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True and False Foodplants of *Callosamia Promethea* (Lepidoptera: Saturniidae) in Southern Michigan

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TRUE AND FALSE FOODPLANTS OF *CALLOSAMIA PROMETHEA* (LEPIDOPTERA: SATURNIIDAE) IN SOUTHERN MICHIGAN

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ABSTRACT

A survey in 1980 of the associations of over 400 cocoons of *Callosamia promethea* Drury in vegetation along and adjacent to southern Michigan roadsides gave evidence for seven species of true larval foodplants (not including two others known in the area from other studies) and 17 species of false foodplants, the latter determined by the (1) rarity of their association with cocoons, (2) only one or two cocoons per plant, and (3) their proximity to a well known true foodplant. Three species, sassafras, black cherry, and buttonbush, are evidently the most important true foodplants in this area. Comparisons are made of the foodplants in terms of past literature, geography, and taxonomic relationships.

Reports of false larval foodplants cause a number of difficulties. By creating misleading impressions about the biology of both the plant hosts and their herbivores, which are persistent once they get into the literature, they interfere with the steady progress of basic research. For example, biologists today are much interested in the nature of those chemical substances in plants which may serve as a means of herbivore defense and are seeking general principles underlying this type of adaptation (Feeny 1976, Janzen 1973, Rhoades and Cates 1976). Also, by correlating the phylogenetic relationships of herbivores and their hostplants, it is possible to gain insights into their co-evolutionary patterns (cf. Ehrlich and Raven 1964). The "parasitological method" in phylogenetic systematics, which may aid in the working out of cladistic patterns (cf. Hennig 1966), is critically reliant on accurate herbivore-hostplant information. In each of these cases, use of false foodplant information can potentially lead to great error. For these reasons it is most desirable that extreme caution be exercised in reporting larval foodplants.

For our purposes, we define "true foodplants" as those plant species upon which larval development occurs in nature, and usually upon or near which the eggs are actually laid. As eggs and larvae are often difficult to find, we adopted the standard convention of using site of pupation as an indicator of the true foodplant. We realize, however, that though highly reliable, site of pupation is not an infallible indicator. Just prior to pupation, a larva may fall from, be knocked off, or leave a true foodplant, crawl to another plant and pupate there. A field worker encounters such a "wanderer" or pupa, jumps to the conclusion that an unrecorded foodplant has been found, and so reports it. In *Antherea polyphemus* (Cramer), for example, 25% of the cocoons we found were spun entirely in grass, which is definitely not a true foodplant (Wagner and Mayfield 1980).

In connection with the study of cocoons of the endemic North American genus of giant silkworms, *Callosamia* (Lepidoptera: Saturniidae), we have become interested in their variation in relation to species-taxonomy, geography, and foodplants. The work reported here is part of that study. Nearly 30 genera of plants have been reported to be hosts of *C. promethea* Drury (see Table 3), most of which occur in Michigan, but a number of which we suspected were not true foodplants for this species. We therefore made a field survey during the period January to May 1980 in an effort to establish what species *C. promethea* actually utilizes in

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southern Michigan and, if possible, whether there are any clear-cut false foodplants, i.e. plants erroneously thought to be true foodplants.

The survey was conducted along roadsides, adjacent fields, and hedgerows as the majority of alleged foodplant species occur there. The cocoons themselves are readily visible, their pendent outlines conspicuous on the branchlets and twigs of their leafless hosts. The foodplant results obtained are representative of the occurrence of cocoons in relation to the respective foodplant species, with one notable exception. The spicebush (*Lindera benzoin* [L.] Blume), a well known true foodplant, tends to grow in rich, shaded swamps and is therefore underrepresented. We have, however, frequently encountered *C. promethea* cocoons on spicebush during field studies of swamp plants, and do not question that it is an important host in southern Michigan. At all sites we collected complete samples of the cocoons, as well as recording host plant species. This totalled 487 cocoons from an estimated 130 plants, including both true and false foodplants.

