COEVOLUTION OF PLANTS AND HERBIVORES: PASSION FLOWER BUTTERFLIES

Woodruff W. Benson[1,2], Keith S. Brown, Jr.[1,2], and Lawrence E. Gilbert[3]

Plant specific insect herbivores are remarkable not only in their ability to locate and identify the appropriate host, but also in that they very often show a "botanical instinct" (Brues, 1920, 1924): closely related insects choose closely related plants. For both insects and plants this statement holds true primarily at the level of higher taxa, and is an outcome of chemical similarities among related botanical groups (Kusnezov, 1929).

The generation of higher level taxonomic correlations between insects and their host plants is thought to be due to concurrent evolution. A hypothesis as to just how coevolution between insects and plants in the past resulted in these present day patterns was suggested by Brues (1920) and developed fully by Ehrlich and Raven (1965) on the basis of butterfly host plant data. The model involves adaptive radiation by plant lines which evolve effective herbivore deterrents, followed by adaptive radiation of insect lines evolving successful methods to circumvent these defenses. Additional evidence on the importance of plant chemistry as a coevolutionary factor in the radiation of herbivorous insects has been presented by Ehrlich (1970), Breedlove and Ehrlich (1968, 1972), Dolinger et al. (1973), and Edgar et al. (1974).

We believe that searching for patterns among insect/plant relationships at finer taxonomic levels (populations, races, species within a tribe rather than tribes and sub-families or families within orders) might help further in the understanding of the relation between evolutionary historic events and on-going dynamic processes of coevolution. In this paper we examine in detail the interactions between the species of a tribe of butterflies, the Heliconiini (Nymphalidae), and a family of plants, the Passifloraceae. We bring together as much up-to-date information on the systematics and ecology of heliconiines and their host plants as possible in hope of answering the following general questions:

1) Were the taxonomic correlations described for butterflies and their host plants (Ehrlich and Raven, 1965) generated only once as butterflies radiated onto already diverse angiosperms, or did multiple adaptive radiations continue within such complexes as the heliconians and the Passifloraceae as both plants and insects evolved?

2) To what extent has herbivory molded the characteristics, especially the taxonomically relevant morphology of natural hosts?

3) Is the coevolutionary contest between insects and their hosts sufficiently dynamic in ecological or recent evolutionary time for racial or populational (i.e.,

geographical) differentiation to be found with respect to coevolved relationships within systems composed of a single insect species and its host plants?

Heliconian butterflies are common, generally successful members of the Neotropical fauna. They are usually regarded as unpalatable to vertebrate predators (Brower et al., 1963; Brower and Brower, 1964), and have adopted gaudy wing coloration and conspicuous behavior patterns to advertise this property. Most are prominent models in local Batesian and Müllerian mimicry rings and have been the subject of many classical studies related to mimicry. On the whole, the cladistics of the Heliconiini are well understood (Emsley, 1963, 1965; Brown, 1972, 1975; Brown and Mielke, 1972). The larvae seem to be uniquely restricted to foodplants in the family Passifloraceae, and as the heliconians are the only major butterfly taxon maintaining this exclusive relationship, they have been termed "Passion Flower Butterflies" (Turner, 1973).

The most recent revision of the Neotropical Passifloraceae (Killip, 1938), while not completely up-to-date, provides an excellent systematic background for interpreting the radiation of the family. Killip's monograph is classificatory, and the species and genera are apparently ordered solely on the basis of key characters, with more specialized traits representing the more evolved species being considered near the beginning of the key. That this can be used to approximate the evolution of species groups is simply a consequence of the robustness of the Darwinian theory (Darwin, 1872). We have introduced only a few changes to the order used by Killip, and these are justified in the Appendix.

The host plant records presented here have come from field observations made in many parts of the Neotropics by ourselves and by co-workers, and from reports in the literature. These data represent the oviposition choices of free-living heliconian females for naturally sympatric passifloraceous species. We report here these

data and interpret them in terms of possible coevolutionary processes. A future paper will treat competitive interactions among heliconian populations for larval host plants.

SYSTEMATICS AND EVOLUTION OF THE HELICONIINI

To evaluate the evolutionary history of the heliconians, we have relied heavily on the works of Emsley (1963, 1965), Brown (1972, 1975), and Brown and Mielke (1972). Our criteria have been based on (1) morphological comparisons and (2) the rationale that small morphologically distinct species groups and genera represent remnants of ancient radiations, and large groups of structurally similar species are the products of more recent radiations of new types. The two methods give very comparable results which can be summarized as follows:

From early radiations, represented today by eleven mostly widespread species divided among six primitive genera (*Philaethria, Dione, Podotricha, Agraulis, Dryadula,* and *Dryas,* in order of their probable evolutionary progression but not necessarily direct lineage) a line gave rise to the ancestors of a still primitive but radiating group of a dozen species (*Eueides*) and of four little-known primitive species of *Heliconius.* The reticulate evolution of this second line has subsequently produced a diversity of species groups and species of the genus *Heliconius* (*H. xanthocles*; wallaceiforms, four species; silvaniforms, five; melpomeneforms, nine; and eratoforms, seven species), apparently climaxing with the *sara-sapho* group (nine species), which shows many unique features and appreciable karyological divergence from the main body of the genus (de Lesse, 1967; Brown, Emmel and Suomalainen, in prep.).

Two offshoots of *Heliconius* probably merit generic separation. The *aoede*-group of three species is being given a name by J. R. G. Turner. The group seems of comparable antiquity to the branching of the *Eueides* line, although it possesses a large

number of characters transitional to *Helico-nius*. The wallaceiform-derived species *Laparus doris* combines polychromatism with karyological variation (de Lesse, 1967; Emmel, pers. comm.) and probably increased palatability (Brower et al., 1963; Benson, 1971). Thus, the herbivore part of the system includes sixty-six species, with several hundred geographical races.

SYSTEMATICS AND EVOLUTION OF THE PASSIFLORACEAE

Following current concepts of angiosperm evolution and using Killip's (1938) monograph as a starting point, we have assumed that long-lived woody forest plants with generalized morphology and simple, multistaminate flowers are more primitive, and short-lived herbaceous, ecologically adaptable plants with more complicated morphology and flower structure (showing specialization or reduction of elements) are more recent derivatives of passion flower evolution. Using these criteria, and refraining from making detailed inferences concerning cladistic relationships, we suggest that the important taxa which include the majority of the more than 360 Neotropical species originated in the following order:

The three small, presumably most primitive genera all consist of slow-growing, woody, often shrubby lianas or bush-like forest plants. The flowers have four styles and five to eight or more stamens. (In contrast, *Passiflora* have three styles and five stamens.) These genera are *Mitostemma*, a poorly known group from the forests of Guiana and southeastern Brazil (probably bitypic); the closely related *Dilkea* (Fig. 1), limited to Amazonian-type forests, including northwestern Colombia and Darién (A. Gentry, *in press*); and the east Brazilian species (probably two) of the biphyletic *Tetrastylis* (Figs. 2, 3 and 5).

The genus *Passiflora* itself consists of 22 subgenera, three of which (*Astrophea*, *Granadilla*, and *Plectostemma*) are diverse enough to be divided into well-marked sections. The most primitive subgenus is

Astrophea, which is largely composed of woody lianas, but also includes some bushes and even trees. The members of this subgenus usually have reduced extrafloral nectaries and few meristems,[4] and frequently bear inflorescences of relatively simple structure. *Astrophea* species are characterized by large biomass of older leaves on individual plants and have a dispersed distribution in the forest canopy. Killip (1938) considers this group as very distinct and hints (p. 520) that it is almost worthy of generic status. The six sections are mostly well defined, although none are very large (up to 17 species), and the species within each section are in general very homogeneous and difficult to separate.

A great deal of diversity is demonstrated by the very large subgenus *Granadilla*, whose members are typically robust, fast-growing, and relatively long-lived vines of forest edges and clearings. The flowers are well developed and showy, bracts and stipules are well differentiated, and extrafloral nectaries, especially on the petioles, show a variety of structure. This group includes most of the fruit-bearing and ornamental species cultivated by man.

A number of smaller subgenera (*Polyanthea, Dysosmia, Dysosmioides, Tacsonioides, Adenosepala, Calopathanthus,* the Central American "*Tetrastylis*," and the ecologically very important *Distephana*), showing varying degrees of primitiveness and specialization, have with *Granadilla* spread out over much of the American tropics and adapted to thrive under many types of soil and climatic conditions. Of these only *Distephana* species (Fig. 9) regularly form a conspicuous part of any flora. Because of the relatively isolated position of *Distephana*, its lignified stems, and the positioning of the styles as in *Astrophea*, we consider this subgenus as more ancient than *Granadilla*.

Several small, high-altitude or other-

---

[4] Throughout this paper, the word "meristem" is employed to indicate "fresh vegetative growth," especially the last 15 cm of a growing branch of a vine.

