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RESPONSES OF NORTH AMERICAN *PAPILIO TROILUS* AND *P. GLAUCUS* TO POTENTIAL HOSTS FROM AUSTRALIA

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ABSTRACT. We tested the abilities of neonate larvae of the Lauraceae-specialist, *P. troilus*, and the generalist Eastern tiger swallowtail, *Papilio glaucus* (both from Levy County, Florida) to eat, survive, and grow on leaves of 22 plant species from 7 families of ancient angiosperms in Australia, Rutaceae, Magnoliaceae, Lauraceae, Monimiaceae, Sapotaceae, Winteraceae, and Annonaceae. Clearly, some common *Papilio* feeding stimulants exist in Australian plant species of certain, but not all, Lauraceae. Three Lauraceae species (two introduced *Cinnamonum* species and the native *Litsea leefeana*) were as suitable for the generalist *P. glaucus* as was observed for *P. troilus*. While no ability to feed and grow was detected for the Lauraceae-specialized *P. troilus* on any of the other six ancient Angiosperm families, the generalist *P. glaucus* did feed successfully on Magnoliaceae and Winteraceae as well as Lauraceae. In addition, some larvae of one *P. glaucus* family attempted feeding on *Citrus* (Rutaceae) and a small amount of feeding was observed on southern sassafras (*Antherosperma moschatum*; Monimiaceae), but all *P. glaucus* (from 4 families) died on Annonaceae and Sapotaceae. Surprisingly, the North American Lauraceae-specialist (*P. troilus*) died on all Lauraceae species by day #12, but some generalist *P. glaucus* larvae survived. Most of the generalist (*P. glaucus*) offspring survived and grew very well on all 3 species of Magnoliaceae assayed (*Magnolia virginiana*, *Michelia champaca*, & *Michelia doltsopa*) and on *Tasmannia insipida* (Winteraceae). The ability of these larvae to feed and grow on *T. insipida* but not *T. lanceolata* suggests significant phytochemical differences may exist within the Winteraceae. Two Monimiaceae "sassafras" plant species were unsuitable to both North American *Papilio* species despite their very close phylogenetic relationship with the Lauraceae.

Additional key words: Annonaceae, detoxification, Lauraceae, Magnoliaceae, Monimiaceae, neonate survival, Papilionidae, Rutaceae, Winteraceae, P. glaucus, P. troilus

Rutaceae-feeding is the primary pattern in 75-80 % of the genus Papilio (Scriber 1984a). In section IV of the Papilionidae (Munroe 1961), Papilio (Heraclides) cresphontes Cramer is constrained to Rutaceae, unable to survive on plants of the Magnoliaceae, Lauraceae, Rosaceae, or Salicaceae (Scriber et al. 1991a,&b). However, in Section III of the Papilionidae, ancestors of the polyphagous North American P.(Pterourus) glaucus L. group and their *P. troilus* L. sister group are believed to have been Rutaceae feeders (Hancock 1983; Scriber et al. 1991a), with subsequent specialization on the Lauraceae and Magnoliaceae, as Rutaceae became scarce after the Cretaceous (Hancock 1983; Scriber 1995). With the Troidini tribe believed to have origins in remnant Gondwana 65-90 mya (Braby et al. 2005), the phylogenetic distances and geological timing (late Jurassic and early Cretaceous; Soltis et al. 2005) of the evolutionary divergence of these plant groups has been recently suggested to be 30-50 million years ago (Gaunt and Miles 2002; Zakharov et al. 2004). Such diversification of the roots of Papilionidae lineages in the Leptocircini (=Graphiini) and Papilionini tribes also corresponds to plate tectonics and subsequent diversification of early Angiosperm families (e.g.

Annonaceae).

There are shared groups of key phytochemicals among the Rutaceae, Lauraceae, Magnoliaceae, Annonaceae, Apiaceae, and Aristolochiaceae (Berenbaum 1995; Brown et al. 1995; Nishida 1995) and these can affect oviposition (Dethier 1941,1954; Feeny 1995) as well as larval survival and growth (Munroe 1961; Nitao et al. 1992; Johnson et al. 1996). Our goal here was to examine neonate larval survival on reported host plants of other Australian Papilionidae and representative species from these chemicallyrelated plant families, including the Australian Winteraceae and Monimiaceae which are ancient angiosperms very closely related to the Lauraceae, Magnoliaceae, and Annonaceae (Bremer et al. 2003) with presumed similarity in phytochemicals. The ancient Doryphora sassafras Endl.(Monimiaceae) and Tasmannia (=Drimys) insipida R.Br. ex DC. (Winteraceae) are reported in Australia as host plants for Graphium sarpedon (L.) and G. macleayanum (Leach) butterflies along with the Lauraceae and Rutaceae (Braby 2000).

Papilio troilus L. (spicebush swallowtail) is a Lauraceae-feeding specialist found across the eastern

half of the USA which naturally feeds on sassafras, Sassafras albidum (Nutt.) Ness, and spicebush, Lindera benzoin (L.) Blume, across most of its range, and red bay, Persea borbonia (L.) Spreng., in Florida and the southeast coastal areas (Scriber 2005). Preliminary bioassays with *P. troilus* in North America confirm that this species is a host plant family specialist and will not initiate feeding on plants other than members of the Lauraceae, including all other families used by Papilio glaucus L. (eastern tiger swallowtail; Scriber et al. 1991b), which also occurs across the eastern USA. P. glaucus is the most polyphagous of all 563 species of swallowtail butterflies in the world (Scriber 1984a, 1995). It feeds occasionally on spicebush and sassafras (Lauraceae; Scriber et al. 1975), but also includes several dozen other host plant species from 9 different families (including the Magnoliaceae, Rutaceae, Oleaceae, Rosaceae, Tiliaceae, Betulaceae, Platanaceae, and others; Scriber 1986, 1988).

Plant species for neonate larval survival and growth bioassays were selected from lists of recorded host plant species for *Papilio aegeus* Donovan and *Graphium* species in Australia (Braby 2000; Edwards *et al.* 2001, Scriber *et al.* 2006, 2007).

Lauraceae feeding and oviposition in *P. troilus* are apparently determined by phytochemical feeding/oviposition stimulants (Lederhouse et al. 1992, Carter & Feeny 1999, Carter et al. 1999, Frankfater & Scriber 1999, 2003). Sassafras and spicebush are the preferred hosts throughout most of the butterfly's range. In Florida, where these plants are scarce, red bay (Persea spp.), is used by P. troilus populations. Preliminary studies indicated that extracts of Persea painted on leaves of *Lindera* depress neonate growth rates of northern populations of *P. troilus* (Nitao *et al.*) 1991). It is clear that among various geographical populations of this Lauraceae specialized butterfly species, there is variation in the suitability of different plant species for oviposition, larval acceptance and larval growth (Nitao et al. 1991; Scriber et al. 1991b; Scriber & Margraf 2005).