RESULTS

The results of our field studies are outlined in Tables 1 and 2. As can be seen from Table 1, the distribution of cocoons was highly clumped. Of the 487 collected, approximately 55% (26) of them occurred on the 16 species of false foodplants, while three of the eight species of true foodplants, sassafras (*Sassafras albidum* [Nutt.] Nees), black cherry (*Prunus serotina* Ehrh.), and buttonbush (*Cephalanthus occidentalis* L.), together accounted for 80% of the total cocoons collected. In fact, sassafras alone accounted for 38.6% of the total cocoons.

The taxonomic unrelatedness of these foodplants will be discussed below. In terms of plant habit, however, we are dealing with a group of plants that have in common a shrubby life form, as can be seen from Table 1. Even those which are trees, black cherry, white ash, (*Fraxinus americana* L.), tulip tree (*Liriodendron tulipifera* L.), and sassafras are utilized as young saplings or stump sprouts, or small shrubs in the case of sassafras. This commonality in growth form suggests that it may be an important factor used in hostplant selection by the promethea moth. Within this growth form the cocoons tended to be located centrally; the vast majority of them occurred between 1–2 m above the ground. A few high cocoons occurred at 5 m up in the branches of white ash and tulip tree. On buttonbush and the introduced lilac (*Syringa vulgaris* L.) cocoons, sometimes numerous, often were hung on branches close to the ground. We sometimes found the same conditions in black cherry where bushy stump sprouts occurred.

The habitats of these foodplants may appear to be strongly different *inter se*, as can be seen in Table 1, although there are some ecological commonalities. Tulip tree tends to be found at the edge of low, rich, hardwood forests. Sassafras occurs most commonly on sterile, upland soils. Lilac does not reproduce in southern Michigan, but is remarkably persistent, remaining for many years after a homestead where it has been cultivated has crumbled away. Large clones are common along roadsides in second-growth places in southern Michigan, but the best cocoon populations are usually in yards and gardens, associated with well-kept landscapes around houses still occupied. The most distinctive habitat for a true foodplant is that of the buttonbush, which is the only aquatic foodplant for *C. promethea*, with edges of marshes, openings in large hardwood swamps, and roadside ditches providing typical sites. All the other foodplants occur along roadsides, hedgerows, and in old fields. Ecologically speaking, these habitats are all early successional ones characterized by a high degree of disturbance. Thus, *C. promethea* appears to be an early successional species.

We looked at the leaf morphology in the different true foodplants to see whether there was a common denominator as this has been shown to be an important component of host plant selection for some Lepidoptera (Rausher 1978). As shown in Table 1, the leaf morphology is strikingly different. The size of the blade varies from large in tulip tree and white ash to small in choke cherry (*Prunus virginia* L.) and spicebush. The case of white ash, however, is unusual in that the large blade is actually compound. Botanically speaking the whole unit is a morphological blade, but both tulip tree and sassafras have a strong tendency toward more

Table 1. True foodplants of *Callosamia promethea.*

Species	Description	Habitat	Cocoons (Approx. No. of plants)
Cephalanthus occidentalis	Clonal shrub, lvs, small, unlobed, simple, opp., entire	Open ditches, marshes, and swamp edges	99 (20)
Fraxinus americana	Small tree, lvs. large, comp'd, opp., nearly entire	Roadbanks, hedgerows	22 (6)
Liriodendron tulipifera	Small tree, lvs. large, simple, 4-lobed, alt. entire	Forest edges, plantings	25 (10)
Prunus serotina	Stump sprouts, saplings, small trees, lvs. small, simple, unlobed, alt., toothed	Roadsides old fields	101 (30)
P. virginiana	Clonal shrub, lvs. large, simple, unlobed, alt., toothed	Roadsides old fields	8 (2)
Sassafras albidum	Clonal shrub or tree, lvs. large, simple, unlobed to 3-lobed, alt. entire	Roadsides, hedgerows, forest edges	188 (40)
Syringa vulgaris	Clonal shrub, lvs. medium, simple, unlobed, opp., entire	Gardens, old homesteads	18 (4)
Lindera benzoin	Shrub, lvs. small simple, unlobed alt., entire	Shaded, mainly hardwood swamps	— (—)
TOTAL			461 (112)

