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FOODPLANT AND OVIPOSITION RECORDS FOR PANAMANIAN LYCAENIDAE AND RIODINIDAE

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ABSTRACT. We present larval foodplant and female oviposition records for 15 Panamanian butterfly species in the Lycaenidae and Riodinidae. Many of these species feed on reproductive parts of plants, e.g. flowers, rather than foliage. Some species are facultatively myrmecophilous, and one species may have an obligate relationship with ants. We discuss possible biological consequences of flower-feeding for lycaenid butterflies.

Larval foodplant records of Lycaenidae and Riodinidae are of particular interest for several reasons. First, many of these species feed as larvae on the flower-buds, flowers, and fruits of plants (Downey, 1962), and thus may exert stronger selective forces on their foodplants than foliage feeders (e.g. Breedlove & Ehrlich, 1968). Plant responses may include changes in flowering phenology (Breedlove & Ehrlich, 1968; Ehrlich et al., 1972) and synthesis of a variety of secondary compounds in flowers (Dolinger et al., 1973). The selective forces acting in turn on the butterflies, however, are unclear at present. Second, larvae of these related families utilize as a group a particularly broad spectrum of foods, including insect prey (Ehrlich & Raven, 1964). In addition, some species are unusually polyphagous (Downey, 1962). And third, the larvae of many lycaenid and riodinid species are tended by ants, a putatively mutualistic interaction (e.g. Hinton, 1951; Callaghan, 1977).

Larval foodplant records for Neotropical lycaenids and riodinids are more poorly known than those for other biogeographical regions (Downey, 1962). Many more records for this species-rich fauna need to be accumulated before general patterns of biological interest can be deduced or tested. We report here foodplant records that we made

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on Barro Colorado Island (BCI), Panama, a research station administered by the Smithsonian Tropical Research Institute, and in surrounding areas of Panama Province, Republic of Panama, during the past few years. We then discuss some possible consequences of flower-feeding by larvae and comment on the extent of myrmecophily in Panamanian riodinids.

Identification and deposition of insects and plants are as follows: Plants were identified by the junior author, by comparison with specimens in the Missouri Botanical Garden's herbarium in Ancon, Panama, and by various visiting botanists. Gordon B. Small of Balboa, Panama, and the senior author identified the butterflies by comparison with type specimens in the U.S. National Museum, with photographs of type specimens in the British Museum (Natural History), and with published plates and descriptions. Taxonomic notes are added where necessary to clarify identifications. Many of the species do not have valid generic names, and are placed for convenience in *Thecla* F., which correctly applies to species in a different tribe (Eliot, 1973). Larval head capsules, pupal skins, and adult specimens for species denoted by "Aiello lot #" are deposited in the collection of the junior author. Adult specimens and some preserved immature stages of other species are retained in the collection of the senior author.

We have had difficulty rearing many of these species from the egg with the notable exception of *Arawacus aetolus* Sulzer. As a result, some of our "foodplant" records are oviposition sightings. Other workers may be able to confirm whether or not these plants are suitable larval foodplants.

Lycaenidae

Arawacus aetolus lincoides (Draudt): We saw females ovipositing on the leaves and twigs of *Solanum lancaeifolium* in Gamboa on 10 September 1979, and 6 & 10 December 1979. Unlike many other lycaenids, females do not lay eggs on flowers or maturing fruits. Females oviposit readily on this plant in the lab, and we have reared more than a hundred individuals from eggs on the leaves of *S. lancaeifolium*. The ithomiine butterflies, *Mechanitis lysimia macrinus* and *M. polymnia isthmia* also oviposit on this plant species.

Although third and fourth instar larvae are often tended by the ants *Ectatomma tuberculatum*, *E. ruidum*, and *Pheidole* sp., they are reared easily in the lab without ants. A final (fourth) instar larva that we found in Gamboa on 2 January 1980 was tended by *Pheidole* and had a chalcidid wasp flying around it. This larva pupated between 4 & 6 January, and a chalcidid emerged on 25 January.

On 18 January 1980 we watched a female of *A. aetolus* oviposit on

Solanum ochraceo-ferrugineum along the road to Cerro Campana at 500 m. We found two other eggs and seven larvae on this plant. Two males and a female reared on leaves eclosed on 10 & 12 February. We switched another larva to *S. lancaefolium* after the third molt. It pupated on 4 February, and eclosed as a female on 14 February. In addition, the female that had oviposited on *S. ochraceo-ferrugineum* laid another 49 eggs on *S. lancaefolium* in the lab. Thirty-five of these eggs were reared to adult.