FIGS. 1–10. Interactions between Heliconiini and Passifloraceae. (1) A pair of eggs of *Heliconius erato* on a small branch of *Dilkea*, a primitive passifloraceous genus. *H. erato* generally prefers meristems of *Passiflora* (*Plectostemma*) but also often attacks other passion vines. (2) Egg of *Heliconius nattereri* on the tip of a tendril growing from the meristem of its sole host plant species, *Tetrastylis ovalis*. *H. nattereri* is a primitive species, as is its host plant, and both are restricted to a small area in eastern Brazil. (3) Two eggs of *H. nattereri* on the tips of tendrils of *T. ovalis* (oviposition mode F). (4) A raft of approximately 800 eggs of *Laparus doris,* probably laid by more than one female, on the upper surface of a leaf of *Passiflora* (*Granadilla*) *ambigua* (oviposition mode B). Note the scars left by eggs which have been removed. (5) A meristem cluster of about 40 eggs of *Heliconius sara* on *Tetrastylis ovalis* (oviposition mode D). (6) An egg of *Heliconius cydno* (a melpomeneform with oviposition mode F) surrounded by *H. sara* eggs on a meristem of *Passiflora* (*Plectostemma*) *auriculata*. (7) A typical raft of regularly spaced eggs of *Eueides vibilia* under an old leaf of

wise geographically limited subgenera (*Granadillastrum, Deidamioides, Tacsonia, Rathea, Tacsoniopsis, Murucuja, Psilanthus, Pseudomurucuja,* and *Chloropathanthus*) are very rarely sympatric with heliconians (we have found early stages only on the last three, two of which are Caribbean). However, the bitypic subgenus *Tryphostemmatoides* (Fig. 10), which has a restricted range between Costa Rica and western Ecuador, is an important heliconian host plant.

The most evolved major group is the large subgenus *Plectostemma*. These are typically fragile forest edge vines with tender photosynthetic stems and are normally found associated with high humidity conditions. The flowers are usually small and often lack morphological elements such as petals. Extrafloral nectaries are typically limited to leaf surfaces or may be lacking. *Plectostemma* seem to be less persistent than *Granadilla*, although many are widespread and common. In spite of their individual small sizes, they probably represent an appreciable fraction of passion vine productivity in many areas.

FOODPLANT DATA

The foodplant data are summarized in Table 1, and the complete data with additional information are tabulated in the Appendix. The observations have been ordered according to the presumed taxonomic positions of the different higher taxa and the species within them, with the more primitive taxa preceding more advanced ones. The lined columns in the tables represent the approximate limits of the five recognizable overlapping radiations of the heliconians. These are in order of their presumed sequential appearance within the respective evolutionary lines. However, the postulated phyletic relationships among the higher taxa as discussed in the text are not indicated in the tables, and for this reason the data should be read with caution.

We gratefully acknowledge the foodplant observations provided by J. R. G. Turner (Stony Brook), John Smiley (Austin), C. H. Dodson (Miami), G. Lamas M. (Lima), S. S. Tillett (Caracas), and L. Otero (Rio de Janeiro). Literature records were obtained from Müller (1886), Herrera (1950), Beebe et al. (1960), Alexander (1961), Ross (1964), Brown and Mielke (1972, including information from C. M. Biezanko), and Muyshondt et al. (1973). About 90% of the records represent original observations of the authors, and these are for the most part previously unpublished.

ADAPTIVE RADIATION IN THE HELICONIANS

We now wish to develop an ecological scenario for the evolution of the heliconians, making inferences from the ecological and taxonomic status of extant species. Our aims are to identify as nearly as possible the historic origin of the heliconian × passion vine interaction, to postulate pathways of radiation in host plant use which

---

←

Passiflora (Astrophea) mansii (oviposition mode C). (8) A coevolutionary short-circuit? A female *H. ethilla* visits a flower of *Passiflora (Granadilla) kermesina*. The large magenta flowers provide nectar for *ethilla*, which in turn may carry pollen on its wings and fertilize the flowers of other plants. However, larvae of *ethilla* also feed upon and greatly damage *kermesina* vines. (9) A similar but much more specialized mutualism exists between *Heliconius wallacei* (and also *H. burneyi*) and *P. (Distephana) coccinea*. The flowers provide much energy for the adults which are highly adapted to seek them out, and the butterflies appear to serve as pollinators. In addition, the meristems of larger *Distephana* plants are probably the exclusive food of the gregarious larvae of these species. (10) Egg mimics on meristem tendrils of *Passiflora (Tryphostemmatoides) gracillima* consisting of deciduous (note one already fallen) yellow flower buds, which probably serve to discourage oviposition by *Heliconius erato*. Note also the bulbous yellow petiolar glands, which resemble eggs to a lesser degree and may too have a deterrent effect. (11) Egg mimics in the form of bright yellow petiolar glands and swellings on the stipules of *Passiflora (Granadilla)* cf. *guazumaefolia*.

TABLE 1. Summary of Heliconian groups and of the genera and subgenera of Passifloraceae used as larval host plants by each. Bold face numbers indicate the preferred plant taxa which are assumed to have been responsible for past radiation and current ecological success of the respective butterfly groups. Passiflora subgenera for which we have no records are given in the foot of the Table, along with the number of species in each (in parentheses), according to Killip 1938. A dash in the body of the Table indicates allopatry of the respective taxa.

Passifloraceous genera and subgenera	Usual habit and habitat*	Number of species in taxon, following Killip (or recent work)	Number of species already observed being used by the Heliconiini	Number of known insect-plant interactions (IX/75)	Philaethria	Dione juno	Dione moneta, glycera	Prodoticha	Agraulis vanillae	Dryadula phaetusa	Dryas iulia	Eueides (primitive)	Eueides (advanced)	Aoede-group	Hel. hierax, hecuba	Hel. xanthocles	Wallaceiforms	Laparus doris	Hel. nattereri	Silvaniforms	Transitional and melpomene-group	Hel. hermathena	Heliconius erato (red-banded forms)	Other erato- and charitonia-group	Sara-group	Sapho-group	TOTAL SPECIES
Number of species in group					3+	1	2	2	1	1	1	7	5	3	2	1	4	1	1	5	9	1	1	7	4	5	66
Species with known foodplants					3+	1	2	0	1	1	1	2	4	3†	0	1	4†	1	1	5	8	1	1	6	3	3	51
Mitostemma	A	3	1	1																							
Dilkea	A	5(2)	2	6																							
Tetrastylis	B	1(2)	2	8					1			1		3†					1	1					1		
Passiflora (Astrophea)	AB	47(>60)	17	50	7				2		4	3					1†			3	12		1	1†	11†	5†	
(Polyanthea)	D	1	1	1																							
(Distephana)	B	8	5	38	3	4			3				6				9†			11			1		1		
(Dysosmioides)	D	5	2	5					1		1																
(Dysosmia)	C	11	2	2					2																		
(Granadilla)¹	D	96(>100)	49	180	11	14	3		18	2	5		34			2		5		44	27		10		5		
(Calopathanthus)²	B	1	1	1																1							
(Tryphostemmatoides)	D	2	1	3							1												1		1		
(Psilanthus)	E	4	1	1			1																1				
(Pseudomurucuja)³	E	5	2	2																				2			
(Chloropathanthus)	D	2	1	1							1																
(Plectostemma)	DE	115(>100)	35	86		1	4		7	6	16		2							2	4		19	24			
("Tetrastylis") lobata⁴	D	1	1	2			1																	1	1		
TOTALS		364	123	387	21	19	9	0	34	8	28	4	42	3	0	2	10	5	1	70	43	2	33	28	20	5	

* A = Woody forest shrub or tree, B = Woody forest vine, C = Open country, D = Climbing forest-edge vine, E = Fragile humid-glade vine.
† Includes selected isolated records for sake of completeness. All other numbers represent reconfirmed interactions.
Subgenus followed by: ¹Tacsonioides (5); ²Grandillastrum (6), Tasconia (36), Rathea (1), Tacsoniopsis (1), Adenosepala (1), and Deidamioides (1); ³Murucuja (4); ⁴Astephia (1) and Apodogyne (1).

are consistent with known eco-evolutionary mechanisms, and to determine the ways in which different lines may have interacted with their hosts and each other to produce the diverse assemblage of heliconians observed today. We are aware of the philosophical difficulties in applying taxonomically derived phylogenies to mechanistic questions (Ehrlich, 1964); however, we feel that with our present knowledge of the morphological correlates of insect and plant adaptations, we can with some confidence begin to approach these kinds of questions. We do not seek to "prove" the phylogenetic sequences or the importance of ecological processes during evolutionary time. Rather we wish to show that the two approaches are compatible, and because of this, data gathered using one method can serve to evaluate interpretations made using the other. In a sense this is an exploratory essay, and it is hoped that as such it will stimulate more analytic thought on the relationships between phylogenetic evolution and ecological forces and how to formulate and test appropriate hypotheses.

I. The Origin of the Heliconians

Morphological and distributional data show that heliconians originated from a primitive nymphaline stock and radiated principally in tropical America. The one exception is the geographically isolated, probably heliconiine (Müller, 1886; Turner, 1967) genus *Cethosia* which feeds on Passifloraceae in the Indo-Australian region (Barrett and Burns, 1951; Corbet and Pendlebury, 1956). This perhaps dates the tribe from before the South American–Antarctica–Australia fission of over 60 million years ago, when diurnal Lepidoptera as well as flowering plants were probably still early in their evolution (Ehrlich and Raven, 1964; Raven and Axelrod, 1972).

The nymphaline tribe most closely allied to the Heliconiini is the Argynnini. Most argynnine larvae eat Violaceae, a plant family placed close to the Passifloraceae in

angiosperm evolution, and butterflies of the primitive argynnine genus *Euptoieta* attack both Violaceae and Passifloraceae, as well as at least eight other families used by other primitive nymphaline groups (Ehrlich and Raven, 1965; d'Araujo e Silva et al., 1968). The Acraeinae (primitive nymphalids which are in many respects analogous to the heliconiines) abound in Africa where they have radiated to use more than a dozen diverse plant families, including Violaceae and especially the Passifloraceae (Owen, 1972; van Someren, 1974); no heliconiines are known from Africa. New World acraeines attack *Eupatorium*, *Mikania*, and related Compositae (d'Araujo e Silva et al., 1968), not Passifloraceae. It is tempting to speculate that this pattern is more than casual and that the heliconiines are in some way excluding acraeines from passion vines in the Americas.