We wanted to evaluate the abilities of the ancestral Papilionidae, North American section III, Munroe (1961) species *P. troilus* and *P. glaucus* larvae to consume, process and grow on these ancient Australian angiosperm species including unique genera of the Lauraceae that differentiated independently of the North American Lauraceae. In Australia, there exist at least two species of plants called sassafras, *Doryphora sassafras* Endl. and *Antherosperma moschatum* Poir. (southern sassafras). These plants are both in the Monimiaceae, which is an ancient angiosperm family very closely related to the Lauraceae (Bremer *et al.* 2003). Tasmannia insipida and T. lanceolata (Poir.) A.C. Smith are ancient angiosperms in the Winteraceae, which is also closely related to the Lauraceae and Monimiaceae. Both of these ancient plant families have aromatic species used by Australian swallowtail butterflies, such as Graphium macleayanum. Australia seemed to be the best place to evaluate suitability of ancient Angiosperm species (Bremer et al. 2003; see also Grimaldi & Engel 2005) since this may have been the "cradle" of flowering plant evolution, including basal families such as the Winteraceae and Monimiaceae (both used by Australian swallowtail butterfly species) as well as the more widespread Lauraceae, Magnoliaceae, Rutaceae, Annonaceae, and Aristolochiaceae (Bremer et al. 2003). The phylogenetically basal angiosperm families have their origins, when geological plate drifting had not fully separated the continents (Grimaldi & Engel 2005), and the Papilionidae are believed to have roots concurrent with these early flowering plants (Gaunt & Miles 2002; Braby et al. 2005; cf. Miller 1987).

The modern phylogeny and systematics of the ancient Angiosperm families, examined here for their relative suitability as larval host plants, have recently been revised based on many independent molecular analyses (Bremer et al. 2003). The phylogenetically basal angiosperms, including the 4 orders, Laurales, Magnoliales, Canellales, and Piperales are all supported as monophyletic, and molecular analyses put them together in a group called the magnoliids, despite the lack of support using morphological traits alone (Bremer et al. 2003). Within this single basal group (magnoliids), the Laurales includes the Hernandiaceae, Lauraceae and the closely-related Monimiaceae. The Magnoliales includes the Magnoliaceae and Annonaceae. The Piperales includes the Aristolochiaceae and Piperaceae. The Canellales includes the primitive Winteraceae with Tasmannia (=Drimys) species reported as hosts for other species of swallowtails (Scriber 1984a; Braby 2000). All of these families have some swallowtail butterfly species (Papilionidae) reported as feeding on them, but 75% of all swallowtail butterfly species feed on the Rutaceae (Scriber 1984a; Berenbaum 1995). The Rutaceae (including Flindersia, Geijera, Citrus, & Zieria) are believed to have survived the extensive worldwide Cretaceous-Tertiary extinctions in the eastern part of Gondwana (the Australian landmass) of the southern hemisphere, along with other ancient angiosperms, such as the Winteraceae, some Lauraceae, and Monimiaceae (Raven & Axelrod 1974).

This study of the North American *P. troilus* and *P. glaucus* was conducted to validate host use abilities (or

inabilities) of the neonate larvae in their first bites (Zalucki *et al.* 2002) on species of 7 families of ancient angiosperms. In order to determine the relative suitability of each host for larval consumption, growth, and survival, we conducted controlled environment bioassays using neonates from eggs of different wild females. Results provided clues to the historical (phylogenetic) or potential (future) abilities of geographically-widespread specialist and generalist species of North American *Papilio* to use different Australian plant families.

MATERIALS AND METHODS

Adult capture and female oviposition. Females of P. troilus and P. glaucus were captured in Levy County, Florida in March and April of 2006. Using methods as described by Scriber (1993), individual females were placed in clear plastic boxes containing red bay leaves for P. troilus and several species of potential host plants for P. glaucus (including sweet bay, Magnolia virginiana L. (Magnoliaceae), black cherry, Prunus serotina Ehrh. (Rosaceae) and white ash, Fraxinus americana L. (Oleaceae). Eggs were collected daily, counted, and placed in a controlled environment chamber for 1-5 days at 4-6 ° C, until express mailed to our Australian quarantine lab in the School of Life Sciences Goddard Building (Australian DEH and AQIS permits had been obtained previously; also with clearance from Biosecurity Australia). Constraints of the AQIS permit and Biosecurity Australia prevented us from sending adults to Australia for oviposition preference assays on native plants there.

Larval bioassays and rearing. Eggs from each Papilio female were kept in sterile clear plastic Petri dishes (20 mm deep; 100 or 150 mm diameter) in the same controlled environment chamber until they eclosed as neonate larvae. Newly emerged neonates were distributed in a split-brood design across an array of potential host plant species, with 2-3 larvae per dish (each dish containing a new leaf and a mature or fullyexpanded leaf of one plant species supported with their petioles immersed in a water-soaked florist "oasis" foam wrapped tightly with aluminum foil to retain moisture) for each 96-hour period. Neonate larvae were introduced to each species with a fine camel hair brush by gently placing them on the aluminum foil at the base of both petioles (the new leaf and the mature leaf) in order for the larvae to choose which leaf they crawled onto. Daily survival and growth were monitored and recorded. The total number of fecal pellets, the estimated leaf area consumed (mm²), the instar stage (or molt), and the larval weights (for all survivors) were recorded at 96 hours. Fresh, new and mature leaves were introduced at 96 hours for continued larval feeding and growth for another 96 hours, when they were weighed again. These assay methods were used successfully in our previous studies of host use by the Australian *P. aegeus* (see Fig. 1; Scriber *et al.* 2007).

Numbers were assigned for each instar (e.g. 1, 2, 3, 4) and molts were assigned the midpoint (e.g. 1.5 = molting from first to second instar). Survivors of *P. glaucus* and *P. troilus* at 12 days were destroyed because of constraints imposed by the AQIS import permit (#200520165).

Plant species used for bioassays. Plant species for neonate larval survival and growth bioassays were selected from lists of recorded host plant species for P. aegeus and Graphium species in Australia (Braby 2000; Edwards et al. 2001; Scriber et al. 2006, 2007). These native Australian plants were obtained as seedlings from Fairhill Native Plants (Yandina, QL), Barung Landcare Nursery (Maleny, QL). Anthony Hiller at Mount Glorious Biological Centre (Mt. Glorious, QL), Turner's Garden Center at Rochdale, near South Brisbane, and Greening Australia Nursery (near The Gap, QL), and from the University of Tasmania at Hobart. Seedlings were brought to the University of Queensland Glasshouse during mid-October, where they were transplanted into 4-liter pots with standard sterilized potting soil (half sand). Each tree seedling was then fertilized with Flowfeed EX7 fertilizer (Grow Force Australia Ltd; N-P-K, 20.8%, 3.3% and 17.4% respectively). New leaves (not fully-expanded) had developed on all plants by the time the larval feeding bioassays started in mid-March 2006.