Boyce A. Drummond III reared three specimens of *A. aetolus separata* Lathy in Limoncocha (Rio Napo), Ecuador, on *Solanum coconilla*. A larva that he found on 4 June 1974 pupated on 8 June, and eclosed as a male on 19 June. Two larvae that he found on 19 June 1974 pupated on 26 June, and eclosed on 8 July (female) and 9 July (male).

Guppy (1904) reported the larval foodplant of the nominate subspecies from Trinidad as cocoa, but Kaye (1921) corrected the record to *Solanum* sp. It is likely that larvae of *A. aetolus* feed on a number of species of *Solanum* throughout its range.

Taxonomic note: Our identification of this species (and its subspecies) is based on an unfinished ms. of H. K. Clench. The senior author is completing this paper.

Tmolus echion (L.): We found a larva on leaves of *Stigmaphyllon lindenianum* (Malpighiaceae) on BCI on 31 May 1978. It pupated on 16 June, and eclosed on 29 June (Aiello lot 78-67).

A female of *T. echion* oviposited on a flower of *Aphelandra deppeana* (Acanthaceae) among numerous ants (*Ectatomma* sp.) on Taboga Island 12 miles off the southern coast of Panama on 24 December 1978. The ants were feeding on secretions from extra-floral nectaries on the flower bracts. We also found two egg shells on this flower, plus damage similar to that produced by lycanid larvae. No larvae were reared.

T. echion is of economic importance because it feeds on flowers of the weed *Lantana camara* (Verbenaceae). There are specimens reared from *L. camara* in the United States National Museum from Brasil (Sao Paulo, Rio de Janeiro, and Minas Gerais) and Costa Rica (Turrialba). Koebele introduced *T. echion* to Hawaii from Mexico about 1902 to control this weed (Swezey, 1913), and it was later introduced (1922–1923) (now extinct) to the Fiji Islands for the same reason (Robinson, 1975). Other larval foodplants of *T. echion* are the flowers of *Cordia sebestena* (Boraginaceae), *Datura arborea* (Solanaceae), *Solanum nodiflorum* (Solanaceae), and *S. sanitwongsei* in Hawaii (Zimmerman, 1958), and *Mangifera indica* (Anacardiaceae) in Brasil (Lima,

1936, 1947). Zimmerman (1958) and Lima (1947) list parasitoids of this species.

Taxonomic note: The ventral wing pattern of *T. echion* is remarkably similar to that of *Strymon basilides* (Geyer), and has been a continuing source of confusion. We follow Hewitson (1862–1878), Godman & Salvin (1887–1901), Draudt (1919–1920), and Clench (1961) in considering *T. echion* to be a senior synonym of *Thecla crolus* Cr., and not a senior synonym of *S. basilides* (but see Kaye [1908] and Lathy [1926] for a different opinion). *T. echion* lacks the red-orange spot of *S. basilides* located dorsally at the margin of cell Cu_1-Cu_2 .

Larval foodplant records of *T. echion* and *S. basilides* have been somewhat confused as a result of the difficulty in identifying these species (e.g. Harris, 1927; Carter, 1933; Ehrlich & Raven, 1964). To date, however, *T. echion* has been recorded reliably only from dicots, and *S. basilides* only from monocots (see below).

"Thecla" mathewi Hew.: A larva feeding on a fallen corolla of *Cydistia* sp. (Bignoniaceae) pupated on 18 June 1979. A female eclosed before 4 July 1979.

Cyanophrys herodotus (F.): We found a green larva on the leaves of *Mikania* sp. (Compositae) on BCI on 7 May 1980. No flowers were present on the plant, and the larva was successfully reared on the leaves. Pupation took place on 13 May; a male eclosed 25 May (Aiello lot 80-47).

We observed a female bending her abdomen into the flowers of the introduced plant, *Clerodendron paniculatum* (Verbenaceae) on BCI on 1 August 1977 but could find no eggs. Females laid single eggs next to a bud of *Lantana camara* (Verbenaceae) on BCI on 7 June 1979 and on a flower stalk of *Cornutia grandifolia* (Verbenaceae) in Gamboa on 18 June 1979. Neither egg was successfully reared, but we infer that flowers of verbenaceous plants are an important larval food of this common species in Panama.

In Brasil, *C. herodotus* feeds on the flowers of *Mangifera indica* (Anacardiaceae) (three references in Silva et al., 1967–1968).

