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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 *Cinnamomum* 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 chemically-related 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 fully-expanded 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 (mm^2), 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

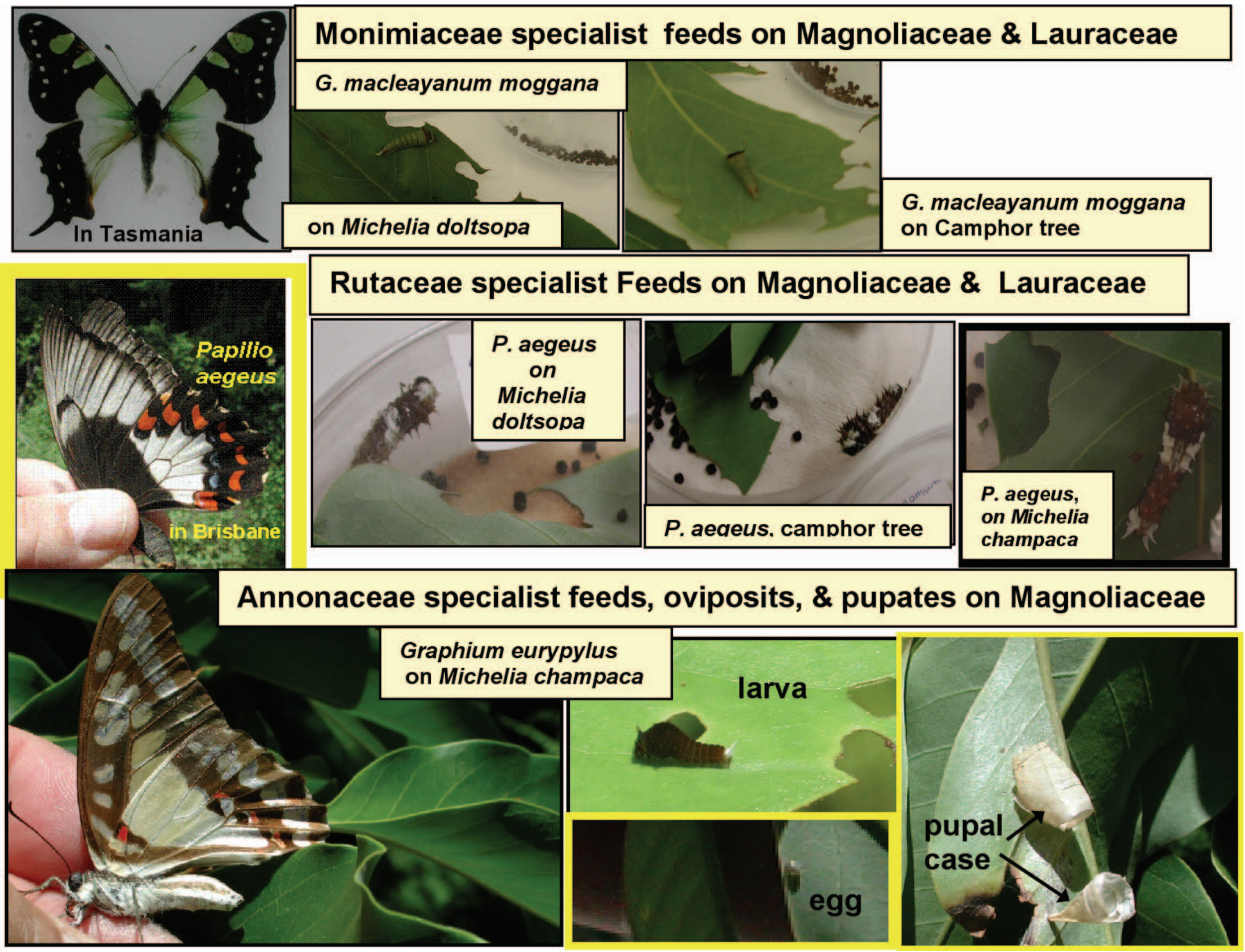

FIG. 1. Feeding assays with family-specialized Australian Lepidoptera that also survived on Magnoliaceae; **1a**) Macleay's swallowtail (Tasmanian subspecies, *G. m. moggana*) is a specialist on the Monimiaceae, but feeds and pupates on Magnoliaceae and Lauraceae (Scriber et al. 2006), **1b**) *Papilio 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).

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.

		4 Days			8 Days			12 Days		
Larval Family	(n)	% surv.	mean wt.	instar	% surv.	mean wt.	instar	% surv.	mean wt.	instar
RUTACEAE										
Citrus sinensis "*joppa*"										
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 australis										
G1	0	na								
G2	3	0	died							
G3	0	na								
G4	0	na								
T1	3	0	died							
T2	0	na								
*Geijera salicifolia**										
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	2	0	died							
MAGNOLIACEAE										
Magnolia virginiana										
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							
T2	3	0	died							
Michelia champaca										
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 doltsopa										
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. (continued)

		4 Days			8 Days			12 Days		
Larval Family	(n)	% surv.	mean wt.	instar	% surv.	mean wt.	instar	% surv.	mean wt.	instar
Michelia doltsopa (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							
T2	3	0	died							
LAURACEAE										
*Beilschmiedia obtusifolia**										
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	2	0	died							
Cinnamomum camphora										
G1	2	0	died							
G2	3	100	8.7	1	100	15.1	2	100	41.3	2.8
G3	0	na								
G4	2	0	died							
T1	2	0	died							
T2	3	66.7	3.8	1.3	66.7	4	1.5	0	died	
Cinnamomum oliveri										
G1	0	na								
G2	3	66.7	4	1	0	died				
G3	0	na								
G4	0	na								
T1	0	na								
T2	3	66.7	3.7	1.3	66.7	4	1.5	0	died	
Cinnamomum virens										
G1	0	na								
G2	3	33.3	2.7	1	0	died				
G3	0	na								
G4	0	na								
T1	0	na								
T2	0	na								
*Cryptocarya glaucescens**										
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	2	0	died							
Cryptocarya microneura										
G1	0	na								
G2	3	0	died							
G3	0	na								
G4	3	0	died							
T1	0	na								
T2	0	na								

