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PAPILIO CANADENSIS AND *P. GLAUCUS* (PAPILIONIDAE) ARE DISTINCT SPECIES

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ABSTRACT. *Papilio canadensis* Rothschild & Jordan is recognized as a distinct species, not a subspecies of *P. glaucus* L., on the basis of physiological and genetic differences despite great similarity in adult appearance of these two taxa. Interspecific hybrids are found in a well-marked zone where the ranges of the species come into contact. The ecological or genetic factors that maintain species integrity despite this natural hybridization are as yet uncertain.

Additional key words: diapause, electrophoresis, hybrid zone, Michigan, Great Lakes region.

In their revision of American Papilionidae, Rothschild and Jordan (1906) described a northern subspecies of *Papilio glaucus* L., *P. g. canadensis*, distinguishable from *P. g. glaucus* by differences in the details of wing color pattern and by its smaller size. Although evidence was scanty, Rothschild and Jordan suggested that *glaucus* and *canadensis* "completely intergrade" in the Great Lakes region. Presumably, the parapatric distribution of these two taxa was a major factor in their decision to treat *canadensis* as a subspecies of *P. glaucus*.

Despite the morphological similarity between *P. glaucus* and *canadensis* adults and the occurrence of natural hybridization, our recent studies lead us to conclude that *canadensis* does warrant recognition as a distinct species. Three lines of evidence support our interpretation: first, there is significant differentiation between *glaucus* and *canadensis* in characters besides adult morphology; second, there appears to be a closer phylogenetic relationship between *glaucus* and *P. alexiars* Hoppfer than between *glaucus* and *canadensis*; and third, intergra-

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dation between *glaucus* and *canadensis* is restricted to a narrow hybrid zone. We discuss this evidence and its implications below.

In contrast to *canadensis*, another currently recognized subspecies of *P. glaucus*, *P. g. australis* Maynard, appears to fully intergrade morphologically and genetically with *P. g. glaucus* in the southeastern United States (Hagen & Scriber 1991, R. C. Lederhouse, J. L. Bossart & J. M. Scriber unpubl.). We suggest that *australis* should be treated as only a form of *P. glaucus*. A more complete discussion of relationships between *australis* and typical *glaucus* populations is in preparation (R. C. Lederhouse, J. L. Bossart & J. M. Scriber unpubl.). In addition, our studies provide no evidence whatsoever to justify resurrection of an Alaskan subspecies, *arcticus* Skinner; all specimens from Fairbanks, Alaska, that we have examined are clearly *P. canadensis*.

***Papilio canadensis* Rothschild & Jordan, new status**

Papilio glaucus canadensis Rothschild & Jordan (1906).

Diagnostic characters for the species are discussed below, and include those which have been used previously for the subspecies.

DIAGNOSTIC CHARACTERS

Color Pattern and Morphology

Overall similarity of adults characterizes taxa within species groups of *Papilio* and contributes to frequent uncertainties in species-level taxonomy of Papilionidae (Rothschild & Jordan 1906, Munroe 1961, Sperling 1987, 1990). Two features of the wing pattern originally noted by Rothschild and Jordan appear to be fairly reliable characters for distinguishing adult *glaucus* and *canadensis*, along with overall size.

The first feature is the form of the forewing underside submarginal spots (Luebke et al. 1988). In *P. glaucus* the yellow spots centered in each cell are distinct; in *P. canadensis*, the spots form a nearly continuous yellow band with black pigment confined to a narrow line of scales at each vein. The yellow band in *canadensis* is similar to that on the forewing underside of *P. rutulus* Lucas. However, both *canadensis* and *glaucus* can be distinguished from *rutulus* by the presence of orange in the first submarginal spot of the hindwing (Rothschild & Jordan 1906).

The second diagnostic feature for *canadensis* is the width of the black band along the anal margin of the hindwing (Scriber 1982). For *P. glaucus* males, widths are in the range 10 to 50 percent of the width from wing margin to the CuA2 vein; whereas for *P. canadensis* males, the range is 50 to 90 percent (Scriber 1982, R. Hagen, unpubl. data). The width of the black band is greater in females than males, though the relative difference between species persists.

