

BUTTERFLIES AND PLANTS: A STUDY IN COEVOLUTION¹

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One of the least understood aspects of population biology is community evolution—the evolutionary interactions found among different kinds or organisms where exchange of genetic information among the kinds is assumed to be minimal or absent. Studies of community evolution have, in general, tended to be narrow in scope and to ignore the reciprocal aspects of these interactions. Indeed, one group of organisms is all too often viewed as a kind of physical constant. In an extreme example a parasitologist might not consider the evolutionary history and responses of hosts, while a specialist in vertebrates might assume species of vertebrate parasites to be invariable entities. This viewpoint is one factor in the general lack of progress toward the understanding of organic diversification.

One approach to what we would like to call coevolution is the examination of patterns of interaction between two major groups of organisms with a close and evident ecological relationship, such as plants and herbivores. The considerable amount of information available about butterflies and their food plants make them particularly suitable for these investigations. Further, recent detailed investigations have provided a relatively firm basis for statements about the phenetic relationships of the various higher groups of Papilionoidea (Ehrlich, 1958, and unpubl.). It should, however, be remembered that we are considering the butterflies as a model. They are only one of the many groups of herbivorous organisms coevolving with plants. In this paper, we shall investigate the relationship between butterflies and their food

plants with the hope of answering the following general questions:

1. Without recourse to long-term experimentation on single systems, what can be learned about the coevolutionary responses of ecologically intimate organisms?
2. Are predictive generalities about community evolution attainable?
3. In the absence of a fossil record can the patterns discovered aid in separating the rate and time components of evolutionary change in either or both groups?
4. Do studies of coevolution provide a reasonable starting point for the understanding of community evolution in general?

FACTORS DETERMINING FOOD CHOICE

Before proceeding to a consideration of the relationships between butterfly groups and their food plants throughout the world, it is necessary briefly to consider some of the factors that determine the choice of food plants in this group and in phytophagous insects in general. Any group of phytophagous animals must draw its food supply from those plants that are available in its geographical and ecological range (Dethier, 1954). For instance, the butterflies are primarily a tropical group, and therefore there is a relatively greater utilization of primarily tropical than of temperate families of plants. The choice of oviposition site by the imago is also important. Many adult butterflies and moths lay their eggs on certain food plants with great precision as stressed by Merz (1959), but on the other hand, numerous "mistakes" have been recorded (e.g., Remington, 1952; Dethier, 1959). In such cases, larvae have either to find an appropriate plant or perish. There is an obvious selective advantage in oviposition on suitable

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plants, but inappropriate choices can be overcome by movement of the larvae. Furthermore, larvae feeding on herbs often consume the entire plant, and then must move even if the adult originally made an appropriate choice.

Larval choice therefore plays an important role in food plant relationships. An excellent review of a long series of experiments pertinent to this subject has recently been presented by Merz (1959); much of the following is based on his account. The condition of a given larva often has an effect on what foods it will or will not accept. In addition, many structural and mechanical characteristics of plants modify these relationships, mostly by limiting the acceptability of those plants in which they occur. For example, Merz (1959) found that larvae of *Lasiocampa quercus*, a moth that normally feeds along the edge of leaves, could not eat the sharply toothed leaves of holly (*Ilex*, Aquifoliaceae). When these same leaves were cut so that untoothed margins were presented, the larvae ate them voraciously. In other cases, larvae eat the young, soft leaves of plants but not the old, tough leaves of the same plants. Many Lycaenidae feed on flowers, and these butterflies may be unable to utilize the tough foliage of the same plants. Numerous similar examples could be given, but it must be borne in mind that chemical factors are operative in the same plants that present mechanical difficulties to larvae (Thorsteinson, 1960), and actually may be more important.

Chemical factors are of great general importance in determining larval food choice. In the first place, potential food sources are probably all nutritionally unbalanced to some extent (Gordon, 1961). The exploitation of a particular plant as a source of food thus involves metabolic adjustments on the part of an insect. These render the insect relatively inefficient in utilizing other sources of food and tend to restrict its choice of food plants. Secondly, many plants are characterized by the presence of secondary metabolic substances.

These substances are repellent to most insects and may often be decisive in patterns of food plant selection (Thorsteinson, 1960). It has further been demonstrated that the chemical compounds that repel most animals can serve as trigger substances that induce the uptake of nutrients by members of certain oligophagous groups (Dethier, 1941, 1954; Thorsteinson, 1953, 1960). Presence of such repellent compounds may be correlated with the presence of the nutrients. Both odor and taste seem to be important.

The chemical composition of plants often changes with age, exposure to sunlight, or other environmental factors (Merz, 1959; Flück, 1963), and this may be critical for phytophagous insects (Dethier, 1954). For example, insects that feed on Umbelliferae prefer the old leaves, which appear to us less odorous than the young ones. Some insects that feed on alkaloid-rich species of *Papaver* (Papaveraceae) prefer the young leaves, which are relatively poor in alkaloids. Diurnal chemical cycles, influenced by exposure of the plant to sunlight, may be of prime importance in determining the habits of night-feeding groups, such as Argynnini.

Merz (1959, p. 159) has given a particularly interesting case of chemical repellents at the specific level. The larvae of the moth *Euchelia jacobaeae* feed on many species of *Senecio* (Compositae), but not on the densely glandular-hairy *S. viscosus*. When the glandular substance was dissolved in methyl alcohol, the larvae ate *S. viscosus*. When the same substance was painted on the leaves of other normally acceptable species of *Senecio*, these were refused. In an extensive study of the food plants of *Plebejus icarioides* (Lycaeninae), Downey (1961, 1962) showed that larvae would feed on any species of *Lupinus* (Leguminosae) in captivity, but populations in the field normally utilized only one or a few of the possible range of *Lupinus* species growing locally. This work suggests the subtle interaction of ecological, chemical, and mechanical factors that doubtless

characterizes most natural situations. Relationships with predators (Brower, 1958), parasites (Downey, 1962), or, at least in the case of Lycaenidae, ants (Downey, 1962), may further modify patterns of food plant choice.

Despite all of these modifying factors, there is a general and long-recognized pattern running through the food plants of various groups of butterflies, and it is this pattern with which we shall be concerned. It certainly should not be inferred from anything that follows that all members of a family or genus of plants are equally acceptable to a given butterfly (for example, see Remington, 1952). We have placed our main emphasis on positive records, especially at the level of plant species and genera.

THE DIVERSITY OF BUTTERFLIES

The butterflies comprise a single superfamily of Lepidoptera, the Papilionoidea. In comparison with many other superfamilies of insects they are uniform morphologically and behaviorally. Table 1 gives a rough idea of the taxonomic diversity of this superfamily.

Papilionoidea are divided into five families. Two of these, Nymphalidae and Lycaenidae, contain at least three-quarters of the genera and species; it is uncertain which family is the larger. Two smaller families, Pieridae and Papilionidae, include virtually all remaining butterflies. Pieridae, although containing many fewer genera and species than either Lycaenidae or Nymphalidae, form a prominent part of the butterfly fauna in many parts of the world, making up in number of individuals what they lack in number of kinds. Papilionidae are a group about half the size of Pieridae, but gain prominence through the large size of the included forms. The tiny family Libytheidae, closely related to Nymphalidae, is obscure to everyone except butterfly taxonomists.

The Papilionidae lead the butterflies in morphological diversity. Nymphalidae probably take second place, with Pieridae and

Lycaenidae about tied for third. Difficult as this diversity is to estimate, it is clear that Papilionidae are a more heterogeneous group of organisms than any of the other families, whereas, considering the number of species and genera included, Lycaenidae are remarkably uniform. A rough idea of the phenetic relationships of the major groups of butterflies is given by Ehrlich (1958).

With food plant records from between 46 and 60% of all butterfly genera (table 1), it seems highly unlikely that future discoveries will necessitate extensive revisions of the conclusions drawn in this paper. The food plants of Riodininae are very poorly known, however, and it will be interesting to have more information about them and records for other outstanding "unknowns" such as *Styx* and *Pseudopontia*. It is, however, difficult to imagine any additional food plant record that would seriously distort the patterns outlined here.

BUTTERFLY FOOD PLANTS

Sources of Information

The food plant information abstracted in this paper is derived principally from two sources. First, we have examined all the extensive and scattered literature that we could uncover with a library search and through the recommendations of various lepidopterists. Particularly helpful have been the volumes of Barrett and Burns (1951), Corbet and Pendlebury (1956), Costa Lima (1936), Ehrlich and Ehrlich (1961), Lee (1958), Seitz (1906-1927), van Son (1949, 1955), Wiltshire (1957), and Wynter-Blyth (1957), as well as the *Journal of the Entomological Society of South Africa*, the *Journal of the Lepidopterists' Society* (formerly *Lepidopterists' News*), and the *Journal of Research on the Lepidoptera*.