II. The Radiation of the Heliconians

Specialization on passion vines.—The original transition of the heliconiines or their precursors to Passifloraceae-feeding was probably taken by a large forest canopy butterfly similar to present day *Philaethria* species, during an evolutionary period when the canopy *Astrophea* group of *Passiflora* and other woody genera were likely to have been the dominant members of the family. It seems probable that very few insect groups were using this resource at that time (and, indeed, there are few which use it today), so that it represented a potentially "open" ecological niche. Like many other primitive Nymphalidae, *Philaethria* spreads out its reproductive effort over a large area. The females hunt out oviposition sites separately, often in the upper levels of the forest, and place eggs singly under older leaves, frequently several to a plant. The large biomass of the woody passion vines would have offered sufficient energetic incentive for the evolution of acceptance of these plants (Southwood, 1960, 1961), and specialization

would have been promoted as the chemical defenses were overcome. (We have observed a similar contemporary phenomenon with some especially common and available passion vines that are usually attacked by a very wide range of sympatric heliconians, including species which refuse to use the same plants where they are rare.) *Philaethria* continues to concentrate heavily upon woody passion vines today (Table 1), although some radiation to other large biomass species has occurred.

As new heliconian species were generated through normal evolutionary mechanisms (Mayr, 1963), displacement and ecological shifts may have occurred as a consequence of competition. The same force has probably played an important role in the extinctions and fragmentations of earlier heliconian radiations.

Division of plants by oviposition patterns.—*Dione juno* and the primitive *Eueides* lay large rafts of eggs on older leaves of their foodplants (Fig. 7), which are generally species more primitive than those used by their close relatives. We suspect that this strategy is derived, and relates to probable search times for finding suitable oviposition sites on their relatively dispersed hosts.

It seems likely that as *P.* (*Granadilla*) and *P.* (*Distephana*) species (Figs. 8 and 9) came into prominence along forest edges, other components of these radiating lines moved onto them and continued to spread out their eggs under older leaves as does *Philaethria*.

Only one *Eueides* species has included in its diet the last major radiation of *Passiflora*, the *Plectostemma*. Most plants of this subgenus are small and grow close to the ground, making them effectively unavailable for under-leaf or multiple oviposition. Two monotypic primitive genera (*Dryas* and *Dryadula*) depend heavily on a diversity of *Plectostemma* for larval food, using these plants in a specialized manner.

The general tendency in the small primitive genera, and in the larger genus *Eueides*, has been a movement from primitive

passifloraceous groups onto the structurally advanced *Passiflora* of the subgenera *Distephana* and *Granadilla*. We believe that these present-day patterns of association between the insects and plants are truly indicative of coevolutionary advance, and that the morphological modifications used to define the "advanced" taxa of these heliconians are in part a consequence of changes in ecological strategies related to host plant usage.

Given the saturation of the available canopy and edge leaf resources, innovation would have been a necessary condition for further radiations and perhaps a prerequisite for additional species to coexist with their more ancient relatives. Two important adaptations correlate with the radiation of *Heliconius*: one is meristem[4] usage which manifests itself in even the most primitive *aoede*-group, and the other is pollen feeding (Gilbert, 1972, 1975) which is present in all but the *aoede*-group.

Extensive field observations on adult *Heliconius* have proved that these butterflies possess many sophisticated behavioral traits related to meristem use. Females only oviposit on or near to meristems, and their attraction toward objects which resemble host plants and flowers indicate the presence of innate or learned searching images. On several occasions a *Heliconius* has been observed to fly right by an inconspicuous host plant to inspect something which resembled a *Passiflora* structure, such as an inappropriate vine or a grass inflorescence which looked like a tendril. A female often spends considerable time tapping, flying around, and landing upon a host plant before ovipositing on or else abandoning it. Even when a vine is tangled among a leafy mass of vegetation, a butterfly will nearly always find and respond to the appropriate *Passiflora* leaves. Sometimes a female will continue to "inspect" a plant even after the meristem has been landed upon, and only later is she observed to return to oviposit. Plants with ants present or spider webs are generally avoided and are rarely found with any eggs

upon them. Eggs of *Heliconius* with aggressive larvae almost never occur more than one to a meristem. It is certain that these patterns are mediated by complex visual and chemotactic responses of the butterflies.

Occasionally females are observed making "bee-lines" to rather inconspicuous plants up to five or more meters away, or even to plants completely hidden from direct view, in the absence of noticeable wind. (We have no compelling evidence to indicate that *Heliconius* are attracted from any distance to host plants by smell.) Every *Heliconius* so far studied in any detail (except perhaps *L. doris*, if one cares to consider this insect a *Heliconius*) has been shown to possess home-range behavior. This and site specific nocturnal roosting would indicate that these insects have a strong locational sense, perhaps determined by learned visual cues. Such behavior would permit, as we believe and the data suggest, the "staking out" of newly discovered host plants which could be visited periodically until meristems suitable for oviposition were produced. Ehrlich and Gilbert (1973) have shown this to be an important mechanism in flower visiting. These characteristics, while demonstrating considerable variation in expression in different populations, are widespread and perhaps universal in the genus, and are evident to some degree even in the *aoede*-group. The wide spectrum of discriminative behavior possessed by *Heliconius* is mirrored in their complex nervous systems (Swihart, 1972) and serves to set these butterflies apart from all other Lepidoptera.

It is probable that many aspects of host finding behavior were promoted by (or coevolved with) increased unpalatability (Benson, 1971; Brower et al., 1963), since efficient predator deterrence would be necessary for undertaking the time consuming and conspicuous egg laying sequence. Perhaps concomitantly, pollen was incorporated as a new nitrogen source in the diet of the advancing stock (Gilbert, 1972). Rapid flower finding and memory

of location became important requirements to maintain high reproductive outputs and perhaps increase adult lifespans (Gilbert, 1975), and probably contributed to the evolution of larger egg size and competitively superior larvae. Evidence for the central role of pollen feeding in the radiation of *Heliconius* has been presented and argued by Gilbert (1972, 1975).

Early radiation of the genus Heliconius. —The *aoede*-group and relict species of two later radiations of *Heliconius* (*nattereri* and *hermathena*) seem restricted to woody Passifloraceae, as are some *Philaethria* and the primitive *Eueides*. Like the more successful species of the primitive genera, and the more evolved *Eueides*, the silvaniform and melpomeneform *Heliconius* have radiated principally onto *Granadilla* and *Distephana*. These plants, with their diversity of species and abundance of rapidly growing meristems, were certainly key elements in the advancement and proliferation of successful contemporary *Heliconius*, as they were for *Eueides*. The great dependence of the melpomeneforms and silvaniforms on species of *Granadilla* and *Distephana*, and the scarcity of clearcut patterns of host plant specialization within these butterfly groups (see Appendix), suggest that the radiations that were responsible for many of the extant species may have occurred fairly recently in evolutionary time. The relative facility in obtaining interspecific crosses and the natural occurrence of hybrids between many of these species add support to this interpretation. On the other hand, the generic separation between *Heliconius* and *Eueides* has been long standing, and even though they commonly share the same host species, competition has been practically eliminated because of the pronounced differences in feeding sites.

The move to Plectostemma.—The perfection of host plant finding apparently enabled a number of populations to transfer onto the fragile, ephemeral *Passiflora*, notably the *Plectostemma* species of forest glades. These species have most of their

biomass in the form of small packets of fresh, soft growth, similar to *Granadilla* meristems. The epitome of this adaptation is found in *Heliconius erato*, with its strong preference for small *Plectostemma*, avoidance of previously occupied plants by ovipositing females, and intolerant and cannibalistic larvae (Alexander, 1961; pers. obs.). The abundance of the *Plectostemma* group is undoubtedly a principal factor in the spectacular contemporary success of *Dryadula phaetusa* and *Dryas iulia*, in addition to *Heliconius charitonia* and *erato*, and has probably helped to spread out many other species. Only a single species of *Eueides* (*E. aliphera*) is known to feed upon *Plectostemma*, and its attacks are restricted to two robust and closely related species placed near the beginning of the subgenus. A somewhat diversified usage of *Plectostemma* by heliconians and the maintenance of alternative hosts by most populations has apparently permitted these butterflies to invade broad geographical areas and many biotopes, and to become abundant. All occupy to some degree the humid shady/sunny habitats in which *Plectostemma* are found. Moreover, most have a reduced per plant ovipositional intensity, usually placing only one egg on any given plant, except for *H. sara* which tends to search out unusually large vines. As noted above for *H. erato*, those species which have specialized on *Plectostemma* efficiently locate small plants that are often just large enough for a single larva to complete development. The large number of dwarfs of these species in collections indicates that the calculations of the ovipositing females are not always perfect.