Smaller adult size is a third criterion useful for distinguishing specimens of *P. canadensis* from *P. glaucus*. Luebke et al. (1988) estimated size from the forewing chord length (FCL), the distance from wing apex to base: FCL for male *P. canadensis* ranged from 41 to 50 mm (median = 45 mm; n = 91); FCL for male *P. glaucus* ranged from 46 to 59 mm (median = 54 mm; n = 72). (Females were not measured in this study.) In both species the upper limits to size appear to be determined by intrinsic developmental constraints, but variation in larval food plant quality can produce wide variation among individuals below this limit; thus, small *P. glaucus* may be similar in size to *P. canadensis*.

Use of wing pattern characters for species diagnosis also must be tempered with caution. Adult *P. glaucus* that diapaused as pupae have greater anal band widths than individuals that did not undergo diapause, and more closely resemble *P. canadensis* adults in other wing pattern features (Scriber 1990). This effect undoubtedly contributes to similarity between *P. canadensis* and "spring brood" (i.e., overwintered) *P. glaucus*, noted by Rothschild and Jordan (1906) and discussed at length by Clark and Clark (1951). It is even possible that some early season individuals collected within the range of *P. glaucus* may be *P. canadensis*, or hybrids (Scriber 1990).

At least one larval character appears useful for distinguishing *glaucus* and *canadensis*. Very young larvae (1st or 2nd instar) of *canadensis* possess three transverse white bands on the dorsal side, whereas *glaucus* larvae have only a single, central, band (Fig. 1). A possible difference in the mature larvae (4th and 5th instar) is the presence of a distinct pale yellow or white pigment around the dorsal anal tubercles of *canadensis* that is fainter or absent in *glaucus* larvae. However, we are uncertain of the reliability of this character difference. The form and color of the metathoracic "eyespot" of mature larvae do not differ between *glaucus* and *canadensis*, though they differ markedly from those of *P. eurymedon* Lucas, *P. rutulus*, and *P. multicaudatus* Kirby larvae (Brower 1959).

Male genitalia of *glaucus* and *canadensis* cannot be distinguished by shape, independent of overall size (Brower 1959). Female genitalia and internal morphology have yet to receive careful study.

Diapause

The most striking differences between *glaucus* and *canadensis* involve physiological and developmental characters (Table 1).

Populations of *canadensis* and *glaucus* differ in the control of pupal diapause (Scriber 1982, Hagen & Lederhouse 1985, Rockey et al. 1987a, Hagen & Scriber 1989). In *P. glaucus*, diapause appears to be determined environmentally: larvae that experience long daylength, good