Our second major source of information has been provided by the following scientists, who have aided us in this ambitious undertaking not only by sending unpublished data and reprints of their works, but by helping to evaluate the validity of cer-

TABLE 1. *Summary of the taxonomic diversity of Papilionoidea*

Taxon	Approximate number of		Distribution
	Genera*	Species	
Papilionidae	24(22)	575-700	
Baroniinae	1(1)	1	Central Mexico
Parnassiinae	8(8)	45-55	Holarctic and Oriental; greatest diversity, Asia
Papilioninae	15(13)	480-640	Worldwide; mainly tropical. Greatest diversity, Old World tropics
Pieridae	58(40)	950-1,150	
Coliadinae	11(8)	225-250	Cosmopolitan; greatest diversity tropics outside of Africa
Pierinae	43(29)	650-750	Cosmopolitan; greatest diversity tropics
Dismorphiinae	3(3)	80-120	Primarily Neotropical; one small Palearctic genus
Pseudopontiinae	1(0)	1	West equatorial Africa
Nymphalidae	325-400 (ca. 202)	4,800-6,200	
Ithomiinae	30-40(10)	300-400	Neotropical; <i>Tellervo</i> Australian
Danainae	10-12(10)	140-200	Cosmopolitan; greatest diversity Old World tropics
Satyrinae	120-150 (ca. 70)	1,200-1,500	Cosmopolitan; greatest diversity extratropical
Morphinae	23-26(12)	180-250	Indomalayan and Neotropical
Charaxinae	8-10(8)	300-400	Tropicopolitan, few temperate
Calinaginae	1(1)	1	Oriental
Nymphalinae	125-150 (ca. 85)	2,500-3,000	Cosmopolitan
Acraeinae	8(6)	225-275	Tropical; greatest diversity, Africa
Libytheidae	1(1)	10	Cosmopolitan
Lycaenidae	325-425 (ca. 167)	5,800-7,200	
Riodininae	75-125(17)	800-1,200	Tropical, few Nearctic and Palearctic. Metropolis, Neotropical
Styginae	1(0)	1	Peruvian Andes
Lycacninae	250-300 (ca. 150)	5,000-6,000	Cosmopolitan; greatest diversity, Old World tropics
Total	730-930 (ca. 432)	12,000-15,000	

* Number in parentheses indicates number of genera for which food plant records are available.

tain published records and commenting on other aspects of the work. The cooperation of these people has been truly extraordinary, and we are particularly indebted to them: Remauldo F. d'Almeida (Brazil), Peter Bellinger (USA), C. M. de Biezanko (Brazil), L. P. Brower (USA), C. A. Clarke (England), H. K. Clench (USA), J. A. Comstock (USA), C. G. C. Dickson (Africa), J. C. Downey (USA), Maria Etcheverry (Chile), K. J. Hayward (Argentina), T. G. Howarth (England), Taro

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To our knowledge, the data assembled here represent the most extensive body of information ever assembled on the interactions between a major group of herbivorous animals and their food plants.

EVALUATION OF THE LITERATURE

Extreme care has been taken in associating insects with particular food plants, as the literature is replete with errors and unverified records. In evaluating records, preference has been given to those which are concerned with the entire life cycle of a particular insect on a wild plant. Laboratory experiments and records from cultivated plants demonstrate only potentialities, not necessarily natural associations. In the laboratory, larvae may be starved or plants abnormal. In the wild, larvae are often misidentified, especially if not reared to maturity (cf. Brower, 1958b). Even more serious is the lack of precise plant identifications, or their identification in the vernacular only, which almost inevitably leads to confusion (Jørgensen, 1932). Any serious student of phytophagous animals should preserve adequate herbarium specimens of the plants with which he is concerned (cf. Remington, 1952, p. 62); only by doing this can the records be verified. Despite the extremely erratic oviposition behavior often shown by butterflies (Dethier, 1959), oviposition records have all too frequently been accepted as being equivalent to food plant records. Finally, nomenclatural difficulties, including changes in name and careless misspellings (e.g., "Oleaceae" for Olacaceae), have given rise to serious errors. In the literature on butterfly food plants, errors have often been compounded when copied from one source to another, and they are difficult to trace back to their origins. All of these problems make quantitative comparisons unreasonable. We therefore have been exceedingly conservative about accepting records, and focused our attention primar-

ily on broad, repeatedly verified patterns of relationship.

The Food Plants of Butterflies

In this section, we will first outline the main patterns of food plant choice for each family, and then discuss what bearing these patterns have on our interpretation of relationships within the various butterfly families. It is necessary to give the data in considerable detail, as no comprehensive survey on a world basis is available elsewhere.

Papilionidae.—There are three subfamilies. *Baronia brevicornis*, the only species of Baroniinae, occurs in Mexico and feeds on *Acacia* (Leguminosae; Vazquez and Perez, 1961). In Parnassiinae, all five genera of Zerynthiini (Munroe, 1960; Munroe and Ehrlich, 1960) feed on Aristolochiaceae, as does *Archon* (Parnassiini). *Hypermnestra* (Parnassiini) is recorded from *Zygophyllum* (Zygophyllaceae). *Parnassius* feeds on Crassulaceae and herbaceous Saxifragaceae, two closely related families, with one small group on Fumariaceae. In view of the discussion below, it is of interest that Zygophyllaceae are close relatives of Rutaceae, and Fumariaceae are rich in alkaloids similar to those of woody Ranales (Hegnauer, 1963).

The third and last subfamily, Papilioninae, is cosmopolitan but best developed in the Old World, and consists of three tribes: Troidini, Graphiini, and Papilionini. The eight genera of Troidini feed mostly on Aristolochiaceae, with individual species of *Parides* also recorded from Rutaceae, Menispermaceae, Nepenthaceae, and Piperaceae. *Parides* (*Atrophaneura*) *daemonius* is reported to feed on *Osteomeles* (Rosaceae), and *P. (A.) antenor*, a Malagasy butterfly that is the only representative of its tribe in the Ethiopian region, feeds on *Combretum* (Combretaceae). Both of these last-mentioned records need confirmation. At least two species of *Battus* have been recorded from Rutaceae in addition to the usual Aristolochiaceae. Records available for five of the seven genera of Graphiini

(*Eurytides*, *Graphium*, *Lamproptera*, *Protographium*, *Teinopalpus*) are mostly from Annonaceae, Hernandiaceae, Lauraceae, Magnoliaceae, and Winteraceae. This is clearly a closely allied group of plant families referable to the woody Ranales. In addition, some species of *Graphium* feed on Rutaceae, and others both on Apocynaceae (*Landolphia*) and Annonaceae (one of the latter also on *Sphedamnocarpus*, Malpighiaceae). Several species of *Eurytides* feed on *Vitex* (Verbenaceae) and one on *Jacobinia* (Acanthaceae). *Eurytides lysithous* feeds both on Annonaceae and on *Jacobinia*, and *E. helios* both on *Vitex* and Magnoliaceae. The bitypic Palearctic *Iphiclides* departs from the usual pattern for the group in feeding on a number of Rosaceae-Pomoideae.

The third and last tribe, Papilionini, consists only of the enormous cosmopolitan genus *Papilio*. Two of the five sections recognized by Munroe (1960; II, IV) are primarily on Rutaceae, with occasional records from Canellaceae, Lauraceae, and Piperaceae. Members of the circumboreal *Papilio machaon* group are not only on Rutaceae but also on Umbelliferae and *Artemisia* (Compositae). The African *P. demodocus*, in another group, is known to feed on Rutaceae and Umbelliferae, as well as *Pseudospondias* (Anacardiaceae), *Ptaeroxylon* (Meliaceae), and *Hippobromus* (Sapindaceae). Another African species, *P. dardanus*, is recorded from Rutaceae and also from *Xymalos* (Flacourtiaceae; Dickson, pers. comm.). The Asian and Australian *P. demoleus* is mostly on Rutaceae but also locally on *Salvia* (Labiatae) and *Psoralea* (Leguminosae). The other three sections (Munroe's I, III, V) are primarily associated with Annonaceae, Canellaceae, Hernandiaceae, Lauraceae, and Magnoliaceae, with a few records from Berberidaceae, Malvaceae (*Thespea*), and Rutaceae. The North American temperate *Papilio glaucus* group (sect. II) feeds not only on Lauraceae and Magnoliaceae like its more southern relatives but also on Aceraceae, Betulaceae, Oleaceae, Platanaceae, Rhamnaceae, Rosa-

ceae, Rutaceae (*Ptelea*), and Salicaceae (Brower, 1958b).

In Papilionidae, Munroe and Ehrlich (1960) have argued that the red-tuberculate, Aristolochiaceae-feeding larvae of Papilioninae-Troidini and Parnassiinae-Zerynthiini, plus *Archon* (Parnassiinae-Parnassini) are so similar, and the likelihood of their converging on Aristolochiaceae so remote, that these probably represent the remnants of the stock from which the rest of Papilioninae and Parnassiinae were derived. Viewed in this context other food plants of these groups are secondary. The two remaining tribes of Papilioninae (Papilionini, Graphiini) are above all associated with the group of dicotyledons known as the woody Ranales. This is a diverse assemblage of plant families showing many unspecialized characteristics. Thorne (1963) has used the food plant relationships of Papilionidae as a whole to support his suggestion of affinity between Aristolochiaceae and Annonaceae (one of the woody Ranales). He appears to have established the existence of this similarity on morphological evidence. Likewise, similar alkaloids are shared by Aristolochiaceae and woody Ranales (Hegnauer, 1963; Alston and Turner, 1963, p. 170). Recently, Vazquez and Perez (1961) described the life cycle of *Baronia brevicornis*, the only member of the third subfamily of the group. *Baronia* feeds on *Acacia* (Leguminosae) and has tuberculate larvae like those of the forms that feed on Aristolochiaceae. Considering its morphological distinctness, and in accordance with the scheme of relationships presented by Munroe and Ehrlich (1960, p. 175), it appears likely that *Baronia* represents a phylogenetic line which diverged early from that leading to the rest of Papilionidae. It may thus be the only member of the family neither feeding on Aristolochiaceae nor descended from forms that did.