The return to Astrophea.—Finally, with the appearance of the *sara-sapho* group, the *Heliconius* line apparently moved back onto and radiated across the infrequent but large biomass primitive species (especially *Astrophea*). Possibly excluded from the more productive Passifloraceae by competition, this advanced group took advantage of a poorly used part of these large plants by adopting cluster oviposition on the scattered meristems (Fig. 5), located by the efficient *Heliconius* searching methods. Perhaps because suitable *Astrophea* meristems are infrequent in time and space, the majority of these butterflies are rather rare and localized. The abundant and near ubiquitous *H. sara* is an exception in that from the Amazon Basin northwards it has adapted to include a common plant *P.* (*Plectostemma*) *auriculata* in its normal fare, and in the south may use some of its close relatives.

Most other *Heliconius* groups are apparently very restricted in the number of eggs they can lay at any one time because of morphology and behavior related to the optimal use of their normal hosts. When *Astrophea* are occasionally included within the larval food niches of such species, these plants must be used in a rather inefficient manner, and for this reason the *Astrophea* meristem-clustering specialists are most certainly able to overcome these more aggressive competitors with their masses of cooperatively docile larvae (Fig. 6).

Multiple oviposition in primitive Heliconius.—Butterflies of the relatively primitive and homogeneous wallaceiform group also cluster eggs on meristems, in this case on species of *Passiflora* (*Distephana*) upon which they seem to specialize. In addition the robust adults are frequently observed visiting the large red *Distephana* flowers, where they drink the abundant nectar. All the wallaceiforms seem to be adapted to and dependent upon these flowers. Although most species of the *wallacei*-group are inhabitants of the upper forest canopy, they are easily caught at *Distephana* flowers, and both sexes are readily attracted down to ground level with a suitable flower mimic, such as a large red handkerchief. Although it is supposed that *Distephana* flowers are adapted specifically for hummingbird pollination (Janzen, 1968), they are also proportioned to enable feeding butterflies to scrape pollen from the anthers with their wings. This is obviously an important mutualism where wallacei-

forms occur, and may represent the ancestral adaptation of the unusual *Distephana* flowers to butterfly and bird pollination. Thus, it is not surprising that *Distephana* might possess a curious mixture of "advanced" characters, related to pollination, a number of "primitive" morphological traits, and a relict-type distribution. We suspect that the association between the wallaceiforms and *Distephana* is very old. This corresponds with our postulation that these plants are considerably more ancient in their origin than *Granadilla*, although no authoratative opinion has been published on this point.

Like the *sapho-sara* species group, the wallaceiforms may have guaranteed their success on the much-sought-after *Distephana* by preempting meristems with clusters of eggs. Their use of larger branches may be a consequence of competition with *Heliconius* having more reduced egg numbers. *Laparus doris*, an evolved derivative of the *wallacei* line, specializes upon certain large-growing species of *Granadilla*, but it only uses occasionally encountered very large branches, upon which it places hundreds of eggs. There is no doubt that the large masses of resulting larvae enjoy several advantages related to competition and protection from parasites and predators, although the strategy carries an important liability. Large meristems are rare, and to reproduce, the butterflies are forced to disperse widely or wait long periods for the growth of suitable vines. As a consequence, *doris* may suffer large variations in abundance in a given locality (Benson, 1971).

We are not able to say whether or not multiple oviposition in the wallaceiforms is a primitive character. However, it appears that the tendency to use larger branches of their preferred host plants is derived and may be associated with competition. Multiple oviposition certainly helps these species, and *L. doris*, make better use of their limited larval food supplies. Not enough is known about the larval ecology of *aoede* and its relatives to comment upon.

Broad Taxonomic Correlations between Heliconians and Passifloraceae

We can now return to and suggest an answer for the first question posed above. The data show that the most primitive members of all five important radiations of the heliconians (*Philaethria*, primitive *Eueides*, *aoede*-group, *Heliconius nattereri*, and *H. hermathena*) are all primarily associated with the presumably most ancient Passifloraceae (*Dilkea, Mitostemma, Tetrastylis*, and *Astrophea*). The morphologically more derived butterflies of each radiation (*Dione* and *Agraulis*, advanced *Eueides*, and advanced *Heliconius* with the exception of the *sara-sapho* group) are associated with more recently radiating *Passiflora* groups. The most advanced *Heliconius* (*sara-sapho* group) are found again on the primitive plants, but use them in a specialized way which is fundamentally different from that of all other lines, and seemingly unavailable to them. Thus, our first question is in part answered: There are a number of strong associations between subgroups of heliconians and passion vines, and these can be ordered to produce an ecologically pleasing pattern of heliconian evolution. The radiations have been several in number often across the same plant groups, and each radiation centers around similar morphological types having similar ecological strategies of plant utilization. Moreover, morphological and ecological features of the plants correlate with their susceptibilities to the insect strategies, seemingly with the effect of promoting a diversity of such strategies and resulting in a rich assemblage of heliconians.

The scenario proposed here for the coevolutionary radiation of the heliconians is based on gross morphological and ecological considerations; however, up until now we have not made reference to what is possibly a reasonable and important alternative: that the radiation of the modern taxa of Passifloraceae preceded occupation of these plants by heliconians. This second

hypothesis would imply that the sequential radiations of heliconians would have each centered on abundant contemporary passion vine taxa (such as *Granadilla*) and that the relict remnants of each previous radiation would be restricted to marginal ecological situations. This is of course what we see. However, the coevolution hypothesis gives the same prediction and is even more restrictive in that it predicts that relict heliconians should be found using systematically primitive passion vines. The evidence tends to support the hypothesis of concurrent evolution with the relict heliconians persisting in part because of long-evolved specializations on their ancestral plant groups, and not merely because they found refuge in marginal habitats. We consider this idea (which is really just a modification on a theme borrowed from biogeography) to be of considerable theoretical significance in the historical analysis of insect/plant interactions and in addition has important implications in the study of present day insect community structure. Moreover, we wish to suggest that, in this form, coevolution is testable as an hypothesis, and we therefore predict that the relict species *Eueides procula, E. emsleyi, Heliconius hierax* and *H. hecuba* will also be discovered to feed upon primitive Passifloraceae.

We have, as yet, no firm evidence that herbivore attacks have significantly influenced the formation of higher groups in the Passifloraceae. However, to answer our second question, there is no doubt that heliconians and other herbivores have been prime movers in promoting and maintaining geographically specific morphological adaptations in passion vines during recent evolutionary time, and in this way are contributing to race and species characters of the plants. These include chemical defenses (still poorly studied), egg and larva mimics, deciduous stipules, leaf mimicry, and other devices such as the indirectly functioning extrafloral nectaries, which, although perhaps not interpretable outside of an ecological context, have contributed

greatly to taxonomically significant diversification in the Passifloraceae. We shall now consider in some detail the coevolved defense mechanisms of passion vines as they function today.

COEVOLVED ANTIHERBIVORE DEVICES IN PASSION VINES

The Passifloraceae have evolved many ways of protecting themselves against attacks by heliconians and other insects. Apparently many species produce a variety of toxic chemicals such as saponins, alkaloids, and phenolic and cyanogenic glycosides (Gibbs, 1974). A few species such as *P. foetida* and *P. lonchocarpa* are extremely foul smelling. The within and between species nutritional qualities as well as the "taste" of a plant to an individual insect probably vary greatly, making it more difficult for a butterfly to include a wide spectrum of foodplants in the larval diet without "specialization for generality." This seems to have occurred only in a few species, such as *Agraulis vanillae* and *Heliconius numata*, and is far from perfect even here as local populations reject plant species used by other populations. Female heliconians, before ovipositing, are always observed to assay foodplant acceptability with foreleg chemoreceptors. In the absence of specific metabolic adaptations by the butterfly, many chemical components of the plant could serve to discourage oviposition through evolved (preprogrammed) avoidance responses or straightforward repellency.

Mechanical defense against general herbivory occurs in the tough older leaves of many species of plants (Merz, 1959), and probably also in *Passiflora*, or in the form of protective hairs. Gilbert (1971) has shown that in *P. (Plectostemma) adenopoda* and related species the modified hooked leaf hairs (trichomes) are capable of puncturing the larval cuticle, resulting in the death of most heliconian larvae placed on these otherwise acceptable plants.

More elegant forms of defense, seemingly directed specifically at *Heliconius*, occur in

a few species of passion vines. Some *Granadilla* of the *laurifolia*-group (e.g., *P. ambigua*) develop filiform stipules which resemble small tendrils on the meristem and are larger than the true tendrils at this stage of development. These are soon deciduous, and could function to stimulate egg placement by a *Heliconius* and then slough the eggs off. Even more striking is the production of credible mimics of eggs and small larvae by a wide variety of *Passiflora*. Thus, *P. (Granadilla) cyanea* has swollen yellow projections on the stipules which exactly resemble in form and color the eggs of *Heliconius ethilla*, the normal herbivore of this Trinidadian plant (Gilbert, 1975), and more pertinently those of *H. melpomene* which (as a consequence?) only occasionally oviposits on *cyanea* (Alexander, 1961). In *P. (G.) guazumaefolia* (Fig. 11) and *P. (Plectostemma) warmingii* the yellow structures are egg-shaped petiolar glands, and in some populations of *P. (G.) ambigua* the tendril tips are yellow. *P. (Plectostemma) punctata* and related species have yellow ocelli (nectar glands on the ventral leaf surface), with the coloration also being expressed dorsally. The most exceptional case of egg mimicry is found in *P. (Tryphostemmatoides) gracillima* which produces abundant supernumerary yellow flower buds on meristem tendrils. These are deciduous soon after attaining a diameter of a millimeter or so, suggesting that their function is primarily for deception (Fig. 10). *P. (G.) miersii* presents a similar case with axillary flower buds. *P. (G.) platyloba* and *maliformis* have yellow-orange serrulate stipules which seem to mimic young heliconian larvae. These structures range from crude to excellent egg and larva mimics and must discourage sharp-sighted mothers of intolerant larvae (e.g., *H. erato*, *H. melpomene*, and many silvaniforms) from laying eggs on already "overpopulated" meristems.