or less deeply lobed leaves. The others are unlobed. Three of the eight species have opposite leaves, the remainder alternate. Only two of the species, black cherry and choke cherry, have toothed leaf margins, but the margins of the leaflets in white ash may show shallow teeth. The remainder of the species have perfectly entire blade margins. Thus, there is little similarity in the foliar morphology of the true foodplants suggesting it is an unimportant factor in hostplant selection.

We based our conclusion that the plants listed in Table 2 are false foodplants on circumstantial evidence. Whether or not the larvae of *C. promethea* can be induced to feed upon any of them in captivity is not the question as induction is a well known phenomenon in the lab. We were concerned with what actually happens in the wild; what do the caterpillars normally feed upon in the natural state? For the true foodplants listed, the majority have actually been observed with *C. promethea* caterpillars feeding upon them, and all have been reported previously by authors elsewhere in the range of this moth (Ferguson 1972, Tietz 1952). Our criteria for false foodplants were as follows: (1) observations of cocoons on the plant exceedingly rare, (2) cocoons 1–2 per plant, and (3) the plant growing next to well known true foodplants upon which there are *C. promethea* cocoons.

With one exception there were no more than two cocoons per false foodplant, and the average was 1.1. For the true foodplants, however, the average number of cocoons per plant

Table 2. Probable false foodplants of *Callosamia promethea* in Southern Michigan.

Species	Provenance and Habit[a]	Number of Cocoons	Nearby True Foodplant
Acer rubrum (1)	Native tree	2	*Cephalanthus*
A. saccharum (1)	Native tree	1	*Sassafras*
Berberis thunbergii (1)	Exotic shrub	1	*Sassafras*
Carya ovalis (1)	Native tree	1	*Sassafras*
Celtis tenuifolia (1)	Native tree	1	*Sassafras*
Cornus racemosa (1)	Native shrub	1	*Prunus*
C. stolonifera (1)	Native shrub	1	*Cephalanthus*
Corylus americana (1)	Native shrub	1	*Sassafras*
Lonicera tatarica (1)	Exotic shrub	1	*Cephalanthus*
Quercus alba (1)	Native tree	1	*Sassafras*
Q. coccinea (1)	Native tree	1	*Sassafras*
Q. rubra (1)	Native tree	2	*Sassafras*
Rhus typhina (2)	Native shrub	2	*Sassafras*
Thalictrum dasycarpum (3)	Native herb	6	*Cephalanthus*
Ulmus americana (2)	Native tree	2	*Prunus* (1), *Cephalanthus* (1)
Vitis riparia (2)	Native vine	2	*Sassafras* (1), *Cephalanthus* (1)

[a]In all cases, those listed as trees were actually saplings or stump sprouts, none over 3 m tall.

was 4.1 for all species (range 2.5 [*Liriodendron*] to 4.9 [*Cephalanthus*]). As will be discussed below, all of the false foodplant species were associated with one or another of the three most common true foodplants, sassafras, buttonbush, and black cherry, which in all cases had several cocoons. The black cherry was the least common of the true foodplants associated with false foodplants, but it is also the plant, being non-clonal, that is most likely to occur isolated from other woody plants in fields and hedgerows. The other two, sassafras and buttonbush, are notable cloneformers, the clones abutting upon and intergrowing with other species.

All of the false foodplants are woody with the exception of the tall herb, *Thalictrum dasycarpum* Fisch. and Lall. Also, in early winter 1980, R. Stewart and K. Gover discovered an herbaceous vine, the yam *(Dioscorea villosa* L.) in Jackson County, Michigan, serving as a support for a *C. promethea* cocoon near a sassafras clone. This is an unusual record not only because it is an herbaceous plant but also because it is the only monocot we have encountered that was a false foodplant. All of the rest of the species are trees or shrubs with the exception of riverside grape (*Vitis riparia* Michx.), which is a woody vine. All of the false foodplants are natives with the exception of Japanese barberry (*Berberis thunbergii* DC) and Tatarian honeysuckle (*Lonicera tatarica* L.), both of which are becoming naturalized in southern Michigan and spreading widely, especially in second-growth woods. All of the species are common except for dwarf hackberry (*Celtis tenuifolia* Nutt.), a highly localized species known from only a few counties.