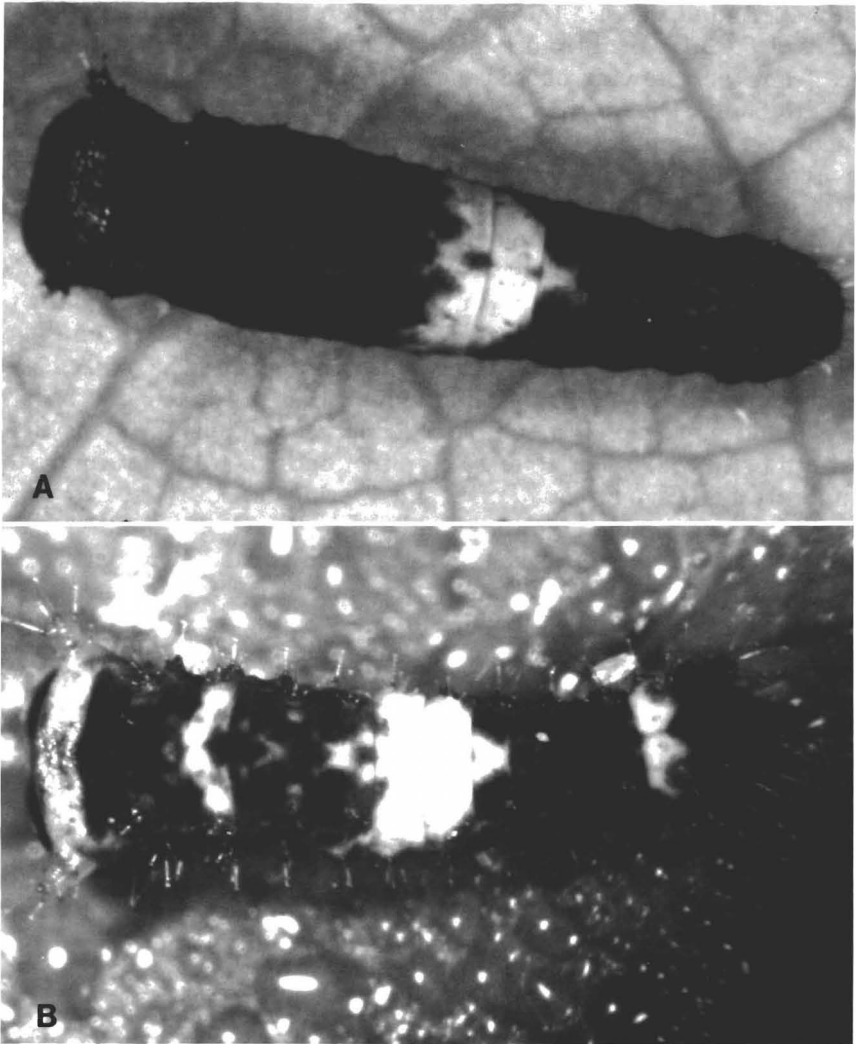


FIG. 1. First instar larvae of (A) *P. glaucus*, from Lawrence County, Ohio and (B) *P. canadensis*, from Cheboygan County, Michigan, showing diagnostic banding patterns (reared June–July 1991).

quality food, and perhaps warm temperatures are much more likely to develop directly into adults, without diapause, than are larvae that experience short days, poor food, or low temperatures. Under standard rearing conditions of 16 h light : 8 h dark, the proportion of larvae developing directly decreases among populations of *P. glaucus* with increasing latitude (Hagen & Lederhouse 1985, Rockey et al. 1987a).

TABLE 1. Summary of physiological and biochemical differences between *P. glaucus* and *P. canadensis*, and their modes of inheritance, if known. See text for fuller explanation.

Character	<i>P. glaucus</i>	<i>P. canadensis</i>	Inheritance	Reference
(Physiological/Developmental)				
Environmental determination of pupal diapause	yes	no	X-linked	1, 2
Lower lethal temperature for diapausing pupae	-23°C	-23 to -27°C	?	3
Larval survival on aspen foliage	very low	high	polygenic	4, 5, 6
Larval survival on birch foliage	low	high	polygenic	5, 7
Larval survival on tuliptree foliage	high	very low	polygenic	4, 5
Polymorphism for female color	present	absent	Y-linked	8, 9
Suppression of melanic color	absent	present	X-linked	1, 9, 10
(Biochemical)				
Hexokinase (<i>Hk</i>) alleles	"100"	"110"	autosomal	11
Lactate dehydrogenase (<i>Ldh</i>) alleles	"100"	"80," "40"	X-linked	1, 7, 11
6-Phosphogluconate dehydrogenase (<i>Pgd</i>) alleles	"100," "50"	"125," "80," "150"	X-linked	1, 7, 11

1. Hagen and Scriber (1989); 2. Rockey et al. (1987a); 3. Kukul et al. in press; 4. Scriber (1986); 5. Scriber (1988); 6. Scriber et al. 1989; 7. Hagen 1990; 8. Clarke and Sheppard (1962); 9. J. M. Scriber, R. H. Hagen and R. C. Lederhouse, unpublished; 10. Scriber et al. (1987); 11. Hagen and Scriber 1991.

This pattern is presumably an adaptive response to latitudinal variation in day length, similar to that shown by many other insects (Tauber et al. 1986).

In *P. canadensis*, however, pupal diapause appears to be obligate: regardless of rearing conditions, all individuals enter pupal diapause (Rockey et al. 1987a). The genetic basis for obligate diapause is an X-linked, recessive allele present in *P. canadensis* (Rockey et al. 1987b, Hagen & Scriber 1989). (The sex chromosomes of males are here denoted as XX; those of females as XY.)

The obligate diapause allele of *P. canadensis* has an obvious benefit for individuals of this species, since the growing season throughout its range is too short to permit more than one generation to develop successfully each year (Hagen & Lederhouse 1985, Scriber 1988). The obligate diapause allele would be highly disadvantageous for *P. glaucus*, because *glaucus* occurs in areas where the growing season should permit two or more generations per year.