It is noteworthy that no plant species in which egg mimics are known to occur is used by meristem clustering *Heliconius* and that the *Astrophea*, the preferred food of

these *Heliconius*, do not seem to bear egg mimics. Butterflies of the *sara-sapho* group might be expected not only to ignore previous occupation by eggs but also even to be stimulated to oviposit in their presence. This can be concluded from the fact that small age differences in larvae would not be as critical as in aggressive species, and group facilitation in feeding and defense and general meristem rarity would give further impetus to join in. Turner (1971) thought that his observation of multiple rafting by several females of *H. sara* might relate to cooperative social behavior, although he did not propose any specific adaptive mechanism. Rafts of up to 800 eggs have been found in *L. doris* (Fig. 4), representing a volume which exceeds that of the abdomen of an average female.

Other cruder mimics of eggs and even larger caterpillars have been suggested (M. Rothschild, pers. comm.) to operate in protecting many species of *Granadilla*. Since many *Heliconius* females assess both egg and caterpillar loads on meristems before ovipositing, they would be subject to all types of plant treachery towards dissuasion of the placement of "further" juveniles.

Leaf shape in the Passifloraceae, both between species and within a given plant, is among the most variable observed in any plant group. Gilbert (1975), noting the high degree of visual acuity and behavioral sophistication of *Heliconius*, has speculated that different passion vines have diverged in their appearance and even come to mimic the leaf shapes of other groups of common tropical plants to escape detection by these butterflies.

The great majority of Passifloraceae produce sugary secretions from extrafloral nectaries. These are most frequently found on the petioles, but also occur on leaf margins, surfaces, and tips, and on bracts and stipules. The nectaries are highly attractive to many kinds of predaceous ants which attack and carry off small larvae, and some myrmecines (e.g., *Crematogaster* spp.) also eat heliconian eggs (Benson,

1967). In a series of ingenious experiments, B. Carroll (unpub. thesis) has related the function of extrafloral nectaries to the protection of plants by ants against herbivore attacks, and has shown that the vine growth form, especially in open or forest edge habitats, is especially favorable for the recruitment of protecting ants to the nectaries. This may help explain the general reduction of such glands in many forest *Astrophea*. Nectaries may also help in sustaining the microhymenopteran parasites of heliconian eggs (Gilbert, 1975) as has been shown to be of importance in other plants (Leius, 1967).

The form and dynamics of passion vine growth also have important consequences for heliconian egg laying strategies. Tendril coiling tends to pull meristems close to adjacent plants and into foliage, making discovery and access more difficult for butterflies, while facilitating access by ants. It may also crush eggs or kill ecdysing larvae, although this is probably no more than a simple byproduct of vine growth.

In more seasonal (subtropical or wet/dry) areas, some passion vines are dormant for long periods, followed by sudden growth, often associated with reproduction, during the warmer or wetter part of the year. The ovipositional capacity of heliconian and other insect populations is "satiated," and the plant can subsequently preserve its capital gains by growth stoppage. *P. (G.) sidaefolia* in Rio de Janeiro presents an example of this mechanism. Woody *P. (Astrophea)*, *Dilkea*, and *Mitostemma* species appear to have a similar growth strategy, but each plant produces only one or a few meristems at a time, and a large proportion of the energy used in this comes from previously stored reserves. This is indicated by the fact that new growth is very rapid, even under shaded conditions, and it is often devoid of leaves (or has only a few basal leaves) until considerable height is attained. After the initial burst of growth over one to several meters, the increase diminishes to more usual rates.

We do not have sufficient observations to determine if this pattern is seasonal as with *P. sidaefolia*; however, growth is not necessarily directly associated with the production of reproductive structures, since many of these forest lianas are cauliflorous (Killip, 1938). Thus, *Astrophea* meristems, rare in space, may also be uncertain and/or satiating in time.

The heliconians in turn have developed many counterstrategies against passion vine defenses. The complex behavioral adaptations of these butterflies make it difficult for even the rarest and most inconspicuous passion vines to escape detection. In addition to well developed vision and learning ability, the butterflies apparently use probing with the antennae and proboscis as well as tapping with the forelegs for such purposes as distinguishing real from false eggs and discovering small larvae. Therefore eggs are very seldomly found on plants which are unsuitable for larval development because of insufficient total biomass, poor physiological condition, disease, or the presence of predators such as ants, spiders, and other *Heliconius* larvae.

Many *Heliconius* place eggs on tendrils, especially near the tips (Figs. 2 and 3), apparently to help protect them from predaceous ants, and young larvae of some species such as *Philaethria dido* and *Dryas iulia* chew out peninsular-shaped slivers from leaf margins where they feed and rest. Ants are much less likely to take insect prey from tendril tips than from vine meristems or leaf surfaces (B. Carroll and W. Benson, unpubl. experiments). Some species, notably *Dryas iulia* and *Agraulis vanillae*, place eggs on adjacent plants, dead leaves or other objects near to the host plants, which perhaps also reduces losses to predators. *Dryadula phaetusa* similarly avoids green leaves for oviposition, often placing eggs at the base of the stem. Newly hatched heliconian caterpillars will often wander for many hours if the immediate substrate is found to be inedible.

Physical defenses, such as hooked tri-

chomes in *P. adenopoda, P. warmingii* and "Tetrastylis" *lobata*, are not always effective deterrents, and indeed the larvae of *Dione moneta* seem to be closely associated with these plants in both Central America and southern Brazil. They and other larvae walk between the trichomes when small and over them when large, eating principally between the veins and using silken pads (universal in heliconiine and most other lepidopterous larvae, even when on smooth substrates; Alexander, 1961) to aid in movement and resting.

With respect to plant chemistry, the secondary substances of passion vines, probably evolved as insect deterrents, may not only have become recognition symbols for heliconians, but also seem to be used by the larvae and adults to protect themselves against vertebrate predators (Brower and Brower, 1964) and may even be of importance in pheromone synthesis for the butterflies (Brown, unpubl.).

DYNAMICS OF THE COADAPTIVE PROCESS BETWEEN HELICONIANS AND PASSION VINES

We now turn to our third and last question. What is the evidence for racial patterns within species which might indicate recent coadaptive evolution between heliconians and their host plants? Although extensive information is not available, we shall cite a few cases turned up through studies in our laboratories.

Adaptive evolution is evident in host plant utilization by *Eueides isabella*. While Mexican populations of *E. isabella* feed on *Passiflora (G.) serratifolia*, their larvae refuse new growth, developing only on older leaves. *E. isabella* larvae from Trinidad, however, when tested on the same plant, feed on the young leaves and are killed. Presumably this difference between populations is due to the fact that *P. serratifolia* is not present in Trinidad, and thus *isabella* there has had no reason to evolve an avoidance response or detoxification mechanisms for the substances in the young leaves. Strangely enough, *P.*

serratifolia is a "supernormal" ovipositional stimulus for at least five non-Mexican races of *H. melpomene* tested (i.e., it is chosen over normal hosts or plants used for rearing), yet the larvae are killed.

Further evidence of intraspecific differences is found in the wide selection of host plants by the southeastern Brazilian *Heliconius erato phyllis* in comparison with other races. This red-banded form presumably has had to adjust to much harsher and more uncertain seasonal variations than the differently colored Amazonian races. The genes which produce the adaptive (detoxifying?) enzymes in *phyllis* seem to be linked to its behavior and color-pattern genes in test crosses with Amazonian forms. Some northern races with red-banded forewings also lack these biochemical adaptations and do not develop on those *Granadilla* and *Astrophea* tested, although many species of *Plectostemma* are universally satisfactory as larval foodplants for *Heliconius erato*. Judging from our laboratory observations, the potential food niche of larval *phyllis* is even wider than its realized usage in nature, covering many additional groups and species in the Passifloraceae present in the insectary. Moreover, preliminary data indicate that, despite the generalized feeding of *phyllis*, geographic patterns exist even within this subspecies. Thus *P. (G.) alata* is used in Santa Catarina and Rio Grande do Sul (Biezanko, quoted in Brown and Mielke, 1972) and in São Paulo, whereas no *phyllis* populations in Espírito Santo or Rio de Janeiro are known to use this frequently encountered plant. In comparisons made under relatively similar conditions, insectary populations obtained from near the town of Linhares (Espírito Santo, Brazil) differed considerably in their ovipositional preferences from other *phyllis* collected in Rio de Janeiro, about 500 km to the southwest. The last readily accepts *P. (G.) sidaefolia* for egg laying (it is a natural host plant), whereas the former does not (*P. sidaefolia* is not known from Linhares), although the larvae of both feed and develop well when

put on the plant. But even in terms of larval feeding, the two populations differ in subtle ways, for different chemical fractions of leaf extracts of *P. sidaefolia* act differently in stimulating the feeding response of larvae from the two areas (R. M. Caire, pers. comm.). The same plant must therefore "taste" differently to both the female butterflies and larvae from different local populations, and the different life history stages apparently use different criteria for evaluating host plant suitability.