Following this reasoning, we suggest that the original transition to Aristolochiaceae opened a new adaptive zone for Papilionidae. Their further spread and the multi-

plication of species was accompanied by the exploitation of other presumably chemically similar plant groups, such as woody Ranales, in areas where Aristolochiaceae were poorly represented, like Africa today. The site of greatest diversity for both Aristolochiaceae and Papilionidae is Asia. It is likely that the major diversification of Papilionidae (involving differentiation into Parnassiinae and Papilioninae) took place after the evolution of Aristolochiaceae. When this might have been is entirely uncertain, despite the unfounded speculations of Forbes (1958).

Another interesting problem is posed by the many representatives of Papilionini and Graphiini feeding on Rutaceae, in addition to woody Ranales. Rutaceae are morphologically very different from woody Ranales, and have not been closely associated with them taxonomically. Recently, however, Hegnauer (1963) has pointed out that some Rutaceae possess the alkaloids widespread in woody Ranales, in addition to an unusually rich repertoire of other alkaloids. Earlier, Dethier (1941) showed the similarity between the attractant essential oils in Rutaceae and Umbelliferae. Some Rutaceae-feeding groups of *Papilio* seem to have shifted to Umbelliferae, especially outside of the tropics. Dethier also implicated some of the similar-scented species of *Artemisia* (Compositae), another plant group fed on by at least one species of *Papilio*. Although species of *Papilio* link these groups of plants, none is known to feed on Burseraceae, Cneoraceae, Simarubaceae, or Zygophyllaceae, families thought to be related to Rutaceae but not known to contain alkaloids or coumarins (Price, 1963). On the other hand, the record of *Papilio demodocus* on *Ptaeroxylon* (Meliaceae), in addition to numerous Rutaceae, would seem to indicate a promising plant to investigate for the alkaloids suspected (Price, 1963) in Meliaceae.

Pieridae.—Our discussion of Pieridae is based taxonomically on the generic review of Klots (1933) as modified by Ehrlich (1958). There are four subfamilies, but

nothing is known of the biology of the monobasic West African Pseudopontiinae. Of the remaining three, Dismorphiinae, including the Neotropical *Dismorphia* and *Pseudopieris* and the Palearctic *Leptidia*, are recorded only on Leguminosae. Larval food plants are known for 7 of the 11 genera of Coliadinae. *Catopsilia*, *Phoebis*, *Anteos*, *Eurema*, and *Colias* are mostly associated with Leguminosae, but there are a few records from Sapindaceae, Guttiferae, Euphorbiaceae, Simarubaceae, Oxalidaceae, Salicaceae, Ericaceae, and Gentianaceae (the last three with northern and montane species of *Colias*). On the other hand, three genera are associated with non-leguminous plants: *Gonepteryx* with *Rhamnus* (Rhamnaceae), *Nathalis* with Compositae, and *Kricogonia* with *Guaiacum* (Zygophyllaceae). Nonetheless, Leguminosae are decidedly the most important food plants of Coliadinae.

Pierinae, the third subfamily, are divided into two tribes, Pierini (36 genera) and Euchloini (7). In Euchloini, the temperate *Anthocharis*, *Euchloë*, *Zegris*, and *Hesperocharis* (also from *Phrygilanthus*, Loranthaceae) feed on Cruciferae, the tropical *Pinacopteryx* and *Hebemoia* on Capparidaceae. For Pierini, 14 of the 23 genera for which we know something of the food plants (namely, *Appias*, *Ascia*, *Beleinois*, *Ceporis*, *Colotis*, *Dixeia*, *Elodina*, *Eronia*, *Ixias*, *Leptosia*, *Pareronia*, *Pieris*, *Prioneris*, and *Tatochila*) are primarily on Capparidaceae in the tropics and subtropics and on Cruciferae in temperate regions. Some have occasionally been reported to feed on Resedaceae, Salvadoraceae, and Tropaeolaceae. There are also a very few scattered records from other plants, including one or two from Leguminosae. The basis for selecting Capparidaceae, Cruciferae, Resedaceae, Salvadoraceae, and Tropaeolaceae is relatively easy to comprehend, since all of these plants are known to contain mustard oil glucosides (thioglucosides) and the associated enzyme myrosinase which acts in the hydrolysis of glucosides to release mustard oils (Alston and Turner,

1963, p. 284–288). In an early series of food choice experiments, Verschaeffelt (1910) found that larvae of *Pieris rapae* and *P. brassicae* would feed on Capparidaceae, Cruciferae, Resedaceae, and Tropaeolaceae, as well as another family which contains mustard oils but upon which Pierinae are not known to feed in nature: Moringaceae. Verschaeffelt also found that these larvae would eat flour, starch, or even filter paper if it was smeared with juice expressed from *Bunias* (Cruciferae), and Thorsteinson (1953, 1960) showed that the larvae would eat other kinds of leaves treated with sinigrin or sinalbin (two common mustard oil glucosides) if the leaves were not too tough and did not contain other kinds of repellents. Very few butterflies outside Pieridinae feed on these plants, but there is one example in Lycaeninae. In addition, there are at least two records of *Phoebis* (Coliadinae) from Capparidaceae and Cruciferae. Numerous groups of insects other than butterflies are characteristically associated with this same series of plant families (Fraenkel, 1959).

It is not so easy to interpret scattered records of these pierine genera feeding on other plant families: *Belenois raffrayi* on *Rhus* (Anacardiaceae); *Nepheronia argyria* on Capparidaceae, but also *Cassipourea* (Rhizophoraceae) and *Hippocratea* (Hippocrateaceae), with *N. thalassina* reported only from *Hippocratea*; *Ascia monuste* on Rhamnaceae and *Cassia* (Leguminosae), as well as Capparidaceae; and *Tatochila autodice* on *Cestrum* (Solanaceae) and also *Medicago* (Leguminosae). Several species of *Appias* have been reported from different genera of Euphorbiaceae, whereas others feed both on Capparidaceae and Euphorbiaceae, but this probably can be explained somewhat more simply, since mustard oils have been reported in some genera of Euphorbiaceae (Alston and Turner, 1963, p. 285).

The remaining genera of Pierini fall mostly into what has been called the *Delias* group. Of these, *Catantixia* and *Archonias* have been recorded from *Phrygilanthus*

(Loranthaceae) in South America, and *Delias*, a large Indo-Malaysian genus, from "*Loranthus*" (Loranthaceae) and *Exocarpos* of the closely related Santalaceae, with *D. aglaja* on *Nauclea* (Rubiaceae). *Aporia*, a large genus of temperate regions of the Old World, has several species on *Berberis* (Berberidaceae), and one on woody Rosaceae. *Pereute*, South American, feeds on *Ocotea* (Lauraceae; Jörgensen, 1932), Tiliaceae, and Polygonaceae. Two very peculiar genera of the *Delias* group are the monotypic Mexican *Eucheira*, which feeds on woody hard-leaved Ericaceae, and the bitypic western North American *Neophasia*, which feeds on various genera of Pinaceae. It is very interesting that *Cepora*, which falls into the *Delias* group morphologically, feeds on *Capparis* like many other Pierini.

Finally, the large, taxonomically isolated, Ethiopian *Mylothris* feeds on Loranthaceae and Santalaceae (*Osyris*), with *M. bernice rubricosta* on *Polygonum* (Polygonaceae).

It is difficult to understand the reasons for large groups of Pierinae being associated both with plants that possess mustard oils and with Loranthaceae–Santalaceae; neither morphological nor biochemical evidence has been adduced to link these two groups of plants. Perhaps the Loranthaceae-feeders represent an old offshoot of Pierinae; in any case it would appear that the main diversification of this group occurred after it became associated with Capparidaceae Cruciferae.

Nymphalidae.—This enormous family is divided into eight subfamilies which will be discussed one by one in the succeeding paragraphs.

Ithomiinae are primarily American, and there feed only on Solanaceae (many genera). The Indo-Malaysian *Tellervo*, only Old World representative of the group, which is segregated as a distinct tribe Tellervini, has been recorded from *Aristolochia* (Aristolochiaceae). The identity of the plant was inferred from the fact that papilionid larvae normally associated with *Aristolochia* were found on it with *Tellervo*. Solanaceae are rich in alkaloids (as are

Aristolochiaceae), and are very poorly represented among the food plants of butterflies as a whole. The diversification of the ithomiines that feed on them has probably followed a pattern similar to that of Papilionidae on Aristolochiaceae and Pierinae on Capparidaceae–Cruciferae. Many other groups of insects feed primarily on Solanaceae (Fraenkel, 1959).

