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THE INHERITANCE OF DIAGNOSTIC LARVAL TRAITS FOR
INTERSPECIFIC HYBRIDS OF *PAPILIO CANADENSIS* AND *P. GLAUCUS*
(LEPIDOPTERA: PAPILIONIDAE)

J. Mark Scriber¹

ABSTRACT

Traits distinguishing the closely related tiger swallowtail butterfly species, *Papilio canadensis* and *P. glaucus*, include fixed differences in diagnostic sex-linked and autosomal allozymes as well as sex-linked diapause regulation, and sex-linked differences in oviposition behavior. Larval detoxification abilities for plants of the Salicaceae and Magnoliaceae families are dramatically different and basically diagnostic as well. The distinguishing morphological traits of the adults and larvae have not been genetically characterized. Here we describe the segregation of diagnostic larval banding traits in offspring from the 2 species in their hybrid and reciprocal backcross combinations. Elucidation of genetic basis, and linkage relationships of a suite of distinguishing biochemical, physiological, morphological, and ecological traits with regard to their geographic concordance across the hybrid zone is fundamental to understanding the pattern and process of speciation.

Papilio canadensis Rothschild & Jordan has recently been recognized as a distinct species, not a subspecies of *P. glaucus* L. (Hagen et al. 1991). Among the morphological characteristics which are diagnostic for these two tiger swallowtail butterfly species are neonate (first instar) larval banding patterns. In very young larvae of *P. glaucus* there is a single central white band compared to three traverse white bands on the dorsal side of *P. canadensis* caterpillars (Hagen et al. 1991; Fig. 1). The purpose of this study is to determine how these diagnostic larval traits are inherited and affected by interspecific hybridization, such as occurs in the Great Lakes ecotone or hybrid zone (Scriber 1996).

Other diagnostic traits distinguish that these two species include biochemical, physiological, behavioral, and ecological differences. Host plant detoxification abilities are very different for *P. canadensis* and *P. glaucus*. Neonate larvae of *P. canadensis* are essentially not able to survive the instar when fed tulip tree, *Liriodendron tulipifera* (which is the favorite host of *P. glaucus*; Scriber 1982, 1988). The chemical basis of toxicity of another Magnoliaceae species to *P. canadensis* has recently been elucidated for sweetbay, *Magnolia virginiana* (Nitao et al. 1991, 1992). However, the chemical basis of the toxicity of tulip tree and other Magnoliaceae remains undetermined, although numerous biochemical candidates are known (see Scriber et al. 1987, Scriber, Lederhouse, Hagen 1991).

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Figure 1. First instar *P. glaucus* (single white band), *P. canadensis* (3 white bands) (see also enlargements in Hagen et al. 1991).

Conversely, neonate larvae of *P. glaucus* are unable to survive the first instar when fed quaking aspen, *Populus tremuloides*, which is the favorite host of *P. canadensis* (Scriber 1982, 1988). The chemical basis of this toxicity has been described (Lindroth et al. 1988a, b). The detoxification ability is genetically based and appears to be related to the capability of *P. canadensis* to maintain high esterase activities (Lindroth 1989, Scriber et al. 1989). Hybrids of *P. glaucus* and *P. canadensis* can survive on both tulip tree of the Magnoliaceae and quaking aspen of the Salicaceae (Scriber 1982, 1987). Furthermore, it appears that this ability to detoxify tulip tree and aspen is inherited autosomally since the male and female offspring of reciprocal pairings do not differ in survival (Scriber 1986). Additional studies of the inheritance of the aspen phenolic glycoside detoxification abilities in F_1 hybrids and backcrosses revealed a strong correlation of survival and growth rate with the level of esterase activity (Scriber et al. 1989, Scriber, Dowell, and Lederhouse, 1995). Such detoxification of phenolic glycosides by esterase activity was shown to be involved for the western tiger swallowtail, *P. rutulus*, as well (Scriber, Lindroth, Nitao 1991).