Many other more anecdotal examples could be given from our laboratory studies on these and other heliconians, indicating the general occurrence of behavioral and metabolic differentiation in different populations of the same species. Equivalent studies on passion vines have not been undertaken, although we are confident that comparative population studies of coevolutionary interactions will reveal not only adaptive differentiation in these plants, but also bring to light some of the on-going selective processes which cause them.

PERSPECTIVE

Further field work will obviously expand the list of foodplants, and turn up many more intriguing examples of geographical specializations and coadaptive evolution in heliconians and passion vines. We do not expect, however, that the fundamental patterns of foodplant choice will be greatly modified. Restricted primitive heliconians will be found ovipositing on the older leaves of primitive passion vines of large biomass. More evolved species will be found on leaves and meristems of *P. (Granadilla)* and *P. (Distephana)* and their close relatives. Widespread common species of more advanced morphology will be able to use *Passiflora* of the subgenus *Plectostemma*, which are probably among the most recent Passifloraceae. And species of the *sara-sapho* group will be found using meristems of *Astrophea*. A wide diversity of geographical patterns of plant usage and local adaptations of both butterflies and

plants exist, and these should provide excellent subjects for decisive studies on the dynamic processes of present-day coevolution.

SUMMARY

Modern patterns of passifloraceous host plant choice by heliconiine butterflies suggest parallel evolution in the two groups with appreciable mutual influence. There are strong associations between the morphologically primitive and advanced sections of each taxon, with the single exception of the most derived *Heliconius*, which use primitive *Passiflora* in a specialized manner. The tracking of passion vine diversification by heliconians is thought to have involved a series of radiations of the insects onto plant groups containing smaller and smaller vines. We believe that competitive exclusion from larger plants has been an important factor in promoting switches to smaller plants in these protected insects, and that such usage resulted in complex behavioral adaptations enabling the efficient use of small, sporadically appearing meristems for oviposition. The association of many very successful heliconians with the small but fast-growing *Plectostemma* group of *Passiflora* and other similar vines is probably significant, and the reradiation of the *Heliconius* line back onto and across the infrequently occurring *Astrophea* meristems was no doubt necessarily predicated upon the evolution of an efficient search behavior by their more generalized ancestors. The five major recognizable radiations of heliconians seem to be able to successfully coexist today because of fundamental differences in the ways they divide up hosts.

There occur many striking adaptations in passion vines which have evolved in response to selective pressure from heliconians and other insect herbivores. These can only be interpreted in an ecological context, and we are unable at present to perceive relict modifications specifically related to past herbivore defense adaptations

in these plants. Extrapolating from current patterns, however, we conclude that such past adaptations existed and are most certainly being preserved in a cryptic state.

Present day cases of adaptive racial divergences in heliconian species suggest that selective pressures are strong and dynamic coadaptive evolution is actively taking place among heliconians, passion vines, and other components in their complex environments.

ACKNOWLEDGMENTS

LITERATURE CITED

ALEXANDER, A. J. 1961. A study of the biology and behavior of the caterpillars, pupae, and emerging butterflies of the subfamily Heliconiinae in Trinidad, West Indies. Part I. Some aspects of larval behavior. Zoologica 46:1–24.

BARRETT, C., AND A. N. BURNS. 1951. Butterflies of Australia and New Guinea. N. H. Seward Pty., Ltd., Melbourne. 187 p.

BEEBE, W., J. CRANE, AND H. FLEMING. 1960. A comparison of eggs, larvae, and pupae in fourteen species of heliconiine butterflies from Trinidad, W.I. Zoologica 45:111–154.

BENSON, W. W. 1967. Studies on the ecology of Ithomiinae and Heliconiinae in Costa Rica. Student Report, Insect Ecology in the Tropics. Feb.–March, 1967. OTS, Ciudad Universitaria, Costa Rica. Mimeogr.

———. 1971. Evidence for the evolution of unpalatability through kin selection in the Heliconiinae (Lepidoptera). Amer. Natur. 105:213–226.

BREEDLOVE, D. E., AND P. R. EHRLICH. 1968. Plant-herbivore coevolution: Lupines and lycaenids. Science 162:671–672.

———. 1972. Coevolution: Patterns of legume predation by a lycaenid butterfly. Oecologia 10:99–104.

BROWER, L. P., AND J. V. Z. BROWER. 1964. Birds, butterflies, and plant poisons: A study in ecological chemistry. Zoologica 49:137–159.

BROWER, L. P., J. V. Z. BROWER, AND C. T. COLLINS. 1963. Experimental studies of mimicry. 7. Relative palatability and Müllerian mimicry among Neotropical butterflies of the subfamily Heliconiinae. Zoologica 48:65–84.

BROWN, K. S., JR. 1972. The heliconians of Brazil (Lepidoptera: Nymphalidae). Part III. Ecology and biology of Heliconius nattereri, a key primitive species near extinction, and comments on the evolutionary development of Heliconius and Eueides. Zoologica 57:41–69.

———. 1975. Geographical patterns of evolution in Neotropical Lepidoptera. Part II. Systematics and derivation of known and new Heliconiini (Nymphalidae: Nymphalinae). J. Ent. (London), B, 44 (in press).

BROWN, K. S., JR., AND O. H. H. MIELKE. 1972. The heliconians of Brazil (Lepidoptera: Nymphalidae). Part II. Introduction and general comments, with a supplementary revision of the tribe. Zoologica 57:1–40.

BROWN, K. S., JR., P. M. SHEPPARD, AND J. R. G. TURNER. 1974. Quaternary refugia in tropical America: Evidence from race formation in Heliconius butterflies. Proc. Roy. Soc. London, B, 187:369–378.

BRUES, C. T. 1920. The selection of food-plants by insects with special reference to lepidopterous larvae. Amer. Natur. 54:313–332.

———. 1924. The specificity of food-plants in the evolution of phytophagous insects. Amer. Natur. 58:127–144.

CORBET, A. S., AND H. M. PENDLEBURY. 1956. The butterflies of the Malay Peninsula. 2nd Edition. Oliver and Boyd, London. 537 p.

D'ARAUJO E SILVA, A. G., C. R. GONÇALVES, D. M. GALVÃO, A. J. L. GONÇALVES, J. GOMES, M. DO NASCIMENTO SILVA, AND L. DE SIMONI. 1968. Quarto Catálogo dos Insectos que Vivem nas Plantas do Brasil—Seus Parasitas e Predadores. Ministério da Agricultura, Rio de Janeiro, Part II, Volume 1.

DARWIN, C. 1872. The origin of species. 6th Edition. (Reprinted 1958, New American Library, New York, 479 p.)

DE LESSE, H. 1967. Les nombres de chromosomes chez les Lépidoptères Rhopalocères Néotropicaux. Ann. Soc. ent. France 3:67–136.

DOLINGER, P. M., P. R. EHRLICH, W. L. FITCH, AND D. E. BREEDLOVE. 1973. Alkaloid and predation patterns in Colorado lupine populations. Oecologia 13:191–204.

EDGAR, J. A., C. C. J. CULVENOR, AND T. E. PLISKE. 1974. Co-evolution of danaid butterflies and their host plants. Pyrrolizidine

alkaloids and cardiac glycosides as evolutionary markers. Nature 250:646–648.

EHRLICH, P. R. 1964. Some axioms of taxonomy. Syst. Zool. 13:109–123.

——. 1970. Coevolution and the biology of communities, p. 1–11. In K. L. Chambers (ed.), Biochemical coevolution, Oregon State University Press, Corvallis. 117 p.

EHRLICH, P. R., AND L. E. GILBERT. 1973. Population structure and dynamics of the tropical butterfly Heliconius ethilla. Biotropica 5:69–82.

EHRLICH, P. R., AND P. H. RAVEN. 1965. Butterflies and plants: A study in coevolution. Evolution 18:586–608.

EMSLEY, M. G. 1963. A morphological study of imagine Heliconiinae (Lep.: Nymphalidae), with a consideration of the evolutionary relationships within the group. Zoologica 48:85–130.

——. 1965. Speciation in Heliconius (Lep.: Nymphalidae): Morphology and geographic distribution. Zoologica 50:191–254.

GENTRY, A. 1975. Notes on Panamanian Passifloraceae. Ann. Missouri Bot. Gard. (in press).

GIBBS, R. D. 1974. Chemotaxonomy of flowering plants. McGill-Queen's University Press, London. 2372 p.

GILBERT, L. E. 1971. Butterfly-plant coevolution: Has Passiflora adenopoda won the selectional race with heliconiine butterflies? Science 172:585–586.

——. 1972. Pollen feeding and reproductive biology of Heliconius butterflies. Proc. Nat. Acad. Sci. (Wash.), 69:1403–1407.

——. 1975. Ecological consequences of a coevolved mutualism between butterflies and plants. In L. E. Gilbert and P. R. Raven (eds.), Coevolution of animals and plants. Univ. Texas Press, Austin. 245 p.

HERRERA, J. 1950. Dos generos nuevos de ninfalidos para Chile. Rev. Univ. Cat. Chile 35:5–15.

JANZEN, D. H. 1968. Reproductive behavior in the Passifloraceae and some of its pollinators in Central America. Behaviour 32:33–48.

KILLIP, E. P. 1938. The American species of Passifloraceae. Publ. Field Mus. Nat. Hist. (Bot.) 19:1–613.

KUSNEZOV, N. J. 1929. Abhängigkeit der geographischen Verbreitung der Weisslinge, Asciidae, von der Verheitung ihrer Futterpflanzen und der chemisch zusammen der letzteren. Z. f. Morphol. u. Ökol. Tiere 17:778–793.