Some plant species' leaves (3 species of Magnoliaceae, 2 species of Rutaceae) used in these studies were field-collected at the Brisbane Botanical Gardens (with the assistance of Director Phil Cameron). Camphor tree leaves were collected from the UQ Campus nearby the lab. The full list of plants tested is given below.

Rutaceae (native unless noted):

Citrus sinensis Osbeck (sweet orange; "Joppa" introduced.);

Geijera salicifolia Schott (brush wilga);

Flindersia australis R.Br (Australian Teak),

Magnoliaceae (all introduced):

Magnolia virginiana L. (sweet bay; North America);

Michelia champaca L. (yellow magnolia; Asia); Michelia doltsopa Buch.–Hum. ex D.C. (silver cloud) an Asian species endemic to the Himalayan region of China and Tibet,

Lauraceae (native unless noted):

Beilschmedia obtusifolia (F. Muell. ex Meis.)

(Blush walnut);

- *Cinnamomum camphora* (L.) J. Presl (camphor laurel) an introduced tree, abundant in Queensland and NSW;
- *Cinnamomum oliveri* (F.M. Bailey) (Oliver's sassafras);
- Cinnamomum virens R.T. Baker;
- *Cryptocarya glaucescens* R.Br. (jackwood); *Cryptocarya microneura* Meisn. (Murrogun); *Endiandra discolor* Benth. (rose walnut); *Litsea leefeana* (F. Muell.) (bollywood); *Neolitsea dealbata* (R.Br.) Merr. (bolly gum),

Monimiaceae (native):

Doryphora sassafras Endl. (sassafras); Antherosperma moschatum Poir. (southern sassafras) found in Tasmania and Victoria (the only host for Tasmanian swallowtail butterfly subspecies, G. m. moggana Couchman),

Annonaceae (introduced):

Annona muricata L. (soursop); Annona reticulata L. (custard apple),

Winteraceae (native):

Tasmannia insipida R.Br. ex DC. (purple cherry);

Tasmannia lanceolata (=Drimys aromatica) (Poir.) A. C. Smith (mountain pepper, winterberry) found in Tasmania and Victoria and NSW,

Sapotaceae (native):

Pouteria (= *Planchonella*) *australis* (R.Br) Baehni (black apple).

RESULTS

Neonate larvae of the Lauraceae specialist, *P. troilus* died on all species in all families except Lauraceae. While some of the species within this favored family



FIG. 1. Feeding assays with family-specialized Australian Lepidoptera that also survived on Magnoliaceae; **1a**) Macleay's swallowtail (Tasmanian subspecies, *G. m. moggana*) is a specialist on the Monimiaceae, but feeds and pupates on Magnoliaceae and Lauraceae (Scriber et al. 2006), **1b**) *Papilio aegeus* is a Rutaceae specialist, but feeds on 3 species of Magnoliaceae and camphor tree in the Lauraceae (Scriber et al. 2007), **1c**) *Graphium eurypylus* is an Annonaceae specialist that oviposits, feeds, and pupates on Magnoliaceae near Brisbane, Australia (Larsen et al. 2008).

	iguz Im	SINCLE	4 Days	NAL ALABORT		8 Days	unio "Navi	12 Days			
Larval Family	(n)	% surv.	mean wt.	instar	% surv.	mean wt.	instar	% surv.	mean wt.	instar	
RUTACEAE				The loss		and the second	. Indiana	a survey and			
Citrus sinensis "j	oppa"										
G1	0	na									
G2	3	33.3	3.7	1	0	died					
G3	0	na									
G4	0	na									
T1	0	na									
T2	3	0	died								
Flindersia austra	lis										
G1	0	na									
G2	3	0	died								
G3	0	na									
G4	0	na									
T1	3	0	died								
T2	0	na									
Geijera salicifolia	ı°										
G1	2	0	died								
G2	3	0	died								
G3	2	0	died								
G4	2	0	died								
T1	2	0	died								
T2	2	0	died								
MAGNOLIACE	AE										
Magnolia virgini	ana										
G1	2	100	9.9	1.5	100	39.6	2.5	100	147.1	4	
G2	3	66.7	8.4	1.5	66.7	31.8	2.8	66.7	125.1	3.5	
G3	2	50	8.4	1.5	50	27	2.5	50	106.7	3	
G4	2	50	7.6	2	50	44.7	3	50	214.3	4	
T1	2	0	died								
Т2	3	0	died								
Michelia champa	ica										
G1	2	100	10.3	1.5	50	72.8	3	50	427.1	4	
G2	3	66.7	17.7	2	33.3	111.9	3	33.3	450	4	
G3	2	100	10.7	1.8	100	41.4	2.8	100	205.6	4	
G4	2	0	died								
T1	2	0	died								
T2	3	0	died								
Michelia doltsop	a										
G1	2	100	4.9	1	100	9.5	1.8	100	17.1	2	
G2	3	66.7	4.6	1	100	7.4	1.3	100	6.7	1.3	

TABLE 1. Mean survival and growth indices of neonate larvae of P. glaucus families (G1-G4) and P. troilus (T1 & T2) reared on various ancient Angiosperm plant species at 4 days, 8 days, and 12 days.

TABLE 1. (continued)

			4 Days			8 Days		12 Days			
Larval Family	(n)	% surv.	mean wt.	instar	% surv.	mean wt.	instar	% surv.	mean wt.	instar	
Michelia doltsop	a (cont.)										
G3	2	100	7	1.8	100	27.2	2.8	100	136.9	3.3	
G4	2	0	died								
T1	2	0	died								
Τ2	3	0	died								
LAURACEAE											
Beilschmiedia ob	otusifolia°										
G1	2	0	died								
G2	3	0	died								
G3	2	0	died								
G4	2	0	died								
T1	2	0	died								
Т2	2	0	died								
Cinnamomum ca	mphora										
G1	2	0	died								
C2	3	100	87	1	100	15.1	2	100	41.3	2.8	
G2	0	100 na	0.1	1	100	10.1	-	100	41.0	2.0	
G3 C4	0	0	died								
T1	2	0	died								
T2	3	66.7	3.8	1.3	66.7	4	1.5	0	died		
Cinnamomum ol	iveri										
G1	0	na									
G2	3	66.7	4	1	0	died					
G3	0	na									
G4	0	na									
T1	0	na									
Τ2	3	66.7	3.7	1.3	66.7	4	1.5	0	died		
Cinnamomum vi	rens										
G1	0	na									
G2	3	33.3	2.7	1	0	died					
G3	0	na									
G4	0	na									
Т1	0	na									
Т2	0	na									
Cryptocarya glat	ucescens°										
G1	2	0	died								
G2	3	0	died								
G3	2	0	died								
G4	2	0	died								
Т1	2	0	died								
Т2	2	0	died								
Cryptocarya mic	croneura										
G1	0	na									
G2	3	0	died								
G3	0	na	alea								
G4	3	0	died								
Г1	0	na	area								
Т2	0	na									