Danainae are a rather uniform cosmopolitan group, obviously related to Ithomiinae. The danaines feed primarily and apparently interchangeably on Apocynaceae and Asclepiadaceae. In addition, there are records of *Euploea*, *Ituna*, and *Lycorella* on Moraceae and of the last occasionally on *Carica* (Caricaceae). All of these plants have milky juice. There is also a single record of *Ituna ilione*, which normally feeds on *Ficus* (Moraceae), from *Myoporum* (Myoporaceae). Apocynaceae and Asclepiadaceae form a virtual continuum in their pattern of variation and can scarcely be maintained as distinct (Safwat, 1962). Both are noted for their abundant bitter glycosides and alkaloids (Alston and Turner, 1963, p. 258), and share at least some alkaloids (Price, 1963, p. 431) and pyridines with Moraceae. Thus it appears very likely that here too the acquisition of the ability to feed on Apocynaceae and Asclepiadaceae has constituted for Danainae the penetration of a new adaptive zone, in which they have radiated. Numerous distinctive segments of other insect orders and groups likewise feed on these two plant families.

Eleven genera of Morphinae are recorded from a variety of monocotyledons: Bromeliaceae, Gramineae (mostly bamboos), Marantaceae, Musaceae, Palmae, Pandanaceae, and Zingiberaceae. In contrast, most species of *Morpho* feed on dicotyledons, including Canellaceae, Erythroxylaceae, Lauraceae, Leguminosae, Menispermaceae, Myrtaceae, Rhamnaceae, and Sapindaceae, but *M. aega* feeds on bamboos (Gramineae) and *M. hercules* on Musaceae. Whether the progenitors of *Morpho* fed on dicotyledons or monocotyledons cannot be determined.

Closely related to Morphinae are the more temperate Satyrinae, an enormous group that feeds mostly on Gramineae (including bamboos and canes) and Cyperaceae, occasionally on Juncaceae. *Pseudonympha vigilans* feeds on *Restio* (Restionaceae), a family close to Gramineae, *Physcaneura pione* on Zingiberaceae, and *Flymnias* on Palmae. There are no records of this group from dicotyledons. Thus the phenetically similar Morphinae–Satyrinae assemblage is the outstanding example in butterflies of a group associated primarily with monocotyledons.

The distinctive tropicopolitan Charaxinae are often associated with woody Ranales (Annonaceae, Lauraceae, Monimiaceae, Piperaceae), but also with such diverse families as Anacardiaceae, Araliaceae (*Schefflera*), Bombacaceae, Celastraceae, Connaraceae, Convolvulaceae, Euphorbiaceae, Flacourtiaceae, Hippocrateaceae, Leguminosae, Linaceae, Malvaceae, Meliaceae, Melianthaceae, Myrtaceae, Proteaceae, Rhamnaceae, Rutaceae, Salvadoraceae (*Charaxes hansali*), Sapindaceae, Sterculiaceae, Tiliaceae, Ulmaceae, and Verbenaceae. Records (largely Sevastopulo and van Someren, pers. comm.) are available for about 50 African species of *Charaxes*, most of which are associated with dicotyledons. At least three feed on grasses (Gramineae), two of these on dicotyledons also.

The Oriental *Calinaga buddha*, the only species of Calinaginae, feeds on *Morus* (Moraceae).

Nymphalinae are a huge cosmopolitan group with relatively few “gaps” in their pattern of variation which would permit the recognition of meaningful subgroups (cf. Reuter, 1896; Chermock, 1950). The tribes do, however, display some significant patterns in their choice of food plants, with Heliconiini (Michener, 1942) and Argynnini feeding mostly on the Passifloraceae–Flacourtiaceae–Violaceae–Turneraceae complex of families, a closely related group of plants also important for Acraeinae. Acraeinae (see below), Heliconiini, and Argynnini are closely related phenetically,

and their diversification may have taken place from a common ancestor associated with this particular assemblage of plants. No biochemical basis is known for the association of this series of four plant families, but we confidently predict that one eventually will be found (cf. also Gibbs, 1963, p. 63). Melitaeini are often associated with Acanthaceae, Scrophulariaceae and their wind-pollinated derivatives Plantaginaceae, and with Compositae and Verbenaceae. Nymphalini feed on plants of the same families as Melitaeini, but also very prominently on the Ulmaceae-Urticaceae-Moraceae group and the Convolvulaceae, Labiatae, Portulacaceae, and Verbenaceae. A single species in this group, however, *Nymphalis canace*, feeds on Liliaceae and Dioscoreaceae. Apaturini are associated chiefly with Ulmaceae, especially *Celtis*. Cyrestini (*Chersonesia*, *Cyrestis*, and *Marpesia*) and Gynaeciini (*Gynaecia* and *Historis*, but not *Callizona* and *Smyrna*) are often associated with Moraceae, and Hamadryini (*Ectima*, *Hamadryas*), Didonini (*Didonis*), Ergolini (*Byblia*, *Byblis*, *Ergolis*, *Eurytela*, *Mestra*), Eunicini (*Asterope*, *Catonephele*, *Eunica*, *Myscelia*), and Dynamini (*Dynamine*) mostly on the related Euphorbiaceae, which, like Moraceae, have milky sap. In addition to the Eunicini just mentioned, *Diaethria* (*Callicore*, *Catagramma*), *Epiphile*, *Haematera*, *Pyrroggyra*, and *Temenis* feed almost exclusively on Sapindaceae. There is no obvious dominant theme for the last tribe, Limenitini, but it is interesting to note that two species of *Euphaedra* (*Najas*), a group that is mostly on Sapindaceae, are on *Cocos* and other Palmae. Additional families represented among the food plants of Nymphalinae are: Aceraceae, Amaranthaceae, Anacardiaceae, Annonaceae, Berberidaceae, Betulaceae, Bignoniaceae, Bombacaceae, Boraginaceae, Caprifoliaceae, Combretaceae, Corylaceae, Crassulaceae, Cucurbitaceae, Dilleniaceae, Dipterocarpaceae, Ebenaceae, Eleagnaceae, Ericaceae, Fagaceae, Gentianaceae, Geraniaceae, Guttiferae, Icacinaceae, Leguminosae (very uncommonly), Loranaceae, Malvaceae,

Melastomaceae, Melianthaceae, Menispermaceae, Myrtaceae, Oleaceae, Ranunculaceae (*Vanessa* on *Delphinium*), Rhamnaceae, Rosaceae, Rubiaceae, Sabiaceae, Salicaceae, Sapotaceae, Saxifragaceae, Sterculiaceae, Thymeleaceae, Tiliaceae, and Vitaceae.

Some of the butterflies in this group feed on a very wide range of plants, and most of the families mentioned in the above list are represented by one or at most a very few records. For example, *Euptoieta claudia* is known to feed on Berberidaceae (*Podophyllum*), Crassulaceae, Leguminosae, Linaceae, Menispermaceae, Nyctaginaceae, Passifloraceae, Portulacaceae, Violaceae, and even Asclepiadaceae (*Cyanthum*), and *Precis lavinia* is recorded from, among others, Acanthaceae, Bignoniaceae, Compositae, Crassulaceae, Onagraceae (*Ludwigia*), Plantaginaceae, Scrophulariaceae, and Verbenaceae.

Acraeinae, a rather small tropical group, are often associated with Passifloraceae-Flacourtiaceae-Violaceae-Turneraceae, as noted above, but also with Amaranthaceae, Compositae, Convolvulaceae, Leguminosae, Lythraceae, Moraceae, Polygonaceae, Rosaceae, Sterculiaceae, Urticaceae, and Vitaceae. In addition, *Acraea encedon* is reported from *Commelina* (Commelinaceae).

For the very diverse Nymphalidae as a whole, the following groups of plants are especially important: (1) Passifloraceae-Flacourtiaceae-Violaceae-Turneraceae; (2) Ulmaceae-Urticaceae-Moraceae, as well as the closely related (Thorne, pers. comm.) Euphorbiaceae; (3) Acanthaceae-Scrophulariaceae-Plantaginaceae. The second and third of these groups are represented among the food plants of other butterflies, such as Lycaeninae, but not abundantly. Conversely, as will be seen, the groups of food plants commonly represented in Lycaenidae—for example, Fagaceae, Leguminosae, Oleaceae, Rosaceae—are rare in Nymphalidae. Although each of these two families of butterflies is very wide in its choice of food plants, there is a distinctiveness to the two patterns which suggests a history of selection along different lines.

Libytheidae.—This small family consists of a single widespread genus, *Libythea*, which feeds almost exclusively on *Celtis* (Ulmaceae), but in southern Japan on *Prunus* (Rosaceae). *Libythea* is obviously closely related to Nymphalidae (Ehrlich, 1958), as has recently been confirmed by a quantitative study of adult internal anatomy (Ehrlich, unpubl.).

