. 45, June 13, 1977; 3) L. arthemis $\mathcal{Q} \times F_1$ hybrid "rubidus" \mathcal{E} ("proserpina-like" morph), brood 95B, No. 4, Dec. 26, 1968; 4) L. archippus $\mathcal{Q} \times F_1$ hybrid "rubidus" \mathcal{E} ("rubidus-like" morph), brood 757, No. 10, Sept. 15, 1975. Such backcross females also occur in parent-type morphs (see Platt, 1975).

Table 2. Records of nine wild hybrids involving the two western banded species of Limenitis (lorquini and weidemeyerii, respectively) \times L. archippus.

State	County	Locality or Township	Date	No. & Sex	Collector &/or collection	Source and notes
		L. lorqui	ni $ imes$ L. archippus (ınnamed	form)	
Washington	Benton	Richland, nr. Richland "Y"	July 4, 1965	18	E. V. Gage, pers. coll.	Gage, 1970; Perkins and Gage, 1970
Washington	Benton	Richland, nr. Richland "Y"	July 6, 1969	2 8 8	J. C. Montgomery, pers. coll.	Gage, pers. comm.
Washington	Benton	Richland, nr. Richland "Y"	Sept. 4, 1971	1 8	J. C. Montgomery, pers. coll.	Gage, pers. comm.
Idaho	Ada	nr. Lucky Peak Dam	Oct. 7, 1971	1 8	R. Cassingham, pers. coll.	Gage, pers. comm.
		L. weidemeyer	ii $ imes$ L. archippus ("	weidechi	ppus" Cross)	
Colorado	Lorimer	Fort Collins	Aug. 25, 1894	18	C. P. Gillette, C.S.U. Entomol. Mus.	Simpson and Pettus (1976)
Colorado	Lorimer	Fort Collins	June 9, 1973	2 8 8		Simpson and Pettus (1976) 1 caught; 1 seen;
Colorado	Not given	nr. Denver along Platte R.	circa 1936	1 8	C. D. Schryver; pers. coll.	fresh; presumed sibe Cross, 1936; 1937

supposed to be doing so). Such hybridization, perhaps, represents a "last chance" effort to reproduce.

The similar rare natural hybrids reported between both of the western banded Limenitis (L. lorquini and L. weidemeyerii) and L. archippus are listed in Table 2. The eight known dates of siting or capture suggest once again that either 1) the hybrids emerged early enough in the year (June and July dates) so that it is a relative certainty that the larvae from which they arose over-wintered in hibernacula, or 2) the specimens were collected in the late summer or fall months. Gage's (pers. comm.) collection dates for the small "hybrid swarm" near Richland, Washington (Table 2) suggest that the four lorquini × archippus hybrids, in fact, represent progeny from at least three different matings. The same may be said for the four "weidechippus" records from Colorado, as well. All of these wild western hybrids are males, and they closely resemble hybrid from "arthechippus" in possessing a partial postmedial white band dorsally (Fig. 1). Two crosses between Colorado weidemeyerii $9.9 \times Massachusetts$ archippus & & have been made by laboratory hand-pairings to date, yielding 22 && and nine 99 (seven of the latter being malformed). All of these F₁'s, although showing some phenotypic variability, are referrable to hyb. form "weidechippus" (Platt, unpub. data). During the past summer two crosses between Oregon L. lorquini 99 × Maryland L. archippus 33 were carried out. All 16 F₁ progeny were males. An additional cross involving an F₁ hybrid, arthemis-lorquini ^Q (Massachusetts × Oregon stocks, respectively) × Maryland archippus 8, yielded 21 male hybrid-like progeny.

Thus, *L. archippus*, which is broadly sympatric with its congeners, will occasionally hybridize with all of the other allopatric species of *Limenitis* in nature. However, such crosses evidently are rare, leading to the supposition that morphological, behavioral, visual, and possibly pheromonal cues, as well as habitat isolating mechanisms, normally operate to prevent such inter-specific hybridization. These barriers against gene exchange between the viceroy and its close relatives sometimes tend to break down, usually when one or both species are rare, and often toward the end of the breeding season, at times when the majority of developing *Limenitis* larvae are entering diapause.

Laboratory data show that inter-specific strains having different geographic origins may be genetically more compatible than similar strains from the same locality, as judged by either the presence or absence of adult females in the F_1 generation. Thus, genetic incompatibility between the viceroy and its congeneric species is viewed as being of local

origin, suggesting that *archippus* may have arisen from a banded ancestral species by the process of sympatric speciation. (The senior author would appreciate hearing from members of the Society who may have knowledge of other records of wild *Limenitis* hybrids.)

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TAENIDIA INTEGERRIMA, A NEW FOODPLANT RECORD FOR PAPILIO POLYXENES (PAPILIONIDAE)

Host plants recorded for the larval stages of *Papilio polyxenes* Fabricius include a wide variety of species in the family Umbelliferae. Although the dominant foodplants in the northeastern United States are plants naturalized from Europe, e.g., *Daucus carota* Linnaeus and *Anethum graveolens* L. (Tyler, 1975, The Swallowtail Butterflies of North America, Naturegraph Publishers, Heraldsburg, CA), a number of endemic species have been documented as foodplants. Tietz (1972, An Index to the Described Life Histories, Early Stages, and Hosts of the Macrolepidoptera of the Continental United States and Canada, A. C. Allen, Sarasota, FL) lists *Cicuta bulbifera* L., *Cicuta maculata* L., *Angelica atropurpurea* L., *Osmorhiza claytoni* (Michx.), *Osmorhiza longistylis* (Torr.), *Oxypolis filiformis* (L.), *Spermolepis divaricata* (L.), *Ptilimnium capillaceaum* (Michx.), and *Sium suave* Walt. among the native umbellifers; *Cryptotaenia canadensis* (L.) has recently been reported as a foodplant as well (Scriber and Finke, 1978, J. Lepid. Soc. 32: 236–238). The majority of these species are characteristically found in rich damp woods (*Osmorhiza* spp.) or wet thickets and swamps.

The native umbellifer Taenidia integerrima (L.) Drude (yellow pimpernel), hitherto unrecorded as a host plant for P. polyxenes but reported as a host plant of the recently described sibling species P. joanae (Heitzman, 1973, J. Res. Lepid. 12: 1-10), is a plant of dry, gravelly slopes and rocky hillsides (Fernald, 1950, Gray's Manual of Botany, 8th ed., American Book Co., NY). On June 22, 1977, one fifth instar larva of P. polyxenes was found feeding in a patch of T. integerrima growing on a dry, exposed slope bordering a road which cuts through Coy Glen, a forested area 3 km west of Ithaca, Tompkins Co., New York. Two additional fifth instar caterpillars were found in the same patch two days later. All three caterpillars were collected and reared to pupation on T. integerrima collected from the Coy Glen site. Pupation was virtually synchronous on June 24, 1977, indicating that the caterpillars may have developed from eggs laid at approximately the same time, possibly by a single female. On July 2, 1977, one adult male ichneumonid, Trogus pennator (Fabr.), a well-known parasitoid of P. polyxenes (Heinrich, 1964, Canad. Ent. Suppl. 29: 807-853), emerged from each of the three pupae.