TABLE 1. (continued)

			4 Days			8 Days	4		12 Days		
Larval Family	(n)	% surv.	mean wt.	instar	% surv.	mean wt.	instar	% surv.	mean wt.	instar	
Endiandra discol	or°										
G1	2	0	died								
G2	3	0	died								
G3	2	0	died								
G4	2	0	died								
T1	2	0	died								
T2	2	0	died								
Litsea leefeana											
G1	2	0	died								
G2	3	33.3	2.3	1	33.3	2.9	1	0	died		
G3	2	0	died								
G4	2	0	died								
T1	2	50	3.8	1	50	2.4	2	0	died		
T2	2	0	died								
Neolitsea dealbat	a°										
C1	2	0	died								
C ²	3	0	died								
G3	2	0	died								
G4	2	0	died								
TI	2	0	died								
T2	2	0	died								
MONIMIACEA	F										
Antheromerman	L Dochatum										
C1	o o	0	diad								
C?	2	0	died								
C2	0	50	11	1	0	diad					
G3	2	50	1.1 diad	1	0	uleu					
C4 T1	2	0	died								
T1 T2	2	0	died								
12	5	0	uleu								
Doryphora sassaf	fras°										
G1	2	0	died								
G2	3	0	died								
G3	2	0	died								
G4	2	0	died								
T1	2	0	died								
T2	3	0	died								
WINTERACEA	E										
Tasmannia insipi	da										
G1	2	100	4.7	1	100	10	1.8	100	17.1	2	
G2	3	66.7	4.6	1	66.7	7.4	1.3	66.7	6.7	1.5	
G3	2	100	2.3	1	50	7.4	1	50	6.5	2	
G4	3	50	3.7	1	50	7.9	1.5	50	18.1	2	
T1	2	0	died								
TO	0	0	diad								

TABLE 1. (concluded)

			4 Days			8 Days			12 Days	
Larval Family	(n)	% surv.	mean wt.	instar	% surv.	mean wt.	instar	% surv.	mean wt.	instar
WINTERACE	AE (cont.)									
Tasmannia land	ceolata°									
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	2	0	died							
ANNONACEA	ΛE									
Annona murica	uta°									
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	3	0	died							
Annona reticul	ata°									
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	3	0	died							
SAPOTACEAR	E									
Pouteria austra	lis°									
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	2	0	died							

* There was no nibbling or feces in any of the dishes of *Geijera salicifolia* (Rutaceae); *Beilschmiedia obtusifolia*, *Cryptocarya glaucescens*, Endiandra discolor, or Neolitsea dealbata (Lauraceae); Doryphora sassafras (Monimiaceae); Annona muricata or A. reticulata (Annonaceae); Tasmnannia lanceolata (Winteraceae); or Pouteria australis (Sapotaceae).

were unsuitable for survival and growth (e.g. *Beilschmiedia abtusifolia*, *Cryptocarya glaucescens*, *Endiandra discolor* and *Neolitsea dealbata*), *Cinnamomum camphora*, *C. virens* and *Litsea leefeana* supported feeding (producing 327, 398, and 192 fecal pellets, respectively) and some growth of larvae (Table 1). However, even with some feeding stimulants in these 3 hosts, all *P. troilus* larvae died before the third instar and day 12 (Table 1).

One family of the generalist *P. glaucus* also fed (producing 335, 220, and 187 fecal pellets, respectively) and grew on the same 3 Lauraceae species as *P. troilus*. Only *C. camphora* supported growth to the third instar and up to day 12 (when killed in accordance with the

AQIS permit). In addition, neonates from all 4 families of *P. glaucus* could feed and survive on *Tasmannia insipida* (Winteraceae). However, the congeneric *T. lanceolata* was unsuitable for any of the *P. glaucus* larvae and there were no feces. Some attempts to feed on the Monimiaceae and Rutaceae were observed for certain *P. glaucus* families, but this was not successful since all larvae died before day 8. Excellent survival and growth were observed on the Magnoliaceae (Table 1). *Magnolia virginiana* (sweet bay) is a favorite of *P. glaucus* in Florida (Scriber 1986, Scriber *et al.* 2001) and larvae grew well on the leaves of this large tree species from the Brisbane Botanical Gardens. All 4 families of *P. glaucus* also grew very well on leaves of *Michelia* *champaca* and *M. doltsopa*, despite their geographically distant Asian origins. Phytochemical common denominators among *Magnolia* species might largely explain this high suitability of such allopatric plant species for *P. glaucus*.

The phylogenetic closeness of Winteraceae and Magnoliaceae may reflect some phytochemical similarities, as is suggested by the high survival and successful growth of *P. glaucus* on *Tasmannia insipida* as well as the *Michelia* and *Magnolia* species. However, no survival (or feeding) on *T. lanceolata* (= *Drimys aromatica*) was observed, suggesting different suitabilities (or toxicities) within this plant genus.

DISCUSSION

The evolutionary constraints that have restricted *P*. troilus to only Lauraceae, and the ecological opportunities that were taken by P. glaucus on 9 families of plants in North America (see Fig.2; Scriber 1988; Scriber et al. 1991b) were confirmed with our neonate larval assays here using 22 species of Australian plants. With a very narrow host range, the Spicebush Swallowtail, P. troilus, grows with 2-4 times the efficiency and rate of the generalist P. glaucus on the same plant, (Scriber & Feeny 1979; Scriber 1984b). In fact there have been no other species of insects ever reported with significantly higher growth rates and efficiencies in various instars than P. troilus on spicebush (Scriber 2005). Potential loss of abilities to accept and detoxify closely related families (or Rutaceae; Scriber et al. 2008a) is suggested by the unwillingness and/or inability of neonate P. troilus to feed and grow on any plants in the 6 plant families other than Lauraceae in these bioassays. Despite the close phylogenetic relationships of the ancient Australian Monimiaceae and Winteraceae with the Lauraceae, their leaves are unsuitable (repellent or toxic) for the Lauraceae specialist, P. troilus. It was evident that some of the Lauraceae assaved here (Beilschmiedia, Cryptocarya, Endiandra, and Neolitsea species) were unsuitable for neonate growth and survival, although they did feed on one Litsea and two Cinnamomum species (Table 1). Differential utilization abilities of plant species within the Lauraceae has been documented for P. troilus (Lederhouse et al. 1992) and among its geographical populations in the USA (Nitao et southeast The introduced al. 1991). Asian Cinnamomum camphora has elicited oviposition and larval feeding by P. troilus on an ornamental planting of this tree in the USA (Morris 1989). It is known that the furanocoumarin-metabolizing cvtochrome P450 enzymes found in many Rutaceae feeders (including P. glaucus and P. canadensis; Li et al. 2001) are lacking in P. troilus (Cohen et al. 1992). Behavioral cues (stimulants) to P. troilus adults and larvae also seem to be missing in plants other than Lauraceae (Carter & Feeny 1999; Carter et al. 1999; Frankfater and Scriber 1999; Scriber et al. 2001).