LEIUS, K. 1967. Influence of wild flowers on parasitism of tent caterpillar and codling moth. Canad. Entomol. 99:444–446.

MAYR, E. 1963. Animal species and evolution. Harvard Univ. Press, Cambridge. 797 p.

MERZ, E. 1959. Pflanzen und Raupen. Über einige Prinzipien der Futterwahl bei Grossschmetterlingsraupen. Biol. Zentr. 78:152–188.

MÜLLER, W. 1886. Sudamerikanische Nymphalidenraupen. In J. W. Spengel (ed.), Zoologischen Jahrbüchern, G. Fischer, Jena.

MUYSHONDT, A., A. M. YOUNG, AND A. MUYSHONDT, JR. 1973. The biology of the butterfly Dione juno huascama (Nymphalidae: Heliconiinae) in El Salvador. J.N.Y. Entomol. Soc. 81:137–151.

OWEN, D. F. 1972. Tropical butterflies: The ecology and behavior of butterflies in the tropics with special reference to African species. Clarendon Press, Oxford, England. 214 p.

RAVEN, P. H., AND D. I. AXELROD. 1972. Plate tectonics and Australasian palaeobiogeography. Science 176:1379–1386.

ROSS, G. N. 1964. Life history studies on Mexican butterflies. III. Nine Rhopalocera (Papilionidae, Nymphalidae, Lycaenidae) from Ocotal Chico, Veracruz. J. Res. Lepid. 3:207–229.

SOUTHWOOD, T. R. E. 1960. The abundance of Hawaiian trees and the number of their associated insect species. Proc. Hawaiian Entomol. Soc. 17:299–303.

——. 1961. The evolution of the insect-host tree relationship—a new approach. Proc. 11th Int. Congr. Ent., Vienna, 1960, 1:651–654.

SWIHART, S. L. 1972. The neural basis of colour vision in the butterfly, Heliconius erato. J. Insect Physiol. 18:1015–1025.

TURNER, J. R. G. 1967. Some early works on heliconiine butterflies and their biology (Lepidoptera, Nymphalidae). J. Linn. Soc. (Zool.) 46:255–266.

——. 1971. Studies of Müllerian mimicry and its evolution in burnet moths and heliconid butterflies, p. 224–260. In R. Creed (ed.), Ecological genetics and evolution. Blackwell, Oxford.

——. 1973. Passion flower butterflies. Animals 15:15–21.

VAN SOMEREN, V. G. L. 1974. List of foodplants of some east African Rhopalocera, with notes on the early stages of some Lycaenidae. J. Lepid. Soc. 28:315–331.

APPENDIX

The Appendix Table presents all the reliable host plant records that we have been able to accumulate for the Heliconiini in Middle and South America; about 90% of these represent original and unpublished observations of the authors.

The double vertical divisions in the Table represent the five principal radiations in the tribe:

I. Small, morphologically isolated, relatively primitive genera;

II. The genus *Eueides*, an early offshoot of the line leading to *Heliconius*, relatively rich in species;

III. Small isolated groups of primitive *Heliconius* and of closely allied genera;

IV. Silvaniform and melpomeneform *Heliconius*, a tight group of fifteen closely related species;

V. *Heliconius erato* and its allies, including the morphologically uniform *sara-sapho* radiation.

The systematic arrangement of the species follows that of Brown (1975). Widespread and common species are indicated by an asterisk.

Oviposition strategies are given in the form of code letters immediately below the species name:

A. Scattered eggs, usually under older leaves;

B. A very large raft of eggs on a large younger leaf;

C. A raft of eggs under an older leaf;

D. A cluster of eggs covering a meristem;

E. A loose group of eggs scattered about a meristem;

F. A solitary egg on a meristem.

Known larval host plants are segregated into generic and subgeneric groups, in order from presumably more ancient to more recently derived taxa. No attempt is made to infer detailed cladistic relationships among the plant groups. The arrangement that we have used is very nearly the the sequence given in Killip's key (1938), in inverted order of all major taxa. This key tended to consider specialized and derived characters, indicative of more recently evolved and advanced taxa, near its beginning. We have slightly departed from the reverse of the order given by Killip where this seemed justified by accepted evolutionary-botanical criteria: *Mitostemma* and *Dilkea* have been switched, implying that *Mitostemma* is more primitive because of the unfused condition of its floral elements and its disjunct geographic distribution; *Passiflora* (*Astrophea*) and *P.* (*Plectostemma*) sections are left in Killip's original order, whereas the order of the series of *P.* (*Granadilla*) has been slightly modified (*Tiliaefoliae* advanced to after the *Serratifoliae* and *Kermesinae* and *Menispermifoliae* switched in position) so as to better reflect a sequence of increasing specialization in leaf and

stipule characters and flower complexity, terminating with the *Lobatae* and the *Kermesinae*, many of whose members share with *Plectostemma* a relatively fragile habit and a plicate operculum; *P.* (*Distephana*) is presumed more primitive than and is placed before *P.* (*Granadilla*) on the basis of its small number of geographically scattered species, and traits (stigmal placement on the ovary and lignification of the stems) suggesting affinities with the primitive *P.* (*Astrophea*); *P.* (*Deidamioides*) and *P.* (*Tryphostemmatoides*), relatively robust cirrhiflorous forest plants, are judged to be more primitive than *Plectostemma* and its close allies; and the Central American "*Tetrastylis*" *lobata* is clearly related to the advanced *Passiflora*, especially *Plectostemma* (section *Pseudodysosmia*) which it follows. In fact, none of these changes produces significant modifications in the over-all patterns of relationships between Heliconiini and their foodplants, as summarized in Table 1. They represent more an initial attempt at improving the rational ordering of the American Passifloraceae, on the basis of standard concepts of evolutionary botany. Dr. S. S. Tillett, who is currently revising the Passifloraceae, has kindly commented on our classification and permitted us to incorporate some of his preliminary conclusions on "*Tetrastylis*" *lobata* and relationships among the sub-groups of *Astrophea*, *Granadilla*, and *Plectostemma* (Tillett, in preparation), for which we are very grateful.

Plant habit and habitat are indicated following the plant name, according to the following code:

(first letter, usual habit)

A. Long-lived, erect or subscandent shrub or tree with few or no tendrils;

B. Long-lived woody vine with well developed tendrils;

C. Erect, small, subligneous herb;

D. Moderate-lived, scandent or decumbent but robust vine;

E. Short-lived fragile vine with a soft stem;

(second letter, usual habitat)

W. Woods interior, usually climbing to canopy;

X. Woods edge, clearings, and second growth;

Y. Natural scrub or open areas;

Z. Humid glades, often steep well-watered areas with undergrowth in shade and sun.

The geographic localities for the foodplant records are indicated by letters in the body of the Table. The continental areas roughly correspond to the Neotropical Quaternary refugia proposed for heliconian differentiation by Brown et al. (1974) and Brown (1975). The names used in the latter paper are indicated below, in parentheses after the area definitions. North American data have not been considered (except for tropical eastern Mexico). The code letters for the geographic areas are as follows:

M. Mexico to Nicaragua, northern Neotropics (Guatemala);

APPENDIX TABLE. *Known larval foodplants of heliconian butterflies, by species and geographical area (see explanation).*