Oviposition preferences of *P. glaucus* strongly favor tulip tree in a 3-choice study including the toxic quaking aspen and the mutually suitable host black cherry, *Prunus serotina* (Scriber, Giebink, and Snider 1991). This same study showed that *P. canadensis* has an entirely different 3-choice preference profile, showing the highest quaking aspen oviposition preference of any *Papilio* tested (see also Scriber 1991, 1992). This oviposition preference for tulip tree of *P. glaucus*, and the aspen preference profile for *P. canadensis* has recently been shown to be inherited as a sex-linked trait on the X-chro-

mosome, where oviposition patterns of hybrid daughters resemble their paternal host species choice (Scriber 1994).

Other important traits have been mapped to the X-chromosome in the tiger swallowtail butterflies, *P. glaucus* and *P. canadensis* (Hagen and Scriber 1989), including: diapause regulation (Rocket et al. 1987), Y-linked mimetic dark-colored female trait suppressors (Scriber, Hagen, and Lederhouse 1996), and 5 electrophoretic allozymes, 2 of which are diagnostic for the species (Hagen and Scriber 1989, Scriber 1994). Neither the white banding patterns on young larvae nor the Salicaceae/Magnoliaceae detoxification abilities (which are basically diagnostic for the two species) are X-linked, however their mode of inheritance and their possible genetic linkage with each other was the reason for this study.

METHODS

Larvae of field-collected females were reared on black cherry, *Prunus serotina*, to pupation in 150 mm diameter \times 25 mm height plastic petri dishes under controlled-environment conditions of 16:8 photo/scotophase, with a corresponding thermoperiod of 23.5/19.5°C. Foodplant leaves were kept turgid by use of water-filled aquapics, and changed each 2–3 days, or as needed. Pupae were individually weighed and placed in 14 cm diameter screen cages until adult emergence.

Hand-pairings of lab-reared virgin female butterflies to field-collected or lab-reared males were made, and females were subsequently set up in clear plastic boxes (12 cm \times 20 cm \times 30 cm) heated by a 100 W incandescent light bulb placed approximately 0.5 m from the boxes. Eggs of the F_1 hybrids were removed daily and upon eclosion, the neonates were distributed to individual petri dishes using a camel hair brush for larval rearing on black cherry. The F_1 hybrids were reared to pupation and paired to produce the F_2 hybrids for this study.

There were three F_2 pairings (#272, 279 and 288) and 15 *P. canadensis* backcross pairings (see Table 5) that produced sufficient eggs and larvae for this study. The F_2 hybrid brood #272 was the result of a pairing of an F_1 hybrid female (derived from a Dane Co. WI dark mother *P. glaucus* \times a field-captured *P. canadensis* male from Marinette Co. WI) mated to an F_1 hybrid male which was a sibling. The F_2 brood #279 was the result of pairing two non-sibling hybrids, with the F_1 female (derived from a Dane Co. WI dark morph mother paired with a *P. canadensis* male from Marinette Co. WI) mated with an F_1 hybrid male (derived from a yellow morph *P. glaucus* mother from Schuylkill Co. PA mated with a field-captured male from Sawyer Co. WI). The third F_2 family (#288) was the result of a sibling pairing of a F_1 hybrid female with her brother, both from a Dane Co. WI dark morph *P. glaucus* paired with a Marinette Co. WI *P. canadensis* male.

Upon hatching, the neonate larvae were scored for the larval banding pattern in one of 3 categories: the "canadensis" phenotype with 3 distinct bands, the "glaucus" phenotype with a single central band, and the "hybrid" phenotype with the distinctive central band and two additional faint bands anteriorly and posteriorly. These three phenotypes were immediately upon eclosion of neonates apportioned as evenly and carefully as possible across the three foodplants (cherry, aspen, tulip tree) in individual larval rearing petri dishes. Food was changed daily and larval survival was monitored daily throughout the entire 1st instar (about 5–7 days).

RESULTS

The proportion of neonate larval banding phenotypes from the grand totals of the three F_2 broods were: 98 (26%) *P. canadensis* "type" with three distinct bands; 226 (60%) "hybrid" (1 distinct and 2 faint bands); and 54 (14%) *P. glaucus* "type" with a single central white band (Table 1). The segregation of 3 larval phenotypes was not significantly different than expected in a (1:2:1) segregation (Chi-square= $p < .01$) supporting a quantitative inheritance model. This is supported by the equal segregation of larval phenotypes in the 15 backcross broods (Table 2).