Differences in the regulation of diapause induction are accompanied by differences in the cold tolerance of diapausing pupae (Table 1: Kukul et al. in press). Diapausing *P. canadensis* pupae are capable of surviving

lower temperatures than are *P. glaucus* pupae. The species also differ in primary metabolism: labelled glucose injected into diapausing pupae is converted to different compounds in each species (Kukal et al. in press). The genetics of cold tolerance and pupal physiology have not been studied in these species.

Larval Food Plant Use

Larval food plant use by *P. glaucus* and *P. canadensis* also differs (Table 1: Scriber 1988). Laboratory studies have revealed that *P. glaucus* larvae develop poorly on foliage from aspen (*Populus* spp.: Salicaceae) or birch (*Betula* spp.: Betulaceae), good hosts for *P. canadensis*. Conversely, *P. canadensis* larvae are unable to grow on foliage from tuliptree (*Liriodendron tulipifera* L.: Magnoliaceae), an important host for *P. glaucus*.

These reciprocal inabilities are due to differences in the larval detoxication systems of each species. Lindroth et al. (1988) showed that *P. canadensis* larvae possess high levels of a specific esterase enabling detoxication of a glycoside present in extracts of trembling aspen (*Populus tremuloides* Michx.) foliage. Larvae of *P. glaucus* lack this esterase activity and are poisoned by the glycoside; esterase activity is heritable (Scriber et al. 1989). Extracts of tuliptree foliage are similarly toxic to *P. canadensis* larvae, but are tolerated by *P. glaucus* (Lindroth et al. 1986). The toxic components in tuliptree have not yet been characterized, but clearly differ from those present in aspen.

Mimicry

As noted by Rothschild and Jordan (1906), mimetic (black or dark brown) females occur as a polymorphism only in *glaucus*; *canadensis* females are always yellow. The expression of this polymorphism in *P. glaucus* is determined by genes on both the X and Y chromosome (Hagen & Scriber 1989). The phenotypic polymorphism in *P. glaucus* results from a genetic polymorphism at the Y-linked locus (Clarke & Sheppard 1962). Thus, in *P. glaucus*, yellow females produce yellow daughters and black females produce black daughters. (Both produce yellow sons, since males do not carry the Y chromosome.)

However, an X-linked gene is also required for expression of the mimetic form (Hagen & Scriber 1989). A female who inherits the Y-linked allele for black color from her mother but also inherits the X-linked "suppressor" allele from her father will be yellow. The X-linked suppressor allele appears to have no effect on the yellow phenotype of males or of females that inherit the Y-linked yellow allele.

Genetic analysis of *P. glaucus* and *P. canadensis* hybrids suggests that *P. canadensis* populations lack the Y-linked allele for black color

and may be fixed for the X-linked suppressor allele (J. M. Scriber, R. H. Hagen & R. C. Lederhouse unpubl.). Conversely, *P. glaucus* populations appear to lack the X-linked suppressor allele.

Biochemical and Molecular Characters

Papilio glaucus and *P. canadensis* show fixed genetic differences at three enzyme loci detected by allozyme electrophoresis: Hexokinase (*Hk*), Lactate dehydrogenase (*Ldh*), and 6-Phosphogluconate dehydrogenase (*Pgd*) (Table 1: Hagen & Scriber 1989, Hagen 1990, Hagen & Scriber 1991). The distribution of allele frequencies at these loci in samples of butterflies collected from Michigan are given in Table 2 and shown in Fig. 2 (discussed below). Differences between the species may represent either chance fixation of neutral variants or the results of natural selection favoring different enzymes in each species.

Analysis of 26 allozyme loci, including the three noted above, yielded an estimate of genetic identity (Nei 1972) also consistent with species-level differentiation between *glaucus* and *canadensis* (Hagen & Scriber 1991). The estimate, 0.86, was lower than that between *P. eurymedon* and *P. rutulus* (0.91), and the same as that between *P. glaucus* and *P. alexiaries*. A similar range of genetic identities was reported by Sperling (1987) for North American species of the *Papilio machaon* species group. The allozyme data gave no support for the proposal (Scott 1986) that *P. rutulus* is conspecific with *P. canadensis* or *P. glaucus*.

The mitochondrial DNA's of *P. glaucus* and *P. canadensis* also differ (F. Sperling & R. Hagen unpubl.).