While *P. glaucus* can and does use spicebush and sassafras naturally, they are not favored hosts. Survival of 2042 individuals from 44 different populations from 17 different States (and Canada and Mexico) was only 14% overall, compared to 68% for *P. troilus* (6 States, 28 families, 621 larvae: Scriber 2005). While the generalist *P. glaucus* does naturally feed on sassafras and spicebush (Scriber *et al.*1975), red bay (*Persea borbonia*, also of the Lauraceae) is toxic to all neonates tested, killing 228 larvae of the Florida population and 432 larvae of the northern *P. glaucus* populations (Scriber *et al.* 1995, Scriber 2005, Table 2). Although unknown regarding specific toxins for *Papilio*, insect toxins have been identified from *Persea* (Ma *et al.* 1988; Gonzalez-Coloma *et al.* 1990).

		Laur	aceae	Monin	niaceae	Winte	eraceae		
	RB	SP	SA	CT(US)	CT(A)	Dsas	Amos	Tins	Tlan
P. troilus	55%	86%	77%	50%	75%	0%	0%	.0%	0%
	(143)	(156)	(404)	(82)	(4)	(5)	(5)	(4)	(4)
P. glaucus	0%	24%	60%	62%	33%	0%	11%	67%	0%
	(432)	(579)	(306)	(134)	(9)	(9)	(9)	(9)	(9)

TABLE 2. Neonate larval survival of *P. troilus* and *P. glaucus* on plants of North American Lauraceae, and Australian Monimiaceae, and Winteraceae. Data are presented as % survival, and (n= total larvae).

RB= red bay; SP= spicebush; SA = Sassafras albidum; CT= Camphor tree (in USA & in Australia); Dsas= Doryphora sassafras; Amos= southern sassafras, Antherosperma moschatum; Tins= Tasmannia insipida, and Tlan= T. lanceolata. North American data (4 columns at the left) are from Scriber et al (1991, 1995)

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FIG. 2. North American P. glaucus and P. troilus on their favored hosts.

It is apparent that *P. glaucus* and *P. troilus* attempt to feed on Litsea leefeana leaves from Australia as well as 2 species of Cinnamomum (C. camphora and C. oliveri; Table 1). However, these Laurcaeae species are not suitable hosts for either butterfly species. Recent experimental feeding studies with campbor tree (C.camphora) have shown this invasive tree species is acceptable for the Antherosperma moschatum specialist Graphium macleayanum moggana in Tasmania (Scriber et al. 2006), as well as for the Rutaceae specialist, Papilio aegeus in Queensland (Scriber et al. 2007). A fundamental common phytochemical array of nutrients and allelochemicals in camphor tree apparently serves the basic nutritional needs for larvae of phylogenetically divergent Australian and North American taxonomic groups of Papilionidae. However, it remains unknown whether camphor tree has been an ancestral plant for any of the Papilionidae.

Despite the same common names, close phylogenetic origins, and a similar aromatic smell between the Monimiaceae (sassafras= *Doryphora sassafras*; southern sassafras = *Antherosperma moschatum*) and the Lauraceae (sassafras= *Sassafras albidum*), the Australian Monimiaceae were not at all suitable for the North American P. troilus. Both of these plant species are hosts of Graphium macleayanum Leach (Braby 2000; Scriber et al. 2006). However, despite the use of both species of Tasmannia (T. insipida and T. lanceolata) by Graphium macleayanum in Australia, these plants were totally unsuitable for P. troilus. However, the North American P. glaucus grew successfully on T. insipida (but died on T. lanceolata; Tables 1 & 2). The phytochemical basis and geneticallybased differences in feeding behavior and larval detoxification abilities deserve further study. The leaf oil cells of Tasmannia lanceolata are known to contain a sesquiterpene chemical called polygodial, which has been shown to have antimicrobial activity (Kubo & Taniguchi 1988) and piscicidal properties (Cimino et al. 1982). It has also been shown to have antifeedant properties for some insects (Powell et al. 1995).

Species of Magnoliaceae, while toxic to *P. troilus* (Scriber *et al.* 1991), can serve as a host for several Australian Papilionidae even though the plants are not found there naturally. The Rutaceae specialist, *Papilio aegeus* was reared to pupation on Magnoliaceae including *Magnolia virginiana* (sweet bay; from North America), *Michelia champaca* (yellow magnolia; from

Asia), and *Michelia doltsopa* (Asian silver cloud; Scriber et al. 2007). Pupae of P. aegeus were obtained from all 3 Magnoliaceae species and also for C. camphora of the Lauraceae (Fig. 1b). In addition, the Annonaceae specialist, Graphium eurypylus L., has recently been shown to naturally oviposit and feed successfully on introduced Michelia champaca of the Magnoliaceae (Larsen et al. 2008; Fig. 1c), and the Monimiaceae specialist (the Tasmanian subspecies of Macleay's swallowtail) was reared to pupation on Michelia doltsopa (Magnoliaceae; Scriber et al. 2006; Fig. 1a). The Umbelliferae (=Apiaceae) specialist, Papilio polyxenes F., also has the ability to feed and pupate on Magnolia as well as species of Rutaceae in North America (Scriber 1984a).

These examples, and the results with *P. glaucus* in Australia, suggest that some ancient common general phytochemical processing (or detoxification) abilities may be shared in different combinations for the Magnoliaceae, Lauraceae, Monimiaceae, Winteraceae, Annonaceae, Apiaceae and Rutaceae phytochemicals. Such adaptations may involve the very large and diverse furanocoumarin detoxification gene family of CYP6B cytochrome P450 monoxygenases, with differential biochemical inducibilities providing additional plasticity (Berenbaum & Zangerl 1998; Li *et al.* 2001, 2003, 2004).

With the Aristolochiaceae-feeding Troidini tribe of Papilionidae diverging from the Papilionini tribe (with 210 species of Papilio) 80-100 million years ago (Zakharov et al. 2004; Braby et al. 2005), it is not surprising that Aristolochiaceae leaves (e.g. A. elegans) are toxic to all neonate larvae of P. glaucus and P. troilus (Scriber unpubl. data) as well as Papilio aegeus Donovan (Scriber et al. 2007), which have no recent relatives that have ever fed on this family of plants (see also Brown et al. 1995). The earlier diverged Aristolochiaceae-feeding Troidini tribe (including Battus) and the Annonaceae-feeding Leptocircini tribe (including *Graphium* = *Eurytides* = *Protesilaus*; Zakharov *et al.* 2004) apparently lack the furanocoumarin detoxification genes needed for Rutaceae use (Berenbaum & Zangerl 1998).