The overall neonate (1st instar) survival across all three families was 78% of 102 larvae on tulip tree, 87% of 136 larvae on black cherry and only 13% of 140 larvae on quaking aspen (Table 2). The black cherry leaves are generally known to be mutually suitable for both *P. canadensis* and *P. glaucus*. The 87% survival on black cherry in this study is basically the expected level of survival we have seen for several thousand other families of these two species over the 20 years that we have reared them (Scriber, Lederhouse, and Dowell 1995). We rarely see 100% survival even when rearing conditions, hostplant quality, and larval vigor all seem ideal.

It is clear that the low level of survival on quaking aspen is consistent for each of the three families and is consistently low for every one of the larval banding types (including the 3 banded, *P. canadensis* "type" which showed only 5% survival; Table 3). It is not clear why aspen detoxication abilities appear poorer than tulip tree detoxication in these 3 and another 9 F_2 hybrid broods (Table 3), especially since reciprocal primary hybrid crosses do not exhibit sex-linkage in the inheritance (Table 4).

DISCUSSION

The segregation of larval banding phenotypes into three categories ("*canadensis*", "hybrid", "*glaucus*" types), is consistent with a 1:2:1 ratio (Chi-

Table 1. The egg and neonate production of 3 different F_2 hybrid broods derived from (*P. glaucus* female \times *P. canadensis* male) F_1 hybrid parents.

F2 hybrid book #	Total eggs (n)	Infertile eggs (n)	Total larvae (n)	Larval Phenotype (banding-type)*		
				<i>canadensis</i> n (%)	"hybrid" n (%)	<i>glaucus</i> n (%)
272	410	99	217	84 (38.7)	112 (51.6)	21 (9.7)
279	53	1	52	9 (17.3)	33 (63.5)	10 (19.2)
288	150	4	109	5 (4.6)	81 (74.3)	23 (21.1)
Totals (%)	613	104	378	98 (25.9)	226 (59.8)	54 (14.3)

* On the total (n=378) 1:2:1 ratio; Chi-square = 25.0 ($p < 0.01$).

Table 2. Neonate survival of *canadensis* first instar larvae backcrosses in relation to the larval banding phenotypes (East Lansing, MI, 1996).

Backcross and larval banding type		Survival on TT tulip tree (TT)
(P.c. X P.g.) X P.c. (n=14 different broods)		Total survivors/initial
<i>Canadensis</i> -type banding		121/258 = 46.9%
F ₁ hybrid-type banding		111/256 = 43.4%
		Chi-square = 2.754 .10 < p < 0.5
(P.g. X P.c.) X P.c. (n = 1 brood)		
<i>canadensis</i> -type banding		26/68 = 38.2%
F ₁ hybrid-type banding		28/51 = 54.9%
		Chi-square = 1.370 .25 < p < .10

The first 14 broods (P.c. X P.g.) X P.c. were:

12207, 12208, 12252, 12253, 12254, 12255, 12256, 12257, 12259, 12260, 12262, 12263, 122351, 122352, and the single reciprocal cross (P.g. X P.c.) X c was 12251. Chi-square values for the expected 50% (equal) survival of banding types are not significant ($.10 < p < 0.5$ and $.25 < p < 0.10$ respectively for the 1st and 2nd backcrosses).

Table 3. Classification of three larval banding phenotypes segregating from three (Pg X Pc)² F₂ hybrid broods, with associated survival on three host species.

Larval phenotype	Female #	Neonate (1st instar) Survival on:		
		Tuliptree surviving/initial (%)	Black cherry surviving/initial (%)	Quaking aspen surviving/initial (%)
<i>P. canadensis</i> (Type I)	272	15/26 = 57.7	20/24 = 83.3	2/34 = 5.9
	279	1/1 = 100.0	2/2 = 100.0	0/6 = 0.0
	288	4/4 = 100.0	—	0/1 = 0.0
	Subtotals	20/31 = 64.5	22/26 = 84.6	2/41 = 4.9
F ₁ hybrid (Type II)	272	24/30 = 80.0	28/36 = 77.8	7/46 = 15.2
	279	11/15 = 73.3	14/14 = 100.0	0/4 = 0.0
	288	11/11 = 100.0	35/39 = 89.7	6/31 = 19.4
	Subtotals	46/56 = 82.1	77/89 = 86.5	13/81 = 16.0
<i>P. glaucus</i> (Type III)	272	5/6 = 83.3	8/9 = 88.9	1/6 = 16.7
	279	6/6 = 100.0	2/2 = 100.0	1/2 = 50.0
	288	3/3 = 100.0	9/10 = 90.0	1/10 = 10.0
	Subtotals	14/15 = 93.3	19/21 = 90.5	3/18 = 16.7
Grand Totals (by host)		80/102 = 78.4	118/136 = 86.8	18/140 = 12.9
Comparison of other F ₂ host survival studies ¹				
(Pg X Pc) ²	9 broods	82/185 = 65.6	216/299 = 72.2	21/59 = 13.2
(Pc X Pg) ²	5 broods	27/56 = 48.2	46/70 = 65.7	17/44 = 40.9