DISCUSSION

Phylogenetic Evidence

A phylogenetic analysis of tiger swallowtails using allozyme loci gave strongest support for a monophyletic lineage consisting of *P. glaucus* and *P. alexiaries* (Hagen & Scriber 1991). The characters most clearly supporting this lineage were *Hk* and *Ldh*. In both cases, *P. glaucus* and *P. alexiaries* share a form of the enzyme that differs from that present in all other *P. glaucus* group taxa.

Papilio glaucus and *P. alexiaries* also uniquely share the mimetic female form (Beutelspacher-Baigts & Howe 1984). Analysis of interspecific hybrids between *P. glaucus* and *P. alexiaries* indicates that genetic control of female color is similar in the two species (Scriber et al. 1988[89]). It appears likely that presence of mimetic females is a derived character within the *P. glaucus* species group (Scriber et al. 1990).

The "Haldane Effect" is a commonly observed consequence of in-

TABLE 2. Allele frequencies for *Ldh*, *Pgd*, and *Hk* allozyme loci from Michigan samples, separated by county. Counties are listed from north (*P. canadensis* range) to south (*P. glaucus* range), as shown in Fig. 2. N = number of males scored for each locus. Alleles at each locus are named according to enzyme mobility relative to the most common allele in *P. glaucus* (named the "100" allele; Hagen & Scriber 1989, Hagen & Scriber 1991). The *canadensis* alleles for *Ldh* are "80" and "40"; for *Pgd*, "125," "80," and "150"; and for *Hk*, "110." *Hk* was not scored from some samples ("—"). (Electrophoretic methods discussed in Hagen & Scriber 1989 and Hagen & Scriber 1991.)

County	LDH			PGD		
	N	100	80	40	N	100
1. Ontonagon	20	0.0	0.95	0.05	20	0.0
2. Gogebic	2	0.0	1.00	0.0	2	0.0
3. Iron	25	0.0	1.00	0.0	25	0.0
4. Dickinson	10	0.0	1.00	0.0	10	0.0
5. Luce	32	0.0	1.00	0.0	30	0.0
6. Mackinac	8	0.0	1.00	0.0	8	0.0
7. Emmet	28	0.0	1.00	0.0	28	0.0
8. Antrim	18	0.0	0.89	0.11	18	0.0
9. Otsego	16	0.0	0.88	0.12	16	0.0
10. Manistee	16	0.0	0.88	0.12	16	0.0
11. Roscommon	10	0.0	0.70	0.30	10	0.0
12. Ogemaw	2	0.0	1.00	0.0	2	0.0
13. Gladwin	6	0.0	1.00	0.0	6	0.17
14. Newago	24	0.0	1.00	0.0	24	0.0
15. Isabella	34	0.0	0.85	0.15	34	0.0
16. Allegan	24	0.92	0.08	0.0	24	0.96
17. Ingham	61	0.85	0.13	0.02	61	0.93
18. Jackson	4	1.00	0.0	0.0	4	1.00
19. Washtenaw	29	0.93	0.07	0.0	29	1.00
20. St. Joseph	24	1.00	0.0	0.0	24	0.96
21. Lenawee	34	1.00	0.0	0.0	35	0.94

terspecific hybridization (Haldane 1922, Coyne & Orr 1989). In the *P. glaucus* group, the Haldane Effect has been observed when *P. glaucus* females are hand-paired to males of *P. eurymedon*, *P. rutulus*, and *P. multicaudatus*, taking the form of reduced viability of female hybrid offspring (Scriber et al. 1990). The effect was not observed among hybrid offspring of *P. glaucus* females and *P. alexiaries* males (Scriber et al. 1988[89]).

A significant Haldane Effect does occur among hybrid offspring of *P. glaucus* females and *P. canadensis* males. A total of 568 male and 370 female offspring eclosed successfully from 39 hybrid families reared in our laboratory from 1983–88 (39.4% female; Hagen & Scriber in press). There was a significant bias against female hybrids in these families: in 25 families more males than females eclosed, in three an equal number eclosed, and in only 11 did fewer males than females eclose ($P = 0.026$; Wilcoxon test). Backcrosses of hybrid males to *P.*

TABLE 2. Extended.