Despite considerable phylogenetic distance from the basal magnoliids (Bremer *et al.* 2003; Scriber *et al.* 2008a), the Rutaceae seem to be the host family used by the ancestors of the North American *Papilio* (*Pterourus*) glaucus species group and possibly the paraphyletic *Pyrrhosticta* (=*Papilio*) scamander Boisduval, *P. homerus* Fabr. and *P. garamas* Hübner groups in South and Central America (Scriber *et al.* 1991b; Caterino & Sperling 1999), probably due to shared host plant chemistry and shared furanocoumarin detoxification

gene families (Li et al. 2001, 2004). If the North American P. troilus sister group ever possessed such Rutaceae (furanocoumarin) detoxification abilities, they have since lost it (Scriber et al. 1991b; Cohen et al. 1992; Berenbaum & Zangerl 1998). The abilities of the very polyphagous P. glaucus and P. canadensis to expand their host range beyond the ancestral Rutaceae and Magnoliaceae appears to be due to a very few mutational changes, allowing novel catalytic activity without loss of the ancestral furanocoumarin activities (Mao et al. 2007). In adult P. glaucus, oviposition rank order hierarchies are stable over the eastern half of the USA (Mercader and Scriber 2005), but plasticity and genetic variation in "specificities" in preference exist, potentially leading to local host specialization where introgression with P. canadensis occurs (on the cooler side of the hybrid zone where tulip tree is not available) in their hybrid species, P. appalachiensis (Mercader and Scriber 2007; Scriber et al. 2008b).

The variety of secondary chemicals (including very different classes of toxic allelochemicals; Berenbaum 1995; Brown et al. 1995; Feeny 1995) in these basal angiosperm plant families is staggering. The ability to consume and grow on plants in several such families, as seen for P. glaucus in the USA and G. macleayanum and G. sarpedon in Australia, seems truly impressive (whether this is a recently derived, or a 50 million year old residual ancestral capability in any current specialist; Nitao 1995). However, while there may be additional detoxification systems for other classes of phytochemicals, the costs of possessing and operating such systems would seem evolutionarily expensive and inefficient (Scriber 2005). As with most insect herbivores both physiological and ecological costs remain basically unknown, and the evolutionary cost of maintaining polyphagous capabilities for millions of years (even with some pleiotrophic fitness value) is hard to imagine and can only be a matter of speculation (Scriber 2002a).

Of course many other ecological factors in addition to plant chemistry (Scriber 2002a) influence local host plant shifts in the Papilionidae and other herbivorous insects, including natural enemies (Murphy 2004) and thermal constraints on voltinism (Scriber & Lederhouse 1992; Scriber 1996, 2002b). Here we only examined the fundamental physiological capabilities to biochemically detoxify and process nutrients from ancient allopatric angiosperms, with which the North American *P. troilus* and *P. glaucus* have never had direct contact. It is unlikely that there would have been any indirect ecological or evolutionary experience in any of their recent ancestors. Nonetheless, the abilities of the generalist, *P. glaucus*, to feed and grow on such unfamiliar plant species (e.g. *Tasmannia insipida* of the Winteraceae, and camphor tree of the Lauraceae), suggests that the potential to "invade" Australia is feasible, although minimal (except on introduced Magnoliaceae). The Lauraceae specialist, *P. troilus*, would almost certainly fail to establish in Australia, since even the Lauraceae did not support larval survival beyond 8 days.

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LITERATURE CITED

- BERENBAUM, M.R. 1995. Chemistry and oligophagy in the Papilionidae. Pp 27–38 *In*; J.M. Scriber, Y.Tsubaki, & R.C.Lederhouse (eds.), Swallowtail Butterflies; Their Ecology and Evolutionary Biology. Scientific Publ, Gainesville, FL.
 - —. & A.R. Zangerl. 1998. Population-level adaptation to host-plant chemicals: the role of cytochrome P450 monooxygenases. Pp. 91–112 In; S. Mopper & S.Y. Strauss (eds.), Genetic Structure and Local Adaptation in Natural Insect Populations. Chapman and Hall, NY.
- BRABY, M.F. 2000. Butterflies of Australia: Their identification, biology and distribution. Vol.1. CSIRO Publishing, Canberra. 976pp.
- —, J. Trueman, & R. Eastwood. 2005. When and where did troidine butterflies (Lepidoptera: Papilionidae) evolve? Phylogenetic and biogeographic evidence suggests an origin in remnant Gondwana in the late Cretaceous. Invert. Syst. 19: 113–143.
- BREMER, K., B. BREMER, & M. THULIN. 2003. Introduction to phylogeny and systematics of flowering plants. Acta Universitalis Upsaliensis, Symbolae Botanicae Upsalienses. 33(2) Sweden. 102pp.
- BROWN, K.S. JR., C. BERLINGERI, C.F. KLITZKE, &. P.E.R. DOS SANTOS. 1995. Neotropical swallowtails: chemistry of food plant relationships, population ecology, and biosystematics. Pp 405–445 *In*; J.M. Scriber, Y. Tsubaki, & R.C. Lederhouse (eds.), Swallowtail Butterflies; Their Ecology and Evolutionary Biology. Scientific Publ, Gainesville, FL,
- CARTER, M. & P. FEENY, 1999. Host plant chemistry influences oviposition choice of the spicebush swallowtail butterfly, *Papilio troilus*.
 J. Chem. Ecol. 25: 1999–2009.
- , P. FEENY, & M. HARIBAL. 1999. An oviposition stimulant for the spicebush swallowtail butterfly, *Papilio troilus* (Lepidoptera: Papilionidae), from leaves of *Sassafras albidum* (Lauraceae) J. Chem. Ecol. 25: 1233–1245.
- CATERINO, M.S. & F.A.H. SPERLING, 1999. Papilio phylogeny based on mitochondrial cytochcrome oxidase I and II genes. Molec. Phylog. & Evol. 11: 127–137.
- CIMINO, G., S. DEROSA, S. DESTEFANO, G. SODANOAND, & G.VILLANI, 1982. The chemical defense of four Mediterranean nudibranchs. Comp. Biochem. Physiol 73B: 471–474.
- COHEN, M.B., M.A. SCHULER, &. M.R. BERENBAUM. 1992. Hostinducible cytochrome P450 from a host-specific caterpillar: molecular cloning and evolution. Proceedings of the National Academy of Sciences (USA) 89: 10920–10924.