¹Scriber 1986 data.

Table 4. Neonate survival through the 1st instar of reciprocal hybrids² on 3 food plant species.

F ₁ hybrid female parent X male	Food plant species ¹					
	QA	(n)	TT		BC	
P.c. X P.g.	68%	(351)	78%	(249)	68%	(291)
P.g X P.c.	63%	(736)	74%	(977)	82%	(3201)

¹QA = quaking aspen (*Populus tremuloides*), TT = tulip tree (*Liriodendron tulipifera*), and BC = black cherry (*Prunus serotina*).

²Larvae from these reciprocal hybrid pairings are the result from 15 to 120 different isofemale broods, respectively (Scriber, Lederhouse, Dowell 1995).

square = 25.0, $p = 0.01$). Part of the variation observed here might be due to some incorrect category assignments of neonate larvae (especially between the single distinct banded "glaucus" type and the central banded "hybrid" type with 2 faint and 1 central bands). Other possibilities exist of course, including that of differential viability of the eggs or unhatched larvae possessing particular banding phenotypes. For example, 104 of the 613 eggs oviposited by these 3 females were not fertilized or were infertile, and 131 of the fertilized eggs produced inviable larvae which either died in the egg or in the process of eclosion. This infertility and inviability of the F² eggs may be due to genetic incompatibilities (not unexpected in hybrid F² crosses) or due to maternal effects (e.g., differential nutrient provisioning) or due to depleted or weakened sperm from the single mating these 3 female hybrids received. The male hybrid parents were not fed honey-water and ionic supplements before matings as we have done in other studies (Lederhouse et al. 1990). The female hybrid parent could not really be mated to another male for restoring fertility because of the primary purposes of these studies. Therefore it is possible that some of the observed infertility and inviability was simply due to depleted spermatophore contents (see Lederhouse and Scriber 1987).

It is also possible that the observed distribution of larval banding patterns is simply a reflection of a quantitative continuum from the "canadensis" type to the "glaucus" type. The "hybrid" type would simply reflect the broad central mean of a normal distribution. Although attempts were made to place the clear extremes into their appropriate categories (type 1 or type 3), the "hybrid" category may have contained subtle phenotypic variation.

It is known that F₁ hybrids (such as the parent generation of these 3 broods) survive well on all 3 hostplant species (tulip tree kills nearly 100% of pure *P. canadensis*, quaking aspen kills nearly 100% of *P. glaucus*, and black cherry is an excellent host for both species; Scriber 1988). For example, in previously published studies (Scriber, Lederhouse, and Dowell 1995), the reciprocal hybrids perform with virtually identical survival percentages on aspen (63% and 68%) and tulip tree (78% and 74%; see Table 4). In other studies (Scriber 1986), larval survival of hybrid F₁'s backcrossed to *glaucus* on quaking aspen (QA) was intermediate between that seen in pure *glaucus* and that for F₁ hybrids, while larval survival of backcrosses to *canadensis* on tulip tree (TT) was intermediate between pure *canadensis* and F₁ hybrids. Survival on black cherry (BC) was uniformly high, 70–90%, for all backcross types (Table 5). The neonate larval survival of backcrossed offspring on the 3

Table 5. Neonate larval 1st instar survival of reciprocal backcross pairings on 3 host species.