"Thecla" near enenia Hew.: We found a yellow and brown larva on the yellow flowers of *Mascagnia hippocratioides* (Malpighiaceae) on BCI, 31 May 1980. After it molted on 2 June we gave it flowers of a cultivated plant, *Hibiscus rosa-sinensis* (Malvaceae) (flowers of *Mascagnia* were no longer available). The larva ate the *Hibiscus* flowers and pupated 13 June. A small male eclosed at 1400 hours on 24 June. After eclosing the butterfly extruded and withdrew the brush organs (*sensu* Eliot, 1973) at the tip of its abdomen (Aiello lot 80-62).

Taxonomic note: This undescribed species is closely related to *enenia* Hew. Males possess a scent pad at the end of the forewing discal cell; whereas, males of *enenia*

lack the scent pad. Otherwise, the two species are similar; future identification should pose no problems. We have seen specimens of *enenia* from Paraiba (Brasil), "Amazon," and Guiana. The new species is known from Panama and Honduras (Museum of Comparative Zoology).

"*Thecla*" *ericusa* Hew.: Kim Steiner reared a male and female of this common, widespread species on flowers of *Stigmaphyllon lindenianum* (Malpighiaceae). A larva that he found on 11 November 1977 at Gatun pupated on 19 November and eclosed as a female. A larva that he found on 8 April 1980 at Frijoles pupated on 13 April and eclosed as a male on 21 April. *T. ericusa* has been reared in Brasil from flowers of *Antigonum leptopus* (Polygonaceae) (Lima, 1947), where it is parasitized by a wasp of the genus *Tetrastichus*. In addition, there are four specimens in the U.S. National Museum from Trinidad and Tobago that were reared on the flowers of *Dioclea guinensis* and *Gliricidia* sp. (Leguminosae).

Taxonomic note: Identification of species in the *spurina-brescia* species groups (to which *T. ericusa* belongs) has been difficult (Clench, 1961, 1970). Draudt (1919-1920) noted that the proximal part of the duplex male scent pad of *T. ericusa* "has disappeared except some traces of it." This character is distinctive and is the primary basis of the present identification. Although the ventral wing pattern of the Brazilian type specimen (probably from the area around Rio de Janeiro) is considerably different from those in Panama, specimens with "intermediate" wing patterns occur in Bolivia, Colombia, and Venezuela. Male and female genitalia are indistinguishable among localities and differ only slightly from those of the apparently parapatric *brescia* Hew.

"*Thecla*" *hesperitis* (B. & D.): We found two larvae inside fallen corollas of the liana *Cydista* sp. (Bignoniaceae) on BCI on 27 May 1979. Three nematomorph worms emerged from one larva on 30 May. The other larva molted to the final instar on 1 June, and pupated on 15 June. Eclosion occurred 27 June (Aiello lot 79-78).

Beutelspacher (1972) reared this widespread, common species from the leaves of *Tillandsia caput-medusae* (Bromeliaceae) in Mexico.

Strymon basilides (Geyer): A female laid an egg on an inflorescence bract of *Heliconia latispatha* (Musaceae) in Gamboa on 16 October 1979. We had found literally hundreds of eggs on the flowers and bracts of this common species and on the bracts of *H. wagneriana* during August 1979 when these plants first blossomed. Although *H. latispatha* continued to produce flowers until at least January, we found only occasional eggs on this plant after mid-September. Larvae brought into the lab on 6 & 8 September 1979 fed on flowers of *H. latispatha* by boring into them. One pupated on 15 September and another on 19 September. They eclosed as females on 23 & 27 September, respectively.

We watched a female lay a number of eggs on *Xiphidium caeruleum* (Haemodoraceae) in Gamboa on 21 September 1979 and found three larvae which had bored into the immature fruit of this plant. A larva pupated on 8 October and eclosed as a female on 17 October.

Larvae of *S. basilides* appeared to have Newcomer's glands on the 7th abdominal segment (Newcomer, 1912), but we found no ants associated with them. We reared no parasitoids, although others have (Harris, 1927; Carter, 1933; Lima, 1947).

This species has been raised on the bromeliads *Ananas cosmosus* (= *A. sativus*) and *Aechmea bracteata* (Harris, 1927; Carter, 1933; Beutelspacher, 1972; Silva et al., 1967–1968, list 38 Brazilian records) and will probably be recorded from the flowers and fruits of other monocots.

Taxonomic note: Confusion of foodplant records due to misidentifications of *S. basilides* and *T. echion* are noted under *T. echion*. A second source of confusion is that a few undescribed sibling species of *S. basilides* occur in various parts of its range, and some of the numerous records of pineapple (*A. cosmosus*) as a larval foodplant may refer to one or more of these sibling species.