Three genera are well represented among the false foodplants: *Acer* (red maple [*A. rubrum* L.] and sugar maple [*A. saccharum* Marsh.]), *Cornus* (gray dogwood [*C. racemosa* Lam.] and red osier [*C. stolonifera* Michx.]), and *Quercus* (white oak [Q. alba L.], scarlet oak [*Q. coccinea* Muenchh.] and red oak [*Q. rubra* L.]). It is interesting to note that several of the genera we here interpret as false foodplants have previously been reported as true foodplants, including *Acer, Berberis, Corylus*, and *Quercus* (Ferguson 1972, Teitz 1952). To our knowledge, the other taxa have not previously been reported to have promethea cocoons hanging on them.

SUMMARY AND DISCUSSION

In addition to the true foodplants listed in Table 1 for southern Michigan, R. Stewart has kindly given us a report of two collections of *C. promethea* cocoons on privet (*Ligustrum vulgare* L.) in Jackson County. We do not consider this a case of wandering as none of the true foodplants were found in the immediate vicinity. This brings the number of species confidently regarded as true foodplants to nine, of which only three, sassafras, black cherry, and buttonbush, are of major importance. Judging from the incidence of cocoons and the nature of their occurrence, we conclude that there are at least 17 species (including *Dioscorea villosa*) upon which wandering larvae may pupate. The potential number of false foodplants is much greater, of course, since the association is probably casual, and based upon chance. Ferguson (1972) has given a valuable discussion of this phenomenon in connection with the buck moth, *Hemileuca maia* (Drury), "reported to feed on a variety of other plants, almost certainly in error. This is partly explained by the habits of the larvae, which, when about half-grown, lose their gregarious nature and disperse widely in all directions. They are then often found resting on plants upon which they do not normally feed, and in some instances these may have been wrongly assumed to be the host plants." In our studies we based our conclusions upon the incidence of cocoons. It is possible indeed that some of our reports deal actually with secondary foodplants i.e. in which wandering larvae adopted after leaving the primary foodplants. It is also possible that at least some of our "false" foodplants are actually primary foodplants which are very rarely utilized, although the likelihood seems remote.

We should caution that our statistics are based primarily upon roadside observations in which cocoons were recognized from a moving automobile and the site subsequently investigated. We thus mainly surveyed plants growing along the road and in nearby fields and hedgerows. In all likelihood the bulk of *C. promethea* cocoons do, in fact, occur in such habitats, but we did miss one conspicuous foodplant by making our survey in this way, the spicebush.

All of the true foodplants for which we have reports are listed in Table 3. Those marked with question marks are ones which, in our opinion, need further confirmation. Those marked with asterisks are ones that we find to be probable false foodplants in southern Michigan. Ferguson (1972) stated that *C. promethea* has "definite preferences that seem to vary geographically." Based on our correspondence with lepidopterists over the range of this moth, we surmise that the three most important foodplants in southern Michigan are consistently the most utilized throughout the eastern United States. However, as we go farther south, new true foodplants are utilized, including sweet gum (*Liquidambar styraciflua* L.), silverbells (*Halesia carolina* L.), storax (*Styrax americana* Lam.), and sweet leaf (*Symplocos tinctoria* [L.]. L'Her.). Heitzman (*in* Ferguson 1972) reported persimmon (*Diospyros virginiana* L.). We have no reason to question any of these as true foodplants, but more evidence would be welcomed for some of them.