		I-PRIMITIVE GENERA							II-MATURE LEAF RADIATION												III-
HELICONIINE SUBGROUP Genus or (species-group)		Philaethria	Dione		Podotricha	Agraulis	Dry adula	Dryulia	Eueides												New Taxon
PLANT (sub)GENUS, species	mode of foodplant usage, habit and habitat species	pygmalion / wernickei / dido / (plex)	*juno / moneta	glycera	euchroia / telesiphe	*vanillae	*phaetusa	*iulia	procula / emsleyi	vibilia	pavana	lampeto / libitina	lineata / libitina	*isabella	eanes	*lybia / *tales	*aliphera	metharme / godmani / acede		
		A A / A	BC AC	A	A? A?	A	A	A	A? A? C	C	A? A? A?	A A? A	A A	A	D? D D					
MITOSTEMMA glaziovii	AW								B											
DILKEA spp.	AW																			
TETRASTYLIS ovalis	BW			B											Q W (W)A					
*(?)sp.nov.	BW																			
PASSIFLORA (Astrophea) (a) pittieri	BW																			
cerradense	BY						W													
(b) gigantifolia	AW			X X					X X		X X X		X							
(c) *leptopoda	BW																			
(d) candida	BW			o o					o o		o o o		o							
*citrifolia	BW																			
costata	AW	A G					G		G											
hexagonocarpa	BY	A																		
faroana	BY	A																		
mansii	AY	X			X X		X		X											
*haematostigma	BW	S		⊢ ⊢					⊢ ⊢		⊢ ⊢ ⊢		⊢							
pentagona	BW																			
rhamnifolia	AW	S			S		S		S											
*cf. rhamnifolia	BW			X X					X X		X X X		X							
(e) skiantha	AW	O																		
*securiclata	AW						R													
spinosa	BW			⊢⊣ ⊢⊣					⊢⊣ ⊢⊣		⊢⊣ ⊢⊣		⊢⊣							
(Polyanthea) cirrhiflora	DY																			
(Distephana) glandulosa	BX	(A)	W		W		W													
coccinea	BX	A A	W	o o					o o		o o o									
quadriglandulosa	BX		W																	
vitifolia	BX	PCQ	P		PC	P								TG O	YWA	WA				
speciosa	BW	E			R S									PO	T					
(Dysosmioides) villosa	DY			⊢⊣ ⊢⊣					⊢⊣ ⊢⊣		⊢⊣ ⊢⊣ ⊢⊣		⊢⊣			PO					
vellozii	DX				S															
(Dysosmia) clathrata	CY			X																
foetida	EY			X X	X PTG				X X		X X X		X							
(Granadilla) (a) quadrangularis	DX		XBS		GSZ		(Z)									Z				
alata	DX		T		S				> >		> > >			(S)					
(b) serrato-digitata	DX			> >					> >		> > >			TGA >					
(c) capparidifolia	DX																			
ambigua	BX	P		⊢⊣ ⊢⊣					⊢⊣ ⊢⊣		⊢⊣ ⊢⊣ ⊢⊣		⊢⊣	MP T A		OG O A				
laurifolia	DX	VTO														A (A)				
acuminata	BX																			
*cf. acuminata	DX																			
riparia	BW																			
*cf. riparia	DX		B	⊢⊣ ⊢⊣	B				⊢⊣ ⊢⊣		⊢⊣ ⊢⊣ ⊢⊣		B		AW					
*malacophylla	DX		A		A															
nitida	DX			o o					o o		o o o		o	A A					
*cf. nitida	DX															Q				
guazumaefolia	DX																			
(J) bahiensis	DX		B	X X	B				X X		X X X		B M X		B				
serratifolia	DX		M		Y															
(e) ligularis	DX														(P)					
seemani	DX																			
maliformis	DX		P		Q									(C) F					
platyloba	DX																			
(f) menispermifolia	DX															S				
(g) setacea	DX																			
(h) *cincinnata	DY		W		B									B					
*filamentosa	DX	f	B																	
recurva	DX																			
edulis	DX	A M	CLVBS M L		MOCAS									CAS					
(i) sidaefolia	DX	S		S		S								(S)		S			
actinia	DX	S																		
(j) mucronata	DY	S	(B) S		S (S)									S					
lilleki	DX	S			BS	BS													
oerstedii	DX								V ⊢					V		P				
*loretensis	DX	Z	Z	> >	Z		Z		> >		> > >		Z >	Z >		F			
(k) caerulea	DX		X		W															
*corruta	DX				K															
violacea	DX		S	< <	BS	S	S		< <		< < <		S <		WXBS S				
amethystina	DX																			
picturata	DX																			
subpeltata	DX																			
elegans	DX	Z		> >					> >		> > >								
*lonchophora	DX				Y															
eichleriana	DX																			
resticulata	DX																			
cyanea	DX	T	T	⊢⊣ ⊢⊣	T				⊢⊣ ⊢⊣		⊢⊣ ⊢⊣ ⊢⊣		⊢⊣		T T				
cf. cyanea	DX																			
garckei	DX																			
(l) kermesina	DX			⊢ ⊢	B				⊢ ⊢		⊢ ⊢ ⊢		B ⊢		B				
*watsoniana	DX				S		S													
miersii	EZ																			
(Calopathanthus) racemosa	BW																			
(Tryphostemmatoides) gracillima	DX			> >				Q	> >		> > >		>						
(Psilanthus) *sanguinolenta	EZ		N																	
(Pseudomurucuja) perfoliata	EZ			⋈ ⋈					⋈ ⋈		⋈ ⋈ ⋈		⋈							
tacsonioides	EZ																			
(Chloropathanthus) lancifolia	DZ																			
(Plectostemma) (a) coriacea	EZ	(Z)	L	⊢ ⊢	JS	(Z)	JLVS		⊢ ⊢		⊢ ⊢ ⊢		⊢ ⊢						
suberosa	EZ						U													
trinifolia	EZ																			
truncata	EZ																			
(b) auriculata	DX			⋈ ⋈	A		RA		⋈ ⋈		⋈ ⋈ ⋈		⋈						
*apetala	EZ						S													
organensis	EZ				S	BS	S													
misera	EZ						BS													
tricuspis	EZ																			
trifasciata	EZ						NW													
vespertilio	EZ				GA T	WGA T													
tuberosa	EZ																			
cuspidifolia	EZ																			
alnifolia	EZ		N																	
cuneata	EZ																			
chelidonea	EZ				WB	W	WB													
*ichthyura	EZ																			
*candollei	EZ																			
punctata	EZ																			
biflora	EZ						MP													
*glaucescens	EZ				X		WK													
pohlii	EZ																			
(c) costaricensis	DX				P		P									(P)			
capsularis	DX		P		VBS		CVBS								QQO			
rubra	DX					T										T			
(d) hahnii	DZ																			
(e) adenopoda	EX		MP		S		S												
warmingii	DX		S		S	S	S												
("Tetrastylis") lobata	DX		P																

SECTIONS: Astrophea, (a) = Dolichostemma, (b) = Euastrophea, (c) = Leptopoda, (d) = Pseudastrophea, (e) = Botryastrophea.
Plectostemma, (a) = Cieca, (b) = Decaloba, (c) = Xerogona, (d) = Hahniopathanthus, (e) = Pseudodysosmia.

APPENDIX TABLE *(continued). Butterflies in presumed evolutionary order within each of five radiating groups (left to right); plants in presumed evolutionary progression (top to botom), but radiating lines together.*

EARLY HELICONIUS RADIATION	IV-ADVANCED HELICONIUS RADIATION A	V-ADVANCED HELICONIUS RADIATION B

SERIES: Granadilla, (a) = Quadrangulares, (b) = Digitatae, (c) = Laurifoliae, (d) = Serratifoliae, (e) = Tiliaefoliae, (f) = Menispermifoliae, (g) = Setaceae, (h) = Incarnatae, (i) = Imbricatae, (j) = Simplicifoliae, (k) = Lobatae, (l) = Kermesinae.

J. Jamaica and other West Indian islands;

P. Panama and southeastern Costa Rica (Chiriquí, Darién);

Q. Northwestern Colombia, area of Quibdó (Chocó);

C. Central Colombian valleys (Cauca, Magdalena);

E. Western Ecuador (Chimborazo);

L. Lima area of western Peru south to northern Chile;

V. Northern Venezuela (Rancho Grande);

T. Trinidad (eastern part of Sucre/Trinidad);

O. Foothills and llanos in Orinoco drainage of eastern Colombia (Villavicencio);

N. Napo drainage in eastern Ecuadorian Andes (Abitagua, Napo);

U. Eastern Peru (Ucayali, Loreto, Chanchamayo);

Y. Northeastern Bolivia (Yungas);

W. Southwestern Brazil, western Mato Grosso and Rondônia (Guaporé, Rondônia);

X. Central Brazil, eastern Mato Grosso and Goiás (Araguaia);

R. Extreme northern Brazil (Roraima, Parima);

G. Guyana, Surinam, and (French) Guyane (Oyapock, northern part of Manaus/Guiana);

A. Lower and middle Amazon area in Pará and eastern Amazonas, Brazil (Belém, Tapajós, southern part of Manaus/Guiana);

B. Eastern Brazil, Pernambuco through Bahia to northern Espírito Santo (Bahia);

S. Southeastern Brazil, Minas Gerais, Rio de Janeiro and São Paulo (Rio de Janeiro);

Z. Extreme southern Brazil, Santa Catarina and Rio Grande do Sul.

The nature of the foodplant records varies. Most records have been derived by direct observation by the authors of oviposition and/or rearing larvae found on plants in nature, usually more than once. These are indicated by normal letters in the body of the Table. Single isolated records of oviposition and some literature references not documented by us are enclosed in parentheses. Cases of presumed usage, based upon observation and pre-oviposition behavior in the

field and/or acceptance of a naturally sympatric plant in the insectary, have been indicated by italicized letters. Such insectary and other inferrential data have been considered only when judged compelling. Only records in the first category have been considered in the summarizing Table 1.

Insect identification is absolutely accurate. Some of the plants (names asterisked) may have been misclassified with respect to species (or are yet to be classified), a not uncommon occurrence when reproductive structures are not available or do not convincingly correspond with descriptions of known taxa. Names not asterisked were satisfactorily identified, following Killip (1938). Possible errors in plant determinations do not affect in any way our conclusions, based on subgeneric and species-group identifications, plant growth forms, or numbers of different host plant species observed to be used by the butterflies. The data seem to be representative of host plant choice of heliconian species in nature.

NOTE ADDED IN PRESS:

Additional data of interest from Costa Rica (P) in the summer of 1975, mostly collected by Mr. John Smiley of the University of Texas, includes *H. hecale* on *P. pedata* (*Granadilla*, additional series *Pedatae*, just before (i) *cincinnata*); *H. erato* (red-banded) on *P. talamancensis* (*Plectostemma* just before *chelidonea*); *H. charitonia* on *P. pulchella* (*Plectostemma*, additional section *Pseudogranadilla*, just before (e) *hahnii*), and *H. clysonymus* on *P. filipes* (*Plectostemma* before *organensis*) and *P. standleyi* (*Plectostemma* before *pohlii*). Records of interest from extreme southern Texas (marginal to M) include *A. vanillae* on *P. tenuiloba* (*Plectostemma* before *suberosa*) and *P. affinis* (*Plectostemma* before *pohlii*), and *H. charitonia* on *P. lutea* (*Plectostemma* before *organensis*) and *P. affinis*. All of these records, which have been included in the total figures presented in Table 1, serve to reinforce the principal elements of the patterns recorded in the Appendix Table and represented in Table 1.