PCD				HK		
50	125	80	150	N	100	110
0.0	0.80	0.05	0.15	—		
0.0	1.00	0.0	0.0	—		
0.0	0.88	0.12	0.0	—		
0.0	0.90	0.10	0.0	10	0.0	1.00
0.0	0.87	0.10	0.03	—		
0.0	0.75	0.13	0.12	6	0.0	1.00
0.0	0.80	0.14	0.06	26	0.0	1.00
0.0	0.94	0.06	0.0	—		
0.0	0.94	0.06	0.0	—		
0.0	0.94	0.06	0.0	8	0.13	0.87
0.0	0.90	0.10	0.0	—		
0.0	0.50	0.0	0.50	—		
0.0	0.83	0.0	0.0	2	0.0	1.00
0.0	0.88	0.12	0.0	6	0.0	1.00
0.0	0.91	0.03	0.06	4	0.0	1.00
0.0	0.04	0.0	0.0	—		
0.01	0.06	0.0	0.0	39	0.95	0.05
0.0	0.0	0.0	0.0	4	1.00	0.0
0.0	0.0	0.0	0.0	22	0.73	0.27
0.0	0.04	0.0	0.0	—		
0.03	0.03	0.0	0.0	28	0.93	0.07

glaucus females also resulted in significantly lower eclosion success of female progeny (Hagen & Scriber 1989, in press).

Hybrid offspring from the reciprocal cross (*P. canadensis* female with *P. glaucus* male) did not show the Haldane Effect: from 35 families reared over the same interval, a total of 284 male and 300 female offspring eclosed (51.4% female: Hagen & Scriber in press). In 14 families more males eclosed, in seven families an equal number of males and females eclosed, and in 14 families fewer males eclosed ($P = 0.829$; Wilcoxon test). The same absence of Haldane Effect was observed in reciprocal crosses when *P. glaucus* males were paired with *P. eurymedon* or *P. rutulus* females (Scriber et al. 1990).

These observations raise a new question about the status of *P. alexiaries* in relation to *P. glaucus* (Hagen & Scriber 1991). For the present, it seems preferable to retain species designation for *alexiaries*, given the lack of information on interactions between *glaucus* and *alexiaries* in

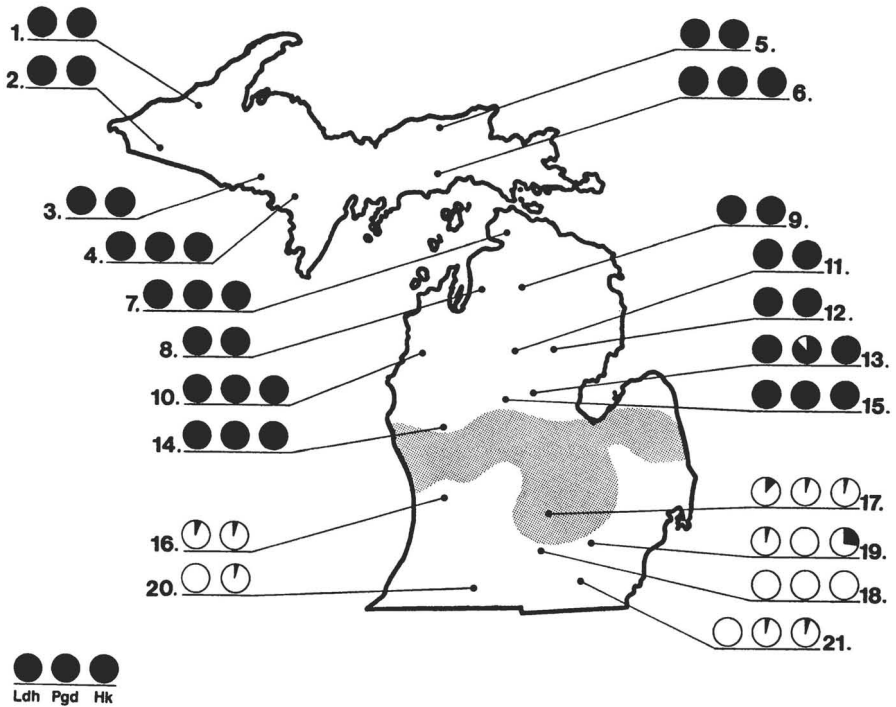


FIG. 2. Proportion of all *canadensis* alleles for *Ldh*, *Pgd*, and *Hk* loci in samples of butterflies from Michigan counties. The number next to each set of circles corresponds to a county listed in Table 2. *Hk* was not scored for samples from all counties; only 2 circles are shown in those cases. Filled circle = 100% *canadensis*; open circle = 0% *canadensis* (=100% *glaucus*); intermediate frequencies of *canadensis* alleles are indicated by the proportion of each circle filled. Sample sizes are given in Table 2, along with frequencies for the separate *canadensis* and *glaucus* alleles. The shaded region indicates the position of 1400–1500°C seasonal isotherm in Michigan, the predicted northern limit for a multivoltine life cycle.

northeastern Mexico, where they are reported to be sympatric (Beutelspacher-Baigts & Howe 1984).