TABLE 1. (continued)

		4 Days			8 Days			12 Days		
Larval Family	(n)	% surv.	mean wt.	instar	% surv.	mean wt.	instar	% surv.	mean wt.	instar
_Endiandra discolor_*										
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 dealbata_*										
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	2	0	died							
MONIMIACEAE										
Antherosperma moschatum										
G1	2	0	died							
G2	3	0	died							
G3	2	50	1.1	1	0	died				
G4	2	0	died							
T1	2	0	died							
T2	3	0	died							
_Doryphora sassafras_*										
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	3	0	died							
WINTERACEAE										
Tasmannia insipida										
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							
T2	2	0	died							

TABLE 1. (concluded)

		4 Days			8 Days			12 Days		
Larval Family	(n)	% surv.	mean wt.	instar	% surv.	mean wt.	instar	% surv.	mean wt.	instar
WINTERACEAE (cont.)										
Tasmannia lanceolata[*]										
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	2	0	died							
ANNONACEAE										
Annona muricata[*]										
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 reticulata[*]										
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	3	0	died							
SAPOTACEAE										
Pouteria australis[*]										
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 assayed 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 al*. 1991). The introduced southeast 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 cytochrome 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).

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).

	Lauraceae					Monimiaceae		Winteraceae	
	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)

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)

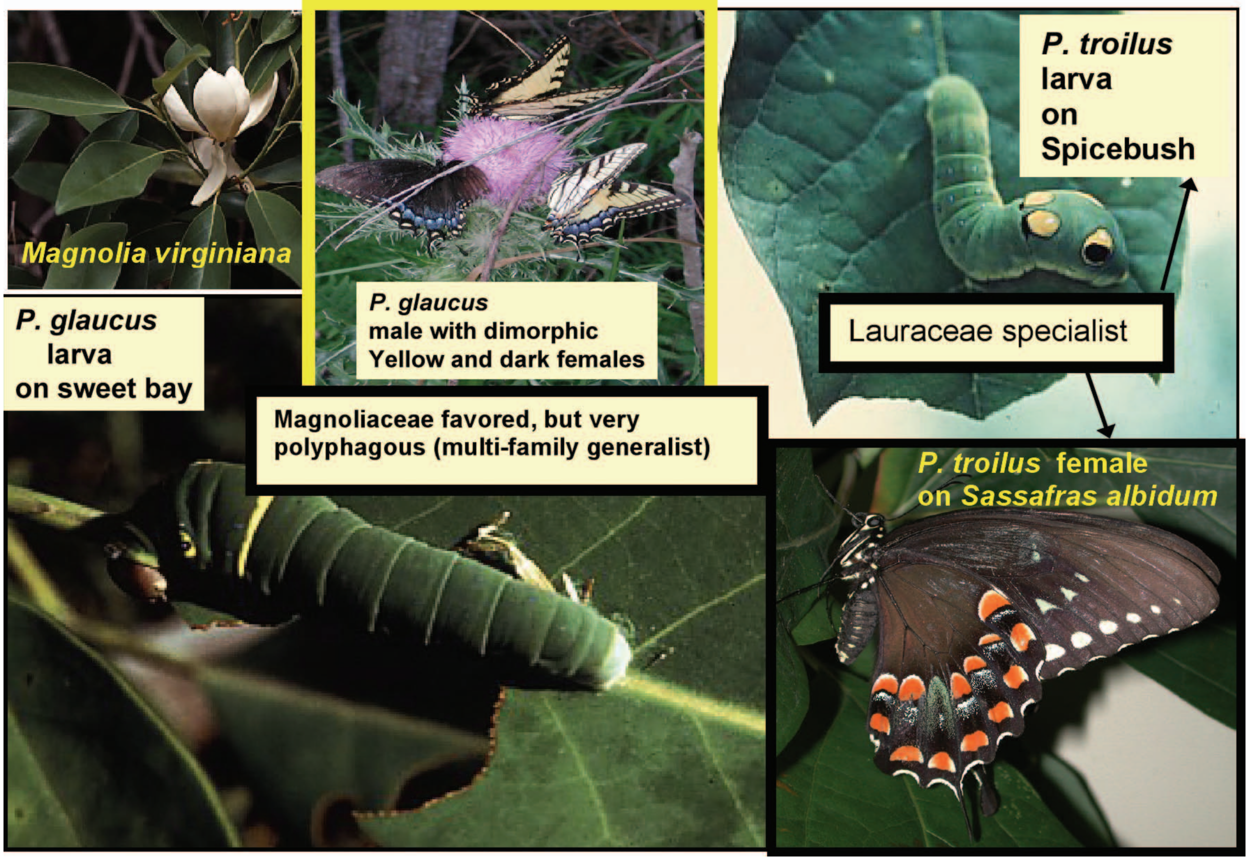

FIG. 2. North American *P. glaucus* and *P. troilus* on their favored hosts.

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 camphor 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 genetically-based 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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