- DETHIER, V.G. 1941. Chemical factors determining the choice of foodplants by *Papilio* larvae. Amer. Nat. 75: 61–73
- ——. 1954. Evolution of feeding preferences in phytophagous insects. Evolution 8: 33–54.
- EDWARDS, E.D., J. NEWLAND, & L. REGAN. 2001. Lepidoptera Hesperioidea, Papilionidae. Pp. 427–428 In; A.Wells & W.W.K. Houston (eds.), Zoological Catalogue of Australia, 31 (6). CSIRO Publishing, Melbourne.
- FEENY, P. 1995. Ecological opportunism and chemical constraints on the host associations of swallowtail butterflies. Pp 9–15 *In*; J.M. Scriber, Y. Tsubaki, & R.C Lederhouse (eds.), Swallowtail Butterflies; Their Ecology and Evolutionary Biology. Scientific Publ, Gainesville, FL.
- FRANKFATER, C.R. & J.M. SCRIBER. 1999. Chemical basis for host recognition by two oligophagous swallowtail butterflies, *Papilio* troilus and *Papilio palamedes*. Chemoecology 9: 127–132.
- & J.M. SCRIBER. 2003. Contact chemoreception guides oviposition of two Lauraceae-specialized swallowtail butterflies (Lepidoptera; Papilionidae). Holarct. Lepid. 7: 33–38.
- GAUNT, M.W. & M.A. MILES. 2002. An insect molecular clock dates the origins of insects and accords with palaeontological and biogeographic landmarks. Molec. Biol. & Evol. 19: 748–761.
- GONZALEZ-COLOMA, A., M. HERNANDEZ, G.A. PERALES, & B.M. FRAGA. 1990. Chemical ecology of Canarian laurel forest toxic diterpenes from *Persea indica* (Lauraceae). J. Chem. Ecol. 16: 2723–2733.
- GRIMALDI, D. & M.S.ENGEL 2005. Evolution of the insects. Cambridge Univ. Press. UK. 796pp.
- HANCOCK D.L. 1983. Princeps aegeus (Donovan) and its allies (Lepidoptera; Papilionidae): systematics, phylogeny and biogeography. Austral. J. Zool. 31: 771–797.
- JOHNSON K.S., J.M. SCRIBER, & M. NAIR. 1996. Phenylpropanoid phenolics in sweetbay magnolia as chemical determinants of host use in saturniid silkmoths (*Callosamia* spp.) J. Chem. Ecol.. 22: 1955–1969.
- KUBO, I. & M.TANIGUCHI. 1988. Polygodial an antifungal potentiator. J. Nat. Prod. 15: 22–29.
- LARSEN, M.L., J.M. SCRIBER, & M.P. ZALUCKI. 2008. Significance of a new field oviposition record for *Graphium eurypylus* (Lepidoptera: Papilionidae) on *Michelia champaca* (Magnoliaceae). Austral. J. Entomol. 47:58–63.
- LI, W., R.A. PETERSON, M.A. SCHULER, & M.R. BERENBAUM. 2001. CYP6B cytochrome P450 monooxygenases from *Papilio* canadensis and *Papilio* glaucus; potential contributions of sequence divergence to host plant associations. Insect Molec. Biol. 11:543–551.
- —, R.A. PETERSON, M.A. SCHULER, & M.R. BERENBAUM. 2003. Diversification of furanocoumarin-metabolizing cytochrome P-450 monooxygenases in two papilionids: specificity and substrate encounter rate. Proc. Nat. Acad. Sci. (USA) 100 (supplement 2), 14593-14598.
- —, J. BAUDRY, M.R. BERENBAUM, & M.A. SCHULER. 2004. Structural and functional divergence of insect CYP6B proteins: from specialist to generalist cytochrome P450. Proc. Nat. Acad. Sci. (USA) 101: 2939–2944.
- MA, W.W., J.E. ANDERSON, C.J. CHANG, D.L. SMITH, & J.L. MCLAUGHLIN. 1989. Majorenolide and majorynolide a new pair of cytotoxic and pesticidal alkene- alkyne δ-lactones from *Persea major*. J. Natur. Prod. 52: 1263–1266.
- MAKITA, H.T., K. SHINKAWA, K. KONDO, L. XING, & T. NAZAZAWA. 2003. Phylogeny of the *Graphium* butterflies inferred from nuclear 28S rDNA and mitochondrial ND5 gene sequences. Trans. Lepid. Soc. Japan 54: 91–110.
- MAO, W., M.A. SCHULER, & M.R. BERENBAUM. 2007. Cytochrome P450s in *Papilio multicaudatus* and the transition from oligophagy to polyphagy in the Papilionidae. Insect Molecular Biology 16: 481–490.
- MERCADER, R. & J.M. SCRIBER. 2005. Phenotypic plasticity in polyphagous *Papilio*: preferences, performances, and potential enhancement by hybridization. Pp. 25–57 *In*; T.N. Ananthakrish-

nan (ed.), Insect Phenotypic Plasticity; Diversity of Responses. Science Publ. Plymouth, UK.

- & J.M.SCRIBER. 2007. Diversification of host use in two polyphagous butterflies: differences in oviposition specificity or host rank hierarchy? Entomol. Exp. et Appl. 129:89–101.
- MILLER, J.S. 1987. Host-plant relationships in the Papilionidae (Lepidoptera): parallel cladogenesis or colonization? Cladistics 3: 105–120.
- MUNROE, E. 1961. The classification of the Papilionidae (Lepidoptera). Can. Entom. (Suppl.) 7: 1–51.
- MURPHY, S.M. 2004. Enemy-free space maintains swallowtail butterfly host shift. Proc. Nat. Acad. Sci. USA 101: 18048–18052.
- MORRIS, M.W. 1989. *Papilio troilus* L. on a new and rare larval foodplant. J. Lepid. Soc. 43: 147.
- NISHIDA, R. 1995. Oviposition stimulants of swallowtail butterflies. Pp. 17–26 In; J.M. Scriber, Y.Tsubaki, & R.C.Lederhouse (eds.), Swallowtail Butterflies; Their Ecology and Evolutionary Biology. Scientific Publ, Gainesville, FL.
- NITAO, J.K. 1995. Evolutionary stability of swallowtail adaptations to plant toxins. Pp 39–52 In; J.M. Scriber, Y.Tsubaki, & R.C.Lederhouse (eds.), Swallowtail Butterflies; Their Ecology and Evolutionary Biology. Scientific Publ, Gainesville, FL.
- —, M.P. AYRES, R.C. LEDERHOUSE, & J.M. SCRIBER. 1991. Larval adaptation to lauraceous hosts: geographic divergence in the spicebush swallowtail butterfly. Ecology 72: 1428–1435.
- —, K.S. JOHNSON, J.M. SCRIBER, &. M.G. NAIR. 1992. Magnolia virginiana neolignin compounds as chemical barriers to swallowtail butterfly host use. J. Chem. Ecol. 18: 1661–1671.
- POWELL, G., J. HARDIE, & J. PICKETT. 1995. Responses of Myzus persicae to the repellent polygodial in choice and no-choice video assays with young and mature leaf tissue. Entomol. Exp. et Appl. 74: 91–94.
- RAVEN, P.H. & D.I. AXELROD. 1974. Angiosperm biogeography and past continental movement. Ann. Missouri Bot. Gard. 61: 539–673.
- READ, C. & R. MENARY. 2000. Analysis of the contents of oil cells in *Tasmannia lanceolata* (Poir.) A.C. Smith (Winteraceae). Ann. Botany 86: 1193–1197.
- SCRIBER, J.M. 1984a. Larval food plant utilization by the world Papilionidae (Lep.): latitudinal gradients reappraised. Tokurana (Acta Rhopalocerologica) 6/7: 1–50.
- —. 1984b. Host plant suitability. Pp. 159–202 In; W.J. Bell & R.T. Carde (eds.), Chemical Ecology of Insects, Sinauer, Sunderland, MA.
- —. 1986. Origins of the regional feeding abilities in the tiger swallowtail butterfly: ecological monophagy and the *Papilio glaucus australis* subspecies in Florida. Oecologia 71: 94–103.
- —. 1988. Tale of the tiger: Beringial biogeography, bionomial classification, and breakfast choices in the *Papilio glaucus* complex of butterflies. Pp. 240–301 *In*; K.C. Spencer (ed.), Chemical Mediation of Coevolution, Academic Press. NY.
- —. 1993. Absence of behavioral induction in oviposition preference of *Papilio glaucus* (Lepidoptera: Papilionidae). Great Lakes Entomol. 26: 81–95.
- —. 1995. Overview of swallowtail butterflies: taxonomic and distributional latitude. Pp. 3–8 In; J.M. Scriber, Y. Tsubaki, & R.C. Lederhouse (eds.), Swallowtail Butterflies; Their Ecology and Evolutionary Biology, Scientific Publishers, Gainesville, FL.
- —. 1996. A new cold pocket hypothesis to explain local host preference shifts in *Papilio canadensis*. Entomol. exp. & appl. 80: 315–319.
- —. 2002a. The evolution of insect-plant relationships; chemical constraints, coadaptation and concordance of insect/plant traits. Entomol. Exp. et Appl. 104: 217–235.
- —. 2002b. Latitudinal and local geographic mosaics in host plant preferences as shaped by thermal units and voltinism. European J. Entomol. 99: 225–39.
- —. 2005. A mini-review of the "feeding specialization/physiological efficiency" hypothesis: 50 years of difficulties, and strong support from the North American Lauraceae-specialist, *Papilio troilus*