Although the true foodplants can be characterized as possessing a shrubby growth form and occurring in highly disturbed and/or secondary succession sites, from a taxonomic viewpoint they are incredibly diverse. As can be seen from Table 3, the actual taxonomic relationships, following current opinion (e.g. Cronquist 1968), are remote indeed. Represented are five widely separated subclasses, and the families seem almost to have been chosen at random. The pair Lauraceae and Magnoliaceae are obviously interrelated; and the trio Ebenaceae, Styracaceae, and Symplocaceae are also interrelated. However, Oleaceae and Rubiaceae are probably quite divergent. Of all the possible woody Rosaceae, why is it that *Prunus* are preferred, indeed the one species, *P. serotina*, against all others? The most isolated foodplant is the sweet gum, the relationships of which to any of the others are probably very distant. Perhaps the plants are similar chemically, such as in nitrogen content in the leaf, percent leaf water content, leaf toughness, or presence of a chemical which acts as a feeding stimulant; all traits which are important components of the nutritive value of the plants. And differences in feeding and growth of larvae have also been shown to be more dependent on the nutritive value than on the taxonomic range of plants used (Fox and Macauley 1977, Onuf et al. 1977).

Table 3. True and false foodplant genera of *Callosamia promethea* in Southern Michigan[a]

PINOPSIDA	MAGNOLIOPSIDA cont.	MAGNOLIOPSIDA cont.
Pinidae	Styracaceae	Hamamelidae
Pinaceae ?	*Styrax*	Hamamelidaceae
Pinus ?	*Halesia*	*Liquidambar*
Thuja ?	Symplocaceae	Anacardiaceae *
	Symplocos	*Rhus* *
MAGNOLIOPSIDA	Ericaceae ?	Juglandaceae *
	Azalea?	*Carya* *
Magnoliidae	Salicaceae ?	Fagaceae ?
Berberidaceae ?	*Populus* ?	*Quercus* *?
Berberis *?	*Salix* ?	Betulaceae ?
Lauraceae	Rosidae	*Betula* ?
Lindera	Rosaceae	*Corylus* *?
Sassafras	*Prunus*	Myricaceae ?
Magnoliaceae	*Amygdalus* ?	*Myrica* ?
Liriodendron	*Malus* ?	Ulmaceae *
Magnolia ?	*Pyrus* ?	*Ulmus* *
Ranunculaceae *	Cornaceae *	*Celtis* *
Thalictrum *	*Cornus* *	Asteridae
Dilleniidae	Vitaceae *	Oleaceae
Tiliaceae ?	*Vitis* *	*Syringa*
Tilia ?	Aceraceae *?	*Ligustrum* *
Ebenaceae	*Acer* *?	*Fraxinus*
Diospyros		Rubiaceae
		Cephalanthus
		Caprifoliaceae ?
		Viburnum ?
		Lonicera *

[a]* = considered a probable false foodplant in the present survey. ? = previously listed by Elliot and Soule (1902), Ferguson (1972) and/or Tietz (1952), but dubious in light of recent reports.

The situation with regard to *C. promethea* is considerably different from another giant silkworm moth we have studied in southern Michigan. The polyphemus, *Antheraea polyphemus*, has 13 known foodplant species in this area belonging to nine genera (Wagner and Mayfield 1980), but not one of them is the same as any of those we regard as true foodplants for promethea. In general, *C. promethea* feeds on low shrubs, saplings, and stump sprouts, while *A. polyphemus* feeds, with one exception, on full-sized trees. Also *A. polyphemus* forms and attaches its cocoon in several different ways, unlike *C. promethea*, which forms its cocoons in a uniform manner. *A polyphemus* is a much more widely ranging species than *C. promethea*, occurring from Canada to Mexico and from coast to coast, while *C. promethea* exists only in the eastern part of North America. *C. promethea* does have a wider range, however, than its congeners, *C. angulifera* and *C. securifera*, both of which, in nature at least, tend to be confined to single foodplants, tulip tree and sweet bay respectively. Thus part of the success of *C. promethea*, which is a much more abundant species than the tulip tree or the sweet bay moths, may be due to its polyphagous nature.

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