The morphology of the male and female genitalia of *basilides* as well as adult behavior clearly indicate a close relationship with *melinus* Hbn., the type species of *Strymon*. *Basilides* will eventually be placed in *Strymon* or a closely related genus.

S. basilides has been misspelled as *S. basalides* by many workers (see Comstock & Huntington, 1959).

Strymon yojoa (Reakirt): We observed females bending their abdomens into flowers and buds of *Desmodium axillare* (Leguminosae) on BCI on 19 June and 15 July 1977 but could not find any eggs. On 19 July 1977, however, we found three larvae boring into the fruits of *D. axillare* where we had seen oviposition behavior. Although the larvae apparently had Newcomer's glands, no ants were tending them. The larvae fed in the lab on fruits and flowers of *D. axillare* and pupated on 23–27 June. Eclosion occurred on 4 July (two males) and 7 July (sex undetermined).

A female deposited a single green egg on an unopened bud of *Kohleria tubiflora* (Gesneriaceae) in Gamboa on 3 December 1979. We took the egg back to the lab but could not find the larva after it hatched. Although we found two eggshells on this plant, plus damage to buds and flowers typical of that done by lycaenids, we could not find any larvae.

This species has been reared previously from *Hibiscus tubiflorus* and *Hibiscus* sp. (Malvaceae) in Mexico (Kendall, 1975).

Michaelus vibidia (Hew.): We collected a yellow larva with brown stripes in a fallen corolla of *Pithecoctenium crucigerum* (Bignoniaceae) on BCI on 6 June 1978. The larva pupated on 10 June. The adult eclosed 24 June (Aiello lot 78-65).

Pseudolycaena damo (Druce): A female oviposited on a stipule of *Pterocarpus* sp. (Leguminosae) on BCI on 7 June 1979. The egg hatched on 11 June, but the larva died two days later. This species has been reared from *Croton niveus* (Euphorbiaceae) in Mexico (Kendall, 1975), but on BCI we found no immature stages of *P. damo* on *Croton bilbergianus* despite extensive searching.

"*Thecla*" *hemon* (Cramer): A female laid three eggs on twigs of *Inga pezizifera* (Leguminosae) on BCI on 8 June 1979. We found five other eggs on this plant. Although four eggs hatched, none was successfully reared. We also found three last instar larvae, presumably *T. hemon*, feeding on the leaves of this same plant on 15 June 1979, but they produced tachinid fly puparia from which no adult flies emerged. Previously recorded larval foodplants for *T. hemon* are *Inga* sp. in Brasil (Müller, 1878; Hoffman, 1930; Silva et al., 1967-1968) and the young shoots of *Theobroma cacao* (Sterculiaceae) in Trinidad (Guppy, 1904).

Riodinidae

Argyrogrammana crocea G. & S.: We found a flat orange-brown larva between two overlapping leaves of *Rheedia edulis* (Guttiferae) on BCI on 28 April 1979. The larva fed by scraping the leaf surface without disturbing the veins, which contain a white latex. The larva stopped eating and turned orange on 2 May. It made a silk girdle, consisting of numerous radiating strands, and pupated on 5 May. The pupa resembled the larva in color and pattern. Eclosion occurred on the evening of 17 May (Aiello lot 79-30).

Audre domina Bat.: A female laid four blue eggs on a twig of *Vismia baccifera* (Guttiferae) near several ants (*Ectatomma* sp.) that were tending membracids on Pipeline Road (five miles north of Gamboa) on 11 June 1977. An ant approached the female, and she flew away. We found 10 other eggs on this plant but found neither eggs nor ants on neighboring plants of the same species. The eggs hatched on 24 June, and the larvae died three days later.

A female flew about plants of *Turnera panamensis* (Turneraceae) on BCI on 18 May 1979 but did not land until she encountered a group of *Ectatomma tuberculatum*. As soon as she landed, several ants approached her. She flew away but returned several seconds later. This time as the ants approached her abdomen, she turned and presented them with her opened wings. While the ants repeatedly attacked her wings with their mandibles, she laid several blue eggs on the branch among some older darker ones. She then flew off to another group of ants. Four of the older eggs hatched on 19 May and

molted on 23 May. These second instar larvae, which resembled ant brood, did not feed and died a week later. The eggs laid on 18 May hatched on 31 May, but the larvae died shortly afterwards.