Lycaenidae.—An enormous group, the family Lycaenidae may be larger even than the Nymphalidae. Lycaenidae are in general poorly known from the standpoint of food plants (Downey, 1962). Our discussion is based largely on the classification of Clench (1955 and pers. comm.). Nothing is known of the life history of the Peruvian *Styx injernalis*, only member of Styginae. Of the two remaining subfamilies, Riodininae, divided into three tribes, will be discussed first. *Euselasia* (Euselasiini) has been recorded from *Mammea* (Guttiferae) and three genera of Myrtaceae. The Old World Hamearini consist of three genera, with *Dodona* and *Zemeros* on *Maesa* (Myrsinaceae) and *Hamearis* on *Primula* (Primulaceae). The two plant families are very closely related, with Myrsinaceae being primarily tropical and woody, Primulaceae primarily temperate and herbaceous. The third and largest tribe, Riodinini, is divided into four subtribes. *Abisara* (Abisariti) feeds, like the Hamearini, on Myrsinaceae; *Theope* (Theopiti) is on *Theobroma* (Sterculiaceae); and *Helicopus* (Helicopiti) is one of two members of the subfamily known to feed on a monocotyledon, in this case *Montrichardia* (Araceae). The remaining genera of Riodinini are in the exclusively New World Riodiniti, with very few records for a great many species. Plant families represented are Acanthaceae, Anacardiaceae, Aquifoliaceae, Chenopodiaceae, Compositae, Euphorbiaceae, Leguminosae, Moraceae, Myrtaceae, Polygonaceae, Ranunculaceae (*Clematis*), Rosaceae, Rutaceae, Sapindaceae, and Sapotaceae. Deserving special mention are the records of *Cariomathus* and *Rhetus* from Loranthaceae, *Napaea nepos* from *Oncidium* (Orchi-

daceae), and *Stalachtis* from *Oxypetalum* (Asclepiadaceae; cf. Jörgensen, 1932, p. 43, however, where it is suggested that associations of larvae of this group with ants may determine the food plant on which they are found). The scanty food plant records for this group are thus sufficiently diverse to suggest that further studies of food plants will be of considerable interest. The most salient feature is the occurrence of Hamearini and Abisariti on Myrsinaceae and Primulaceae, two closely related families that are fed on by very few other butterflies.

Lycaeninae likewise consist of three tribes. Of these, Leptinini are African and feed on lichens, some of them (*Durbania*, *Durbaniopsis*, and *Durbaniella*) even on the low crustose lichens that grow on rocks. Liphyrini, almost entirely confined to the Old World tropics, are predaceous on aphids, coccids, ant larvae, membracids, and jassids. There are no reliable records of phytophagy in this group.

The largest of the three tribes, Lycaenini, presents a bewildering array of forms that can be separated only informally at present. Many of these larvae are closely associated with and tended by ants, and this association may modify their food plant relationships (Downey, 1962; Stempffer, pers. comm.). For the large *Plebejus* group (the "blues"), we have records of the food plants of 45 genera, and 33 of these are known to feed, at least in part, on Leguminosae. Records of special interest in this group include *Nacaduba* on several genera of Myrsinaceae and *Agriades* on Primulaceae; in this way they are like Hamearini and Abisariti of Riodininae. *Chilades* and *Neopithecops* are recorded from Rutaceae. Four genera (*Philotes*, *Scolitantides*, *Talicauda*, and *Tongeia*) are known to feed, at least in part, on Crassulaceae. *Catachrysops pandava* feeds not only on *Wagatea* and *Xylia* (Leguminosae) but also on *Cycas revoluta* (Cycadaceae), a cycad to which it does harm in gardens. *Hemiargus ceraunus* feeds on Marantaceae. Although most species of *Jamides* feed on Legumino-

sae, *J. alecto* feeds on Zingiberaceae (a monocotyledon).

In the Strymon group (Clench *in* Ehrlich and Ehrlich, 1961, plus *Strymonidia*), there is no obvious pattern, but there are several records of interest: *Dolymorpha* on *Solanum* (Solanaceae; Clench, unpubl.); *Eumaeus*, with *E. debora* on both *Dioon edule* (Cycadaceae) and *Amaryllis* (Liliaceae) and *E. atala* on both *Manihot* (Euphorbiaceae; Comstock, unpubl.) and on *Zamia integrifolia* (Cycadaceae); *Strymon melinus*, which feeds on a variety of dicotyledonous plants, but also on the flowers of *Nolina* (Liliaceae); and *Tmolus echion*, which feeds not only on *Lantana* (Verbenaceae), *Cordia* (Boraginaceae), *Datura* and *Solanum* (Solanaceae), *Hyptis* (Labiatae), and *Mungifera* (Anacardiaceae), but also on *Ananas* (Bromeliaceae). The impressive pattern of food plant radiation among the four subgenera of *Callophrys* deserves special mention, for subg. *Callophrys* and *Incisalia* feed mostly on angiosperms—Leguminosae, Polygonaceae, Rosaceae, and Ericaceae—but three species of *Incisalia* have switched to conifers, feeding on *Picea* and *Pinus* (Pinaceae). A third subgenus, *Mitoura*, feeds primarily on another group of conifers, Cupressaceae, with two species surprisingly on the pine mistletoes, *Arceuthobium* (Loranthaceae). Finally, *Callophrys* (*Sandia*) *macfarlandi*, the only species of its group, feeds on the flowers of *Nolina* (Liliaceae) in the southwestern United States.

Lycaena and *Heliophorus*, closely related, feed primarily on Polygonaceae throughout the nearly cosmopolitan but largely extratropical range of both groups.

The theclines, narrowly defined (Shirôzu and Yamamoto, 1956), have recently been treated by Shirôzu (1962), who has demonstrated that Fagaceae are the most important food plants, with a number of genera associated with Oleaceae. One genus (*Shirozua*) has become predaceous on aphids.

Among the remaining genera of Lycaeninae, a few points are especially noteworthy.

The morphologically diverse South American group referred to "*Thecla*" is also extraordinarily diverse in its choice of food plants: Bromeliaceae, Celastraceae, Compositae, Euphorbiaceae, Leguminosae, Liliaceae, Malpighiaceae, Malvaceae, Sapotaceae, Solanaceae, and Ulmaceae. In addition to *Callophrys*, already mentioned, many distinctive and in some cases large genera feed primarily on Loranthaceae and the closely related Santalaceae: *Charana*, *Deudorix*, *Hypochrysois*, *Iolaus* s. str. (also often on *Ximelia*, Olacaceae), *Ogyris*, *Pretapa*, *Pseudodipsas*, *Rathinda*, and *Zesius*. It would appear that the epiphytic mistletoes and their relatives have constituted an important adaptive zone for a number of genera of Lycaeninae (as suggested by Clench, pers. comm.). Some species of *Iolaus* are on *Colocasia* (Araceae). Olacaceae, Loranthaceae, and Santalaceae are presumably closely related (Hutchinson, 1959), and interestingly share some acetylinic fatty acids (Sørensen, 1963) and lipids (Shorland, 1963). *Chliaria* feeds on the buds and flowers of a number of genera of Orchidaceae, and *Eooxylides*, *Loxura*, and *Yasoda* feed on *Smilax*, a hard-leaved member of Liliaceae, and the superficially similar *Dioscorea* (Dioscoreaceae). *Artipe* lives inside the fruits of *Punica* (Punicaceae), and *Bindahara* inside the fruits of *Salacia* (Celastraceae). Finally, *Aphnaeus* inhabits galleries hollowed out by ants in the twigs of *Acacia* (Leguminosae), where it feeds on fungi (van Son, pers. comm.)!

In summary, the plant families that are best represented among the food plants of Lycaenini are Ericaceae, Labiatae, Polygonaceae, Rhamnaceae, and Rosaceae. Other records from families not hitherto mentioned are: Aizoaceae, Amaranthaceae, Araliaceae, Betulaceae, Boraginaceae, Bruniaceae, Burseraceae, Caprifoliaceae, Caryophyllaceae, Chenopodiaceae, Cistaceae, Combretaceae, Convolvulaceae, Coriariaceae, Cornaceae, Diapensiaceae, Dipterocarpaceae, Ebenaceae, Eleagnaceae, Gentianaceae, Geraniaceae, Hamamelida-

ceae, Juglandaceae, Lauraceae, Lecithydaceae, Lythraceae, Meliaceae, Melianthaceae, Myricaceae, Oxalidaceae, Pittosporaceae, Plantaginaceae, Plumbaginaceae, Proteaceae, Rubiaceae, Saxifragaceae, Sterculiaceae, Styracaceae, Symplocaceae, Theaceae, Thymeleaceae, and Zygophyllaceae. As before it must be borne in mind that many of these listings represent single records only; for example, the widespread Holarctic *Celastrina argiolus* has been recorded from food plants belonging to at least 14 families of dicotyledons. Nonetheless, it should be evident that the pattern is very different from that of Nymphalinae, the only subfamily comparable to Lycaeninae in size.

DISCUSSION

What generalities can be drawn from these observed patterns? We shall approach this question from the standpoint of the utilization of different plant groups by butterflies and see what light this throws on patterns of evolution in the two groups. Butterflies, of course, are only one of many phytophagous groups of organisms affecting plant evolution.

Within the appropriate ecological framework, our view of the immediate potentialities of studies of phytophagy has been stated clearly and succinctly by Bourgoigne (1951, p. 330), who, speaking of the patterns of food plant choice in Lepidoptera, said: "Ces anomalies apparentes peuvent parfois démontrer l'existence, entre deux végétaux, d'une affinité d'ordre chimique, quelquefois même d'une parenté systématique. . . ." Thus, the choices exercised by phytophagous organisms may provide approximate but nevertheless useful indications of biochemical similarities among groups of plants. These do *not* necessarily indicate the plants' overall phenetic or phylogenetic relationships. The same can be said of the choice of arrow poisons by primitive human groups (Alston and Turner, 1963, p. 293) and of patterns of parasitism by fungi (Saville, 1954). In many of these cases, biochemists have not yet worked out the bases for the observed

patterns, but as Merz (1959, p. 181) points out, we should nevertheless assume that they probably do have a chemical basis.