The Hybrid Zone Between *glaucus* and *canadensis*

Evidence of natural hybridization between *glaucus* and *canadensis* has come from studies of morphology (Rothschild & Jordan 1906, Luebke et al. 1988), host plant use (Scriber 1986, 1988, Hagen 1990); inheritance of mimetic female color (Scriber et al. 1987, J. M. Scriber, R. H. Hagen & R. C. Lederhouse unpubl.) and allozyme electrophoresis (Hagen 1990). However, hybridization is confined to a relatively narrow zone between 41 and 44°N latitude, extending from New England through the Great Lakes region. The position of the hybrid zone appears to

track closely the seasonal degree-day isotherm corresponding to the predicted northern limit for a multivoltine lifecycle in *P. glaucus* (Scriber 1982, 1983, 1988, Hagen 1990).

The narrowness of the hybrid zone is demonstrated best by allozyme characters, since their frequencies can be estimated more easily than frequencies of physiological or developmental characters. Allele frequencies for *Hk*, *Ldh*, and *Pgd* from samples of males collected in Michigan from 1986–89 are given in Table 2, grouped by county. The county locations are shown in Fig. 2.

The sharp transition in frequencies for all three loci in Michigan coincides with the predicted northern limits to a multivoltine life cycle. Laboratory experiments have shown that successful completion of two generations by *P. glaucus* or *P. canadensis* requires a minimum of 1400 to 1500°C “degree-days” above a threshold of 10°C, on good larval hosts (Hagen & Lederhouse 1985). The shaded band in Fig. 2 indicates the position of this 1400–1500°C band based on a 20 year (1950–70) average of climatic data (J. M. Scriber unpublished data).

Conclusions

Because there is no geographic barrier to prevent dispersal of *P. glaucus* and *P. canadensis* across the hybrid zone, maintenance of the sharp boundary between them must be attributed to more subtle factors that prevent extensive interbreeding or the establishment of sympatric populations. One possible factor may be inability of *P. glaucus* to adapt to the univoltine lifecycle that is essential for survival north of the hybrid zone (Hagen & Lederhouse 1985, Rockey et al. 1987a). This could prevent northward extension of *P. glaucus*' range, but would not prevent *P. canadensis* from extending its range further south.

Another possibility is disruption of development in the offspring of interspecies matings: for example, that which is responsible for the Haldane Effect observed in laboratory-generated hybrids. However, this too may be only a partial barrier, since we have evidence of developmental disruption affecting female offspring in only one direction of hybridization. Additional possibilities include differential mate preference by males or females of the two species, or differing tolerances for extremes of high—or low—temperature encountered on either side of the hybrid zone.

It is probable that a combination of factors will turn out to be responsible for maintaining the species' identities. The range boundary between *P. glaucus* and *P. canadensis* coincides with a complex ecotone between boreal coniferous forest and temperate deciduous forest (Braun 1974, Curtis 1959). This ecotone coincides with a climatic transition between northern areas dominated by relatively cool, dry arctic air

masses and southern areas dominated by warmer, wetter tropical air masses (Bryson & Hare 1974). It also coincides generally with the southern margins of Pleistocene continental glaciation and thus represents a transition in topography and history of occupancy by animals and plants (Braun 1974).

The range limits of a variety of animal taxa coincide with this ecotone (Remington 1968, Scriber & Hainze 1987). Among the best-known examples from Lepidoptera are subspecies of the admiral butterfly, *Limenitis arthemis arthemis* Drury and *L. a. astyanax* Fabricius (Nymphalidae) (Platt & Brower 1968, Waldbauer et al. 1988). We strongly suspect that similar patterns of geographic differentiation occur frequently among eastern North American Lepidoptera. Tiger swallowtails may be atypical only in that they have received the intensive study necessary to detect it.

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