Last instar larvae of two species of *Audre* (= *Hamearis*, in part) pupate and diapause in ant nests (Bruch, 1926; Bourquin, 1953; see Hemming, 1934 for generic taxonomy), and we suspect that *A. domina*, which is apparently single-brooded in Panama, also has an obligate myrmecophilous relationship, including diapause in ant nests.

Thisbe irenea Stoll: Females oviposited on leaves and twigs of *Croton bilbergianus* (Euphorbiaceae) on BCI on 15 June 1977, on 6, 10, & 13 July 1977, and on 29 May 1979. We also found numerous larvae feeding on the leaves of this plant and reared three males and three females. Larvae fed only on younger leaves that had a pair of secreting extra-floral nectaries at their base on the underside of the leaf. Between feeding bouts, larvae rested along major leaf veins with their heads next to a nectary. We found at least five ant species tending both the nectaries and the larvae, although larvae are easily reared in the lab without ants. The larvae have pairs of "tubercles," which are occasionally everted, near their head and at their caudal end. These glands may be homologous with the "honey glands" and "eversible tubercles" reported by Ross (1966). Pupae have polyp-like glands that are tended by ants and have two black spots that give the appearance of holes through which parasitoids emerged. Pupae of the African lycaenid *Argiolaus maesa* also have spots that resemble parasitoid emergence holes (Hinton, 1955). Parasitoids of *T. irenea* include a chalcidid (*Spilochalcis* sp.) and a tachinid fly. In addition, one tachinid puparium had two small holes in it indicating that a hyperparasitoid had emerged from it.

DISCUSSION

Most of the lycaenids we reared oviposit and feed on reproductive parts of plants. A notable exception is *A. aetolus*, which appears to be an obligate foliage feeder; in both the field and lab, females do not oviposit and larvae do not feed on flowers and fruits of their solanaceous foodplants. *T. hemon* and *P. damo* may also feed primarily on foliage. We also found late instar larvae of *T. echion* and *C. herodotus* feeding on leaves, but females of these species have been seen ovipositing only on plant reproductive parts. On the other hand, we have never seen riodinids ovipositing on flower-buds, flowers, or fruits.

The biological consequences of flower-feeding for lycaenid butterflies, particularly in relation to polyphagy, have not been explored.

We tentatively propose three possible consequences that merit further investigation. First, flower-feeding may allow lycaenids, at least as early instar larvae, to feed on plants whose leaves are not available to butterfly larvae (perhaps due to chemical defenses). For example, Ehrlich & Raven (1964) list plant families including the Bignoniaceae, Gesneriaceae, and Begoniaceae that are not used, or are under-utilized by butterfly larvae. We recorded three flower-feeding lycaenid species (*M. vibidia*, *T. hesperitis*, and *T. mathewi*) on Bignoniaceae and one oviposition record (*S. yojoa*) on a flower in the Gesneriaceae. In addition, Zikan (1956) reared *Thecla azaria* Hew. from the flowers of a plant in the Begoniaceae. Many more records will be needed before we properly can assess the range of larval foodplants used by these insects. For evident reasons, we consider it imperative that foodplant records include the plant part fed upon.

A second consequence of flower-feeding is that it may allow individual lycaenid species to feed on a variety of unrelated plants. The range of seemingly unrelated foodplants used by some of the flower-feeding lycaenids discussed in this paper is striking and would be considered highly unusual for butterflies in other groups. In addition, one of the most polyphagous butterfly species known (*Strymon melinus* on 46 genera in 21 families [Howe, 1975]) is a flower-feeding lycaenid. Such polyphagy would be particularly advantageous to weedy, multivoltine species that frequently encounter changing habitats or seasons.

A third possible consequence of flower-feeding is that the abundance and diversity of adult lycaenid butterflies might "track" the abundance and diversity of flowering plants. The peak of flowering on BCI occurs at the end of the dry season (February to May) (Croat, 1978, p. 35), which corresponds to an increase of about two orders of magnitude in the abundance of lycaenid butterflies, at a time when many species in other butterfly families show a marked decrease in abundance (pers. obs.). A consequence of dry season abundance, in turn, is dispersal by strong, sustained dry season trade winds (Robbins & Small, 1981).

Myrmecophily has been recorded in many lycaenid species (e.g. Hinton, 1951) but for only seven species of Neotropical riodinids (Callaghan, 1977). We note that in addition to the records presented in this paper, we have encountered myrmecophilous larvae of at least five other riodinid species but were unable to rear them. We agree with Callaghan (1977) that a large proportion of the Neotropical riodinids will prove to be myrmecophilous.

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