Now let us consider the groups of organisms utilized as food by butterfly larvae, starting with the most unusual diets. Two tribes of Lycaeninae have departed completely from the usual range of foods: Liptenini feed on lichens, Liphyrini are carnivorous. Many other Lycaeninae, however, are tended by ants and in some cases the larvae are brought into the ant nests. It would seem to be a relatively small step for such larvae to switch and feed on the ant grubs or fungi present in these nests. A number of species of the group exhibit well-developed cannibalism (Downey, 1962). Several Lycaenini, such as *Shirozua*, are carnivorous, and at least one species of *Aphnaeus* feeds on fungi in ant galleries. These transitional steps suggest the evolutionary pathways to the most divergent of butterfly larval feeding habits.

Among those groups of butterflies that feed on plants, none is known to feed on bryophytes or on Psilopsida, Lycopsida, or Sphenopsida, nor is any known from ferns. In fact, very few insects feed on ferns at all (cf. Docters van Leeuwen, 1958), a most surprising and as yet unexplained fact with no evident chemical or mechanical basis. At least one genus of moths, *Papaipema*, is known to feed on ferns, however (Forbes, 1958).

There are a few groups of butterflies that feed on gymnosperms. Two genera of Lycaenidae (*Catachrysops*: *Eumaeus*, two species) feed on Cycadaceae, but all three species involved also feed on angiosperms. *Neophasia* (Pierinae) and three species of *Callophrys* subg. *Incisalia* (Lycaeninae) feed on Pinaceae, while *Callophrys* subg. *Mitoura* feeds on Cupressaceae (and also on *Arceuthobium*, Loranthaceae, a mistletoe that grows on pines). It is well established that Cupressaceae and Pinaceae are chemically quite distinct (Erdtman, 1963, p. 120). Judging from the taxonomic distance between these butterfly groups, it

can be assumed that butterflies feeding on gymnosperms had ancestors that fed on angiosperms.

An overwhelmingly greater number of butterfly larvae feed on dicotyledons than on monocotyledons. The only two groups primarily associated with monocotyledons are Satyrinae and Morphinae, closely related subfamilies of Nymphalidae. One genus of morphines (*Morpho*) is more often associated with dicotyledons, but we can think of no way to determine whether this represents a switch from previous monocotyledon feeding. No member of Papilionidae, Pieridae, or Libytheidae is known to feed on monocotyledons, but in Nymphalidae and Lycaenidae numerous genera do so in whole or in part. Among the Nymphalidae, several species of *Charaxes*, one of *Acraea*, one of *Nymphalis*, and two of *Euphaedra* (*Najas*) are known to feed on monocotyledons; all of these genera and some of the same species feed on dicotyledons also. In Lycaenidae, a number of very diverse groups, including at least two genera of Riodiniinae (*Helicopsis* on Araceae, *Napaea* on Orchidaceae) and 11 genera of Lycaeninae (*Jamides* on Zingiberaceae; *Iolaus* on Araceae; *Tmolus* on Bromeliaceae; *Chliaria* on Orchidaceae; *Hemiargus* on Marantaceae; and *Callophrys*, *Eooxylides*, *Eumacus*, *Strymon*, "Thecla," and *Yasoda* on Liliaceae) feed on monocotyledons. Representatives of many of these genera and in some cases the same species feed on dicotyledons also. This pattern strongly suggests that butterflies of two families have switched to monocotyledons from dicotyledons in a number of independent lines (probably at least 18).

A corollary to the observations presented above is that the diversity we see in modern butterflies has been elaborated against a dicotyledonous background. Indeed this is probably true for Lepidoptera as a whole (cf. Forbes, 1958). The dominant themes in this particular coevolutionary situation are therefore of considerable interest. We conclude from this relationship that the

appearance of dicotyledons, as yet undated but surely pre-Cretaceous, must have antedated the evolutionary radiation that produced the modern lines of diversification in Lepidoptera and specifically in Papilionoidea. All utilization of foods other than dicotyledons by butterfly larvae (and probably by any Lepidoptera) is assumed to be the result of changes from an earlier pattern of feeding on dicotyledons.

In general, the patterns of utilization by butterflies of dicotyledonous food plants show a great many regularities. Certain relationships are very constant; the plants are usually fed upon by a single, phenetically coherent group of butterflies or several very closely related groups. As examples we have the Aristolochiaceae-feeding Papilionidae; Pierinae on Capparidaceae and Cruciferae; Ithomiinae on Solanaceae; Danainae on Apocynaceae and Asclepiadaceae; Acraeinae, Heliconiini, and Argynnini on Passifloraceae, Flacourtiaceae, Violaceae, and Turneraceae; and Riodiniinae-Hamearini and Abisariti on Myrsinaceae and Primulaceae. In many of these cases, the broad patterns observed probably support suggestions of overall phenetic similarity among the plants utilized and among the groups of butterflies concerned. Other clusterings on the basis of food plant choice like that of Ulmaceae, Urticaceae, Moraceae, and Euphorbiaceae by certain groups of Nymphalidae, probably also reflect phylogenetic relationship among the plants concerned. In several instances, the patterns of food plant choice of butterfly groups underscore the close relationship between certain sets of tropical woody and temperate herbaceous families elaborated by Bews (1927). Examples are Danainae, feeding interchangeably on Apocynaceae and Asclepiadaceae; Pierinae, on Capparidaceae and Cruciferae; and part of Riodiniinae, on Myrsinaceae and Primulaceae. In the first case, the families are generally thought to be closely related. On the other hand, Hutchinson (1959) widely separated the members of the second and third pairs of plant families in his system, but this

disposition is considered inappropriate by almost all botanists since it is based upon his primary division of flowering plants into woody and herbaceous lines. In making such decisions based on larval food plants, it must be remembered that we are dealing only with an indirect measure of biochemical similarity. For example, Pierinae not only feed on Capparidaceae and Cruciferae, which most botanists would agree are closely related, but also on Salvadoraceae, which contain mustard oil glucosides but otherwise seem totally different from Capparidaceae and Cruciferae. More equivocal cases likewise occur. For example, Pierinae feed on Tropaeolaceae. Not only do Tropaeolaceae share mustard oil glucosides with Capparidaceae and Cruciferae, they likewise have in common the rare fatty acid, erucic acid. Can we, with Alston and Turner (1963, p. 287), dismiss this as coincidence, or do these groups of plants have more in common than is generally assumed? Finally, is there biochemical similarity between Loranthaceae-Santalaceae and Capparidaceae-Cruciferae, both common food plants of different groups of Pierinae (and of the genus *Hesperocharis*).

Whatever conclusions are drawn about the biochemical affinities of plants from the habits of phytophagous or parasitic organisms, little or no weight should be given to individual records. This is true not only because of the numerous sources of error enumerated earlier, but also because of the multiple explanations possible for such switches. For example, *Atella* (Nymphalinae) feeds on Flacourtiaceae and Salicaceae, among other plants. It is quite possible that these two families are fairly closely related, despite the greatly reduced anemophilous flowers of the latter (Thorne, pers. comm.). But to assume that the few records involved indicate biochemical similarity between the groups would be an unwarranted extension of the data; it would be far simpler and safer at that point to make comparative investigations of the biochemistry of the two plant families.

Patterns of food plant utilization provide evidence bearing on the relationship of Araliaceae and Umbelliferae. Some groups of Papilioninae, normally associated with Rutaceae, feed interchangeably on Umbelliferae, or in some cases have switched entirely to this family. As we have seen, these two plant families are chemically similar. But Araliaceae are close relatives of Umbelliferae (Rodríguez, 1957) despite their wide separation in the system of Hutchinson (1959), and are common in many regions where Papilioninae feed on Rutaceae. Despite this, there is not a single record of a papilionid butterfly (indeed very few butterflies of any kind) feeding on Araliaceae. An even more interesting relationship hinges on the suggestion that the three subfamilies of Umbelliferae—Apioideae, Hydrocotyloideae, and Saniculoideae—may represent three phylogenetic lines, derived independently from a group like the present-day Araliaceae. All records of Papilioninae from Umbelliferae are concerned with Apioideae, and indeed Dethier (1941) found that Umbelliferae-feeding papilionine larvae refused *Hydrocotyle* (Hydrocotyloideae). This very strongly suggests that biochemical analysis may go far in elucidating relationships within the Araliaceae-Umbelliferae complex, and that the chemical properties generally ascribed to Umbelliferae as a whole may be characteristic only of one subfamily, Apioideae. Araliaceae and Umbelliferae are known to share certain distinctive fatty acids (Alston and Turner, 1963, p. 121) and acetylinic compounds (Sørensen, 1963), and it might be very instructive to see how these were distributed in Umbelliferae outside of Apioideae.

In further evaluating the patterns of food plant choice in butterflies, it is important to consider those plant families, especially dicotyledons, which are absent or very poorly represented. One outstanding group is that partly characterized by Merz (1959, p. 169) as "Sphingidpflanzen"—plants fed on by moths of the family Sphingidae. These include, among others,

Onagraceae, Lythraceae, Balsaminaceae, Vitaceae, Rubiaceae, and Caprifoliaceae. The first two, and probably the third and fourth, are generally regarded as fairly closely related. Each one of the first five families (Rubiaceae only in part) is characterized by the abundant presence of raphides, bundles of needlelike crystals of calcium oxalate (see discussion in Gibbs, 1963). In a very interesting experiment, Merz (1959) offered mature leaves of *Vitis* (Vitaceae) to larvae of *Pterogon proserpina* (Sphingidae). Young larvae ate these leaves, their pointlike bites falling between the clusters of raphides. Older larvae, which make large slashing bites, could not avoid the raphides and did not eat the leaves. After the raphides were dissolved in very dilute hydrochloric acid, the leaves were accepted by larvae of all sizes. Although it cannot be proven that some other chemical repellent was not removed by this treatment, it is obvious that raphides offer considerable mechanical difficulty for phytophagous insects. A number of families of moths other than Sphingidae feed on this same series of plant families (Forbes, 1958).