Backcross type (Female parent X male parent)	# of broods	Food plant species				
		QA	(n)	TT	BC	
F ¹ hybrid X P.c.	(20)	63%	(330)	18% (521)	83% (748)	
P.c. X F ¹ hybrid	(1)	100%	(16)	38% (42)	91% (65)	
F ¹ hybrid X P.g	(24)	58%	(281)	87% (300)	71% (1705)	
P.g. X F ¹ hybrid	(21)	26%	(341)	87% (358)	75% (815)	

Larvae in these backcross pairings (hybrids were all P.g. X P.c) are the result of 66 different female broods (Scriber 1986). The progressively poorer survival on QA with backcrosses to Pg (compared to the F₁ hybrids in Table 3) is likely due to dilution of carboxylesterase detoxication enzymes (Scriber et al. 1989).

host species exhibit the expected declines on aspen for the *glaucus* backcrosses, and on tulip tree for the *canadensis* backcrosses (Table 5).

The independent trait assortment of larval banding types and host plant (tulip tree) detoxication abilities seen in the F₂ hybrids (Table 1) was again observed with 15 different backcross broods (Table 2). In both types of reciprocal backcrosses to *P. canadensis* males, the 2 larval banding types produced in equal numbers and the survival percentages on tulip tree were virtually identical. This also supports the suggestion that tulip tree detoxication abilities may be of simpler inheritance (the result of fewer genetic loci) than is the case for aspen detoxication abilities (Scriber 1986; Scriber et al. 1989).

When F₁ hybrids are backcrossed to the parental types, two primary larval banding phenotypes appear (the "hybrid" and the corresponding "pure parental" type). In these F₂ offspring the segregation of the different larval banding phenotypes and the differential hostplant detoxification abilities on tulip tree and quaking aspen seem clearly independent of each other (Table 3). These 3 F₂ hybrid broods are, however, comprised of pairings of F₁ hybrid parents which are each *P. glaucus* female and *P. canadensis* male. It is possible that the reciprocal hybrids (i.e., *P. canadensis* female and *P. glaucus* male) would give different results, however these were not available.

In summary, the larval banding phenotypes distinctively characterizing *P. canadensis* and *P. glaucus* outside of the hybrid zone, appear to be inherited independently of the detoxification abilities of quaking aspen and tulip tree, which are thought to be distinctive traits between the species, autosomally controlled by multiple loci. This lack of congruence in larval phenotypes, hostplant detoxification abilities, and distinctive (diagnostic) adult wing traits, makes the precise geographic delineation of the natural zone of hybrid introgression difficult to define (Luebke et al. 1988; Scriber 1996) without other multiple trait analyses. The occurrence of numerous X-linked trait differences between *P. canadensis* and *P. glaucus* (including diapause regulation, wing color polymorphism regulation for females, oviposition preferences) and 5 allozymes which are X-linked (Ldh, Pgd, Acp, Tpi, and P3Gdh), provides a unique and compelling opportunity to determine differences in the patterns of enzyme and other trait concordance patterns at various locations in multiple transects across this long hybrid zone of different widths. This type of analysis has not been done in any hybrid zone (Harrison 1993) and could be valuable for elucidating key evolutionary questions about speciation patterns and processes that have thus far eluded researchers (Fu-

tuyma and Shapiro 1995; Bossart and Scriber 1995; Hagen and Scriber 1995).

We are already aware of a broader blending of *P. canadensis* traits with *P. glaucus* traits across the eastern portions (NY/PA) of this hybrid zone. With regard to allozymes for example, the sharp concordance in geographic delineation of diagnostic alleles observed for LDH, PGD, and HK across the hybrid zone in Wisconsin and Michigan (Scriber 1996) is not seen in the east, where the allozyme clines are not concordant (Hagen 1990). Furthermore, central New York populations of tiger swallowtail butterflies are not clearly univoltine nor bivoltine (Scriber 1975; Hagen and Lederhouse 1985). The hind wing banding (morphometric) pattern is intermediate between *P. glaucus* and *P. canadensis* (Scriber 1982; Luebke et al. 1988). We have also observed partial suppression of dark morph female color traits in hybrids with New York *Papilio* males (Scriber et al. 1996). Results of this study imply that the NY sire was heterozygous for the color suppressor/enable alleles. The X-linked color suppressor gene and the PGD (-140, *canadensis* type) alleles apparently segregated together in the yellow hybrid daughters, with the dark/intermediate hybrid daughters having the PGD (100, *glaucus* type) alleles. Scriber et al. (1996) point out that none of the other female color segregating broods thus far examined from the Great Lakes region had segregating X-linked marker alleles as observed in this NY brood (#3770). These results suggest introgression occurs at very different rates in these areas and that independent hybrid zone transects evaluating a suite of traits (including those that are autosomal such as these larval banding patterns) is the only way to go if we really want to understand the "geographic mosaic" pattern and process of speciation (Thompson 1994; Menken 1996).