(Papilionidae: Lepidoptera). Trends in Entomology 4: 1-42.

- & P. FEENY. 1979. Growth of herbivorous caterpillars in relation to feeding specialization and to the growth form of their foodplants. Ecology 60: 829–850.
- & R.C. LEDERHOUSE. 1992. The thermal environment as a resource dictating geographic patterns of feeding specialization of insect herbivores. Pp. 429–466 In; M.R. Hunter, T. Ohgushi & P.W. Price (eds.), Effects of Resource Distribution on Animalplant Interactions, Academic Press, New York, NY.
- —, R.C. LEDERHOUSE, & L. CONTARDO. 1975. Spicebush, *Lindera benzoin* (L.), a little known foodplant of *Papilio glaucus* (Papilionidae). J. Lepid. Soc. 29: 10–14.
- —, R.C. LEDERHOUSE, & R.DOWELL. 1995. Hybridization studies with North American swallowtails. Pp. 269–282 *In*; J.M. Scriber, Y. Tsubaki, & R.C. Lederhouse, (eds.), The Swallowtail Butterflies: Their Ecology and Evolutionary Biology. Scientific Publishers, Inc., Gainesville, FL.
- —, R.C. Lederhouse, & K. Brown. 1991a. Hybridization of Brazilian Papilio (Pyrrhosticta) (Section V) with North American Papilio (Pterourus) (Section III). J. Res. Lepid. 29: 21–32.
- —, R.C. LEDERHOUSE, & R.H. HAGEN. 1991b. Foodplants and evolution within the *Papilio glaucus* and *Papilio troilus* species groups (Lepidoptera: Papilionidae). Pp 341–373 *In*; P.W. Price, T.M. Lewinsohn, G.W. Fernandes, & W.W. Benson (eds.), Plantanimal Interactions: Evolutionary Ecology in Tropical and Temperate Regions. Wiley, NY.
- M.L. LARSEN, & M.P. ZALUCKI. 2007. Papilio aegeus Donovan (Lepidoptera; Papilionidae) host plant range evaluated experimentally on ancient Angiosperms. Austral. J. Entomol. 46: 65–74.
 & N. Margraf. 2005 (2003). Suitability of Florida redbay (Persea borbonia) and silk bay (Persea humilis) for the Papilio palamedes
- butterfly larvae. Holarct. Lepidopt. 8: 49– 51. —, N. Margraf, & T. Wells. 2001. Suitability of four families of
- Florida "bay" species for *Papilio palamedes* and *P. glaucus* (Papilionidae). J. Lepid. Soc. 54, 131–136.
- —, M.L. LARSEN, G.R. ALLEN, P.W. WALKER, & M.P. ZALUCKI. 2008a. Interactions between Papilionidae and ancient Australian angiosperms: evolutionary specialization or ecological monophagy? Entomol. Exp. et Appl. (SIP-13 conf. issue).
- —, G.J. ORDING, AND R.J. MERCADER. 2008b. Hybrid introgression and parapatric speciation in a hybrid zone. Pp. 69–87 *In*; K.J. Tilmon (ed.), Specialization, Speciation, and Radiation: the Evolutionary Biology of Herbivorous Insects. Univ. California Press.
- —, G.R. ALLEN, & P.W. WALKER. 2006. Ecological monophagy in Tasmanian *Graphium macleayanum moggana* and evolutionary reflections of ancient Angiosperm hosts. Insect Science 13: 325–334.
- SOLTIS, P.S., P.K. ENDRESS, M.W. CHASE, AND D.E. SOLTIS. 2005. Phylogeny of the Angiosperms. Sinauer Assoc. MA. 370pp.
- SPERLING, F.A.H. 2003. Butterfly molecular systematics: from species definitions to higher level phylogenies. Pp. 431–458 In; C.L. Boggs, W.B. Watt, & P.R. Ehrlich (eds.), Butterflies: Ecology and Evolution Taking Flight, Univ. Chicago Press, IL.
- THOMPSON, J.N. 1995. The origins of host shifts in swallowtail butterflies versus other insects. Pp 195–203 *In*; J.M. Scriber, Y. Tsubaki, & R.C.Lederhouse (eds.), Swallowtail Butterflies; Their Ecology and Evolutionary Biology. Scientific Publ, Gainesville, FL.
- ZAKHAROV, E., M.S. CATERINO, & F.A.H. SPERLING. 2004. Molecular phylogeny, historical biogeography, and divergence time estimates for swallowtail butterflies of the genus *Papilio* (Lepidoptera: Papilionidae). Syst. Biol. 53, 193–215.
- ZALUCKÎ, M.P. A.R. CLARKE, & S.B. MALCOLM. 2002. Ecology and behavior of first instar larval Lepidoptera. Ann. Rev. Entomol. 47:361–393.

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Scriber, J Mark, Larsen, Michelle L, and Zalucki, Myron P. 2008. "Responses of North American Papilio troilus and P. glaucus to potential hosts from Australia." *Journal of the Lepidopterists' Society* 62(1), 18–30.

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