Rubiaceae, one of the families mentioned above, is perhaps the most prominent family that is nearly absent from the records of butterfly food plants. Probably the third largest family of dicotyledons, with nearly 10,000 species, it is, like the butterflies themselves, mostly tropical. One can only speculate that some chemical factor, perhaps the rich representation of alkaloids, sharply restricts the ability of butterfly larvae to feed on plants of this family. In this respect, the similarities between the alkaloids of Apocynaceae (which however have milky juice) and Rubiaceae are of interest. Other dicotyledonous families that are very poorly represented or not represented at all among butterfly food plants include Begoniaceae, Bignoniaceae, Boraginaceae, Celastraceae, Cornaceae, Curcubitaceae (with curcubitacins, bitter-tasting terpenes), Gesneriaceae, Hydrophyllaceae, Loasaceae, Menispermaceae

(rich in alkaloids), Myrtaceae, Polemoniaceae, Ranunculaceae (rich in alkaloids), and Theaceae. In addition, very few butterflies feed on Centrospermae, a group characterized both by its morphological and biochemical traits (summary in Alston and Turner, 1963, p. 141-143, 276-279). This group includes such large families as Amaranthaceae, Cactaceae, Caryophyllaceae, Chenopodiaceae, Nyctaginaceae, and Portulacaceae. Although no biochemical basis for this lack of utilization is known at present, one probably exists. For a family such as the enormous Compositae, poorly represented among the food plants of butterflies, the explanation may lie either in their chemical composition or largely extra-tropical distribution, or most likely a combination of these. One prominent family of monocotyledons that is practically unrepresented among butterfly food plants is Araceae (*Helicopsis*, Riodininae, and species of *Iolais*, Lycaeninae, are exceptions).

One can conclude only that at least some of the plant groups enumerated above have chemical or mechanical properties that render them unpalatable to butterfly larvae. Thus far the combination of circumstances permitting a shift into the adaptive zones represented by these groups has not occurred. The assumption that such a shift is theoretically possible is strengthened by the observation that nearly every one of these plant groups is fed upon by one or more families of moths.

CONCLUSIONS

A systematic evaluation of the kinds of plants fed upon by the larvae of certain subgroups of butterflies leads unambiguously to the conclusion that secondary plant substances play the leading role in determining patterns of utilization. This seems true not only for butterflies but for all phytophagous groups and also for those parasitic on plants. In this context, the irregular distribution in plants of such chemical compounds of unknown physiological function as alkaloids, quinones, essential oils (including terpenoids), gly-

cosides (including cyanogenic substances and saponins), flavonoids, and even raphides (needlelike calcium oxalate crystals) is immediately explicable (Dethier, 1954; Fraenkel, 1956, 1959; Lipke and Fraenkel, 1956; Thorsteinson, 1960; Gordon, 1961).

Angiosperms have, through occasional mutations and recombination, produced a series of chemical compounds not directly related to their basic metabolic pathways but not inimical to normal growth and development. Some of these compounds, by chance, serve to reduce or destroy the palatability of the plant in which they are produced (Fraenkel, 1959). Such a plant, protected from the attacks of phytophagous animals, would in a sense have entered a new adaptive zone. Evolutionary radiation of the plants might follow, and eventually what began as a chance mutation or recombination might characterize an entire family or group of related families. Phytophagous insects, however, can evolve in response to physiological obstacles, as shown by man's recent experience with commercial insecticides. Indeed, response to secondary plant substances and extreme nutritional imbalances and the evolution of resistance to insecticides seem to be intimately connected (Gordon, 1961). If a recombinant or mutation appeared in a population of insects that enabled individuals to feed on some previously protected plant group, selection could carry the line into a new adaptive zone. Here it would be free to diversify largely in the absence of competition from other phytophagous animals. Thus the diversity of plants not only may tend to augment the diversity of phytophagous animals (Hutchinson, 1959), the converse may also be true.

Changes in food plant choice would be especially favored in situations where the supply of the "preferred" plant is sufficiently limited to be an important factor in the survival of the larvae. Such situations have been described by Dethier (1959), who showed that the density of *Aster umbellatus* (Compositae) plants was critical

to the success of the larvae of *Chlosyne harrisii*. Similarly, in western Colorado, the density of the small plants of *Lomatium eastwoodiae* (Umbelliferae) is an important factor limiting population size in *Papilio indra* (T. and J. Emmel, pers. comm.). In these, and many similar situations, it is logical to assume that genetic variants able to utilize another food plant successfully would be relatively favored. This advantage would be much enhanced if genotypes arose that permitted switching to a new food plant sufficiently novel biochemically that it was not utilized, or little utilized, by herbivores in general.

The degree of physiological specialization acquired in genetic adjustment to feeding on a biochemically unusual group of plants would very likely also act to limit the choice of food available to the insect group in the general flora (Merz, 1959, p. 187; Gordon, 1961). As stressed by Brower (1958a), moreover, close relationships between insects and a narrow range of food plants may be promoted by the evolution of concealment from predators in relation to a single background. The food plant provides the substrate for the larvae, not just their food (Dethier, 1954, p. 38).

After the restriction of certain groups of insects to a narrow range of food plants, the formerly repellent substances of these plants might for the insects in question, become chemical attractants. Particularly interesting is the work of Thorsteinson (1953), who found that certain mustard oil glucosides from Cruciferae would elicit feeding responses from larvae that fed on these plants if these glucosides were smeared on other, normally unacceptable, leaves. But if these glucosides were smeared on the alkaloid-rich leaves of *Lycopersicum* (Solanaceae), the larvae still refused them. Similarly, Sevastopulo (pers. comm.) was unable to induce the larvae of *Danais chrysippus* to eat anything but Asclepiadaceae even by smearing the leaves of other plants with the juice of *Calotropis* (Asclepiadaceae).

This illustrates clearly that the choice of

a particular food plant or of a spectrum of food plants may be governed by repellents present in other plants (Thorsteinson, 1960) as well as by attractants in the normal food plants: this fully accords with the model outlined above. It should not, however, be assumed without experimental verification that a particular secondary plant substance is an attractant or feeding stimulant for the insects feeding on plants that contain it. Indeed, for the beetle *Leptinotarsa*, the alkaloids of the Solanaceae on which it feeds serve as repellents (summary in Fraenkel, 1959, p. 1467–1468).

In view of these considerations, we propose a comparable pattern of adaptive radiation for each of the more or less strictly limited groups of butterflies enumerated above. It is likewise probable that the elaboration of biochemical defenses has played a critical role in the radiation of those groups of plants characterized by unusual accessory metabolic products.

Further, it can be pointed out that all groups of butterflies that are important in furnishing models in situations involving mimicry are narrowly restricted in food plant choice: Papilioninae–Troidini; Ithomiinae; Nymphalinae–Heliconiini; Acraeinae; and Danainae. This is in accordance with a long-standing supposition of naturalists and students of mimicry that the physiological shifts that enabled the butterfly groups to feed on these plants conferred a double advantage by making the butterflies in question unpalatable. These groups of butterflies have been selected for warning coloration, and once established, this conspicuousness would tend to put anything that would maintain their distastefulness at a selective premium.

Conversely, those groups of butterflies that furnish most of the Batesian mimics—Papilioninae–Papilionini and Graphiini; Satyrinae; Nymphalinae except Heliconiini; Pierinae; and Dismorphiinae—feed mostly on plant groups that are shared with other dissimilar groups of butterflies. It is somewhat surprising that Nymphalinae–Argyn-

nini, which feed on the same plants as Heliconiini and Acraeinae, do not play any prominent role as models for mimetic forms. This may be in part because Argynniini are best developed in temperate regions, where butterflies and therefore mimetic complexes are less common. It may further be suggested that the mimicry supposed to exist between dark female forms of various species of *Speyeria* and the model *Battus philenor* may well be a case of Müllerian rather than Batesian mimicry. Indeed, the results of Brower (1958) with the model *Danais plexippus* and its mimic *Limenitis archippus* suggest that there is in fact no sharp line between Batesian and Müllerian mimicry. These should be thought of as the extremes of a continuum. Thus *Speyeria* females may be somewhat distasteful but can only acquire warning coloration when the selective balance is tipped by the presence of other distasteful forms. This follows logically from numerous experiments and observations on the behavior of predators with mimetic complexes, which rarely reveal an “either/or” type of response (cf. Swynerton, 1919). Assuming a balance of this sort would resolve some of the difficulties of interpretation concerning the two kinds of mimicry (e.g., Sheppard, 1963, p. 145).