Oviposition preferences for tulip trees or quaking aspen in these 2 *Papilio* species are known to be X-linked (Scriber, Giebink, and Snider 1991; Scriber 1994). However, segregation of this and other X-linked traits (including allozymes and obligate diapause) has been observed in Michigan populations. It is again interesting that central New York has too few seasonal thermal unit accumulations to support 2 generations (Scriber and Lederhouse 1992), and that multivariate wing morphometrics (Luebke et al. 1988; Scriber 1982, 1990) and electrophoresis allozymes (Hagen 1990) lead us to believe that these populations are composed primarily of *P. canadensis* types. However, these populations favor oviposition in tulip tree (Scriber 1975) and exhibit excellent abilities to detoxify and grow on this *P. glaucus* host (Scriber and Feeny 1979; Fig 2). These findings suggest more genetic introgression for NY populations. Also noteworthy in this photograph is that the New York larva feeding on tulip tree has the larval banding pattern diagnostic for *Papilio canadensis*. While not examined for electrophoretic allozyme profiles, this larva also apparently reflects the extensive genetic introgression of the eastern hybrid zone. It also represents a potential natural field confirmation of the independent segregation of physiological detoxication abilities and larval banding as well as in the laboratory hybridization studies presented here.

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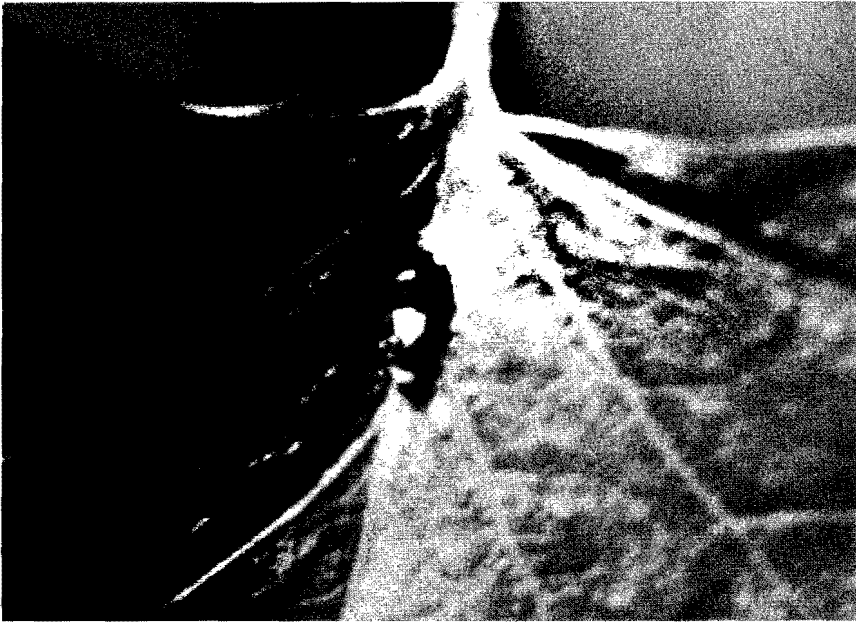


Figure 2. An early instar from a natural population of tulip tree-preferring tiger swallowtail from Ithaca, New York (Tompkins Co.). The larval banding of this individual, the wing patterns of adults in the area (Scriber 1982), the univoltine (obligate diapause) life cycle and electrophoresis profiles of male adults (Hagen 1990), suggest that the population is largely *P. canadensis*, in spite of the oviposition and larval survival on tulip tree (Scriber 1975) and the incomplete suppression of the dark (mimetic) trait in daughters of males from this area (Scriber et al. 1996). More multiple trait clines across this central New York hybrid zone are warranted in future studies.

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