Numerous unusual feeding patterns scattered among butterfly families attest to the frequency of radiation into new groups of food plants. We can, however, only guess at the probability of future radiation in the new adaptive zone. For example, does *Stalactis susanae* (Riodininae), which is known to feed on *Oxypetalum campestre* (Asclepiadaceae) in Argentina, represent the start of a new phylogenetic series of butterflies restricted to this group of plants? Probably not, since the examples of this sort of unusual feeding habit today far exceed the number of radiations observed in the past. Nevertheless, the close patterns of coadaptation we have discussed above must have started in a similar fashion. Comparable patterns can be found among plants with biochemical in-

novations, for example, *Senecio viscosus*, mentioned earlier, or the relationship of *Sedum acre* to other species of its genus (Merz, 1959, p. 160).

In viewing present-day patterns of food plant utilization, however, the historical aspect of the situation must not be neglected. A biochemical innovation might have had a considerable selective advantage for a group of plants in the Cretaceous. Such an advantage would, of course, have been in terms of the phytophagous animals and parasites present in the Cretaceous, and not necessarily those of the present day. The crossing of an adaptive threshold by a member of a living group of phytophagous animals would have an entirely different significance now than that which it would have had in the Cretaceous.

For example, even though a species of *Stalachtis* is able to feed on Asclepiadaceae, it shares the available supply of these plants with representatives of numerous other groups of phytophagous animals. These have, somewhere in the course of geological time, acquired the ability to feed on asclepiads. Further, if the phytophagous organisms switching early to milkweeds became protected from predators by their ingestion of distasteful plant juices, this initial advantage might have been overcome in the intervening years by corresponding changes in prospective predators. A species of bird long selected to like milkweed bugs might find milkweed-feeding *Stalachtis* a gourmet's delight.

As in the occupation of any adaptive zone, the first organisms to enter it have a tremendous advantage and are apt to have the opportunity to become exceedingly diverse before evolution in other organisms sharply restricts their initial advantage. In short, the nature of any adaptive zone is altered by the organisms that enter it. From our vantage point in time we view only the remnants, doubtless often disarranged if not completely shattered by subsequent events, of the great adaptive radiations of the past.

In view of these considerations, we

cannot accept the theoretical picture of a generalized group of polyphagous insects from which specialized oligophagous forms were gradually derived. Just as there is no truly "panphagous" insect (cf. Fraenkel, 1959), so there is no universally acceptable food plant; and this doubtless has always been true. This statement is based on the chemical variation observed in plants and the physiological variation observed in insects. Leguminosae are important food plants for several groups of Lycaenidae and Pieridae, and woody Ranales are well represented among the food plants of Papilionidae and Nymphalidae; but this should not be taken to prove that these groups of plants are "inert" chemically or readily available to other phytophagous groups of insects. The initial radiation of butterfly taxa onto these groups may for a time have produced a pattern just as spectacular as, for example, the close association between Troidini and Aristolochiaceae seen today. We hold that plants and phytophagous insects have evolved in part in response to one another, and that the stages we have postulated have developed in a stepwise manner.

As suggested by Fraenkel (1956, 1959), secondary plant substances must have been formed early in the history of angiosperms. At the present day, many classes of organic compounds are nearly or quite restricted to this group of plants (for example, see Alston and Turner, 1963, p. 164; Harborne, 1963, p. 360; Paris, 1963, p. 357). We suggest that some of these compounds may have been present in early angiosperms and afforded them an unusual degree of protection from the phytophagous organisms of the time, relative to other contemporary plant groups. Behind such a biochemical shield the angiosperms may have developed and become structurally diverse. Such an assumption of the origin of angiosperms provides a cogent reason why one of many structurally modified groups of gymnosperms would have been able to give rise to the bewildering diversity of modern angiosperms, while most other lines became

extinct. It seems at least as convincing to us as do theories based on the structural peculiarities of angiosperms. Although the chemical basis for the success of early angiosperms may no longer be discernible, it can be mentioned that woody Ranales, generally accepted as the most "primitive" assemblage of living angiosperms on other grounds, are as a group characterized by many alkaloids as well as by essential oils. Of course this might also be interpreted only to mean that the development of alkaloids has permitted this group to persist despite its many generalized features.

In turn, the fantastic diversification of modern insects has developed in large measure as the result of a stepwise pattern of coevolutionary stages superimposed on the changing pattern of angiosperm variation. With specific reference to the butterflies, one is tempted in terms of present-day patterns to place more emphasis on the full exploitation of diurnal feeding habits by the adults than on the penetration of any particular biochemical barrier by the larvae. On the other hand, phenetic relationships suggest that Papilionoidea (with Hesperioidea, the skippers) are representatives of a line that is amply distinct from all other living Lepidoptera (Ehrlich, 1958). Thus it is entirely possible that radiation onto a new food plant was decisive at the time Papilionoidea first diverged, even though the feeding habits of the order as a whole are now much wider than those of the butterflies alone. The impossibility of deciding objectively which groups of Papilionoidea are more primitive than others (cf. Ehrlich, 1958, p. 334-335) relegates the task of identifying the original group of food plants for butterflies to the realm of profitless speculation.

We would like to return now to the four general questions posed at the beginning of this paper. First, what have we learned of the reciprocal responses of butterflies and their food plants? The observed patterns clearly point to the critical importance of plant biochemistry in governing the relationships between the two groups. The

degree of plasticity of chemoreceptive response and the potential for physiological adjustment to various plant secondary substances in butterfly populations must in large measure determine their potential for evolutionary radiation. Of secondary, but still possibly major importance, are mechanical plant defenses, and the butterflies' responses to them.

With respect to the second question on the generation of predictions the answer also seems clear. We cannot predict the results of any given interaction with precision—*Stalactis* on Asclepiadaceae or *Neophasia* on pines may or may not form the basis for further patterns of radiation. On the other hand, the basis for a probabilistic statement of "Further radiation unlikely" seems to have been developed. A great many minor predictions can be made, such as the probable presence of alkaloids in *Ptaeroxylon* (Meliaceae), the solanaceous character of the food plants of unknown larvae of Ithomiinae, and so forth.

Although the data we have gathered permit us to make some reasonable sequence predictions about phylogenetic patterns (e.g., diversification of Apocynaceae and Solanaceae before Danainae and Ithomiinae, respectively), these predictions cannot be tested and the relationships cannot be specified further in the absence of a fossil record. The reconstruction of phylogenies on the basis of this sort of information would seem an unwarranted imposition on the data, since evolutionary rate and time are still inseparable.

In response to the fourth question, it seems to us that studies of coevolution provide an excellent starting point for understanding community evolution. Indeed the seeming ease with which our conclusions have been extended to include the complex interactions among plants, phytophagous organisms, mimics, models, and predators leads us to believe that population biologists should pursue similar studies of other systems. Many examples come to mind such as parasitoid-caterpillar, *Plasmodium*—

hemoglobin, tree-mycorrhizal fungus, in which stepwise reciprocal selective response is to be expected. Studying most of these systems experimentally tends to be difficult, and may be complicated by lack of repeatability in the results.

An approach to biology that is concerned with broad patterns quite possibly will lead to a better understanding of some other problems of community ecology. For example, biologists have long been interested in the reasons for the differences in species diversity between tropical and temperate areas. An important factor in maintaining these differences may be the sort of synergistic interactions between plants and herbivores we have been discussing. The selective advantage of living in a tropical climate is evident for insects, which are poikilothermal. Insects are much more abundant in the tropics than elsewhere and doubtless constitute the major class of herbivorous animals. The penetration of relatively cold environments or other environments requiring diapause is probably a rather recent occurrence in most insect groups. That these environments are not always readily entered is attested to by the repeated failure of insects such as the butterfly *Mestra amymone* to survive the winter in localities at the northern fringes of their ranges where summer colonies have been established (Ehrlich and Ehrlich, 1961).

The abundance of phytophagous insects in tropical regions would be expected to accentuate the pace of evolutionary interactions with plants. These interactions may have been the major factor in promoting the species diversity of both plants and animals observed in the tropics today. As this diversity was being produced, it became arrayed in richly varied mixtures of species with relatively great distances between individuals of any one plant species. As Grant (1963, p. 420-422) has suggested, this arrangement would have the additional advantage of providing a maximum degree of protection from epidemic outbreaks of plant diseases and plant pests. It must,

however, also be mentioned that the relatively permissive tropical climate presumably allows a greater diversity of plant life forms and therefore secondarily of animals (Hutchinson, 1959, p. 150).

Probably our most important overall conclusion is that the importance of reciprocal selective responses between ecologically closely linked organisms has been vastly underrated in considerations of the origins of organic diversity. Indeed, the plant-herbivore "interface" may be the major zone of interaction responsible for generating terrestrial organic diversity.

SUMMARY

The reciprocal evolutionary relationships of butterflies and their food plants have been examined on the basis of an extensive survey of patterns of plant utilization and information on factors affecting food plant choice. The evolution of secondary plant substances and the stepwise evolutionary responses to these by phytophagous organisms have clearly been the dominant factors in the evolution of butterflies and other phytophagous groups. Furthermore these secondary plant substances have probably been critical in the evolution of angiosperm subgroups and perhaps of the angiosperms themselves. The examination of broad patterns of coevolution permits several levels of predictions and shows promise as a route to the understanding of community evolution. Little information useful for the reconstruction of phylogenies is supplied. It is apparent that reciprocal selective responses have been greatly underrated as a factor in the origination of organic diversity. The paramount importance of plant-herbivore interactions in generating terrestrial diversity is suggested. For instance, viewed in this framework the rich diversity of tropical communities may be traced in large part to the hospitality of warm climates toward poikilothermal phytophagous insects.

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