

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^{1,2}

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(Plate I; Text-figures 1-8)

[This paper is one of a series emanating from the Tropical Field Station of the New York Zoological Society, at Simla, Arima Valley, Trinidad, West Indies. This station was founded in 1950 by the Zoological Society's Department of Tropical Research, under the direction of Dr. William Beebe. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of undisturbed government forest reserves. The laboratory of the Station is intended for research in tropical ecology and in animal behavior. The altitude of the research area is 500 to 1,800 feet, and the annual rainfall is more than 100 inches.

[For further ecological details of meteorology and biotic zones, see "Introduction to the Ecology of the Arima Valley, Trinidad, B.W.I.," William Beebe, *Zoologica*, 1952, 37 (13): 157-184.

[The success of the present study is a large measure of the cooperation of the staff at Simla, especially of Jocelyn Crane and Constance Carter, the former contributing much of her knowledge of the animals, the latter helping with recording of observations].

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I. INTRODUCTION

THE phylogeny of the neotropical subfamily of butterflies, the Heliconiinae, is interesting, partly because most species are distasteful and aposematically colored, partly because of the possibility of Müllerian mimicry. The determination of relationships within the group must clearly utilize information of behavior, physiology and ecology of the butterflies as well as their anatomy. Indeed, work has already been going on along former lines (see the study of comparative ethology of the adults, Crane, 1955 and 1957) and that of breeding experiments and wing patterns (Beebe, 1955). It is obvious, however, that all such studies must relate not only to the adult stages but also to egg, larva and pupa. The present paper represents an attempt to study comparatively the larval behavior of as many species of heliconiines as were available over a period of four and one-half months spent in the laboratory at Simla. Because of limitations of material and time,

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the project was necessarily of a preliminary nature and there are many unavoidable gaps in information. The significance of some late larval behavior was clearly to be sought in the pupa and possibly the emergent adult; limited observations were thus made on these stages as well. These, together with information on molting of the larvae, will be presented in Part II. Implications of the phylogeny of the species observed are discussed tentatively but in relation to this study only, and it is hoped that a later paper will correlate evidence from the several fields and workers on the subjects of relationships among the Heliconiinae.

For descriptions and illustrations of the external characteristics of the larvae to be discussed, see Beebe, Crane & Fleming (1960) and Fleming (1960).

II. MATERIALS AND METHODS

Of the 14 species of heliconiines known to occur in Trinidad, three were not available at all during the time of this study and any reference to their behavior is from the notebooks of the Simla staff. These species are *Heliconius wallacei wallacei* Reakirt, *Heliconius numata ethilla* Godart and *Philaethria dido dido* Clerck. Of the others, observations on *Heliconius doris doris* (Linnaeus) were limited to two days, while only a single specimen of *Dryadula phaetusa phaetusa* (Linnaeus) was obtained. *Dione juno juno* (Cramer) is gregarious and a single group of 37 healthy individuals was observed; these were, however, already in their second instar when found. Lastly, information on *Heliconius sara thamar* Hübner and, to a lesser extent *Heliconius erato hydara* Hewitson, was limited, as healthy stocks were unobtainable for much of the period. Observations on the emergence of *H. sara* are due entirely to Constance Carter to whom I owe many thanks. The remaining six species consist of *Heliconius melpomene euryades* Riffarth, *Heliconius ricini insulana* Stichel, *Heliconius alipha alipha* (Godart), *Heliconius isabella isabella* (Cramer), *Dryas iulia iulia* (Fabricius) and *Agraulis vanillae vanillae* (Linnaeus).

After initial observations of caterpillars on single leaves in glass jars, it was found more satisfactory to keep the larvae on lengths of vine, one to three feet long, the ends of which were thrust into narrow-necked bottles of water. Fresh vines were added to the bottles every few days and the caterpillars were free to move onto them, or were very occasionally transferred by hand. In such conditions the caterpillars remained on the vines, apparently content. With the exception of the two species mentioned

earlier, all larvae were very healthy. Well-formed butterflies emerged from the pupae and individuals of those species whose normal courtship is known behaved as would be expected of healthy adults.

Most of the observations of larval behavior were made on vines in an isolated room on the fringe of the forest around Simla. Conditions of light, humidity and wind were therefore close to those of the natural habitat of at least some of the species outside (see Beebe, 1952, for details of ecological conditions in the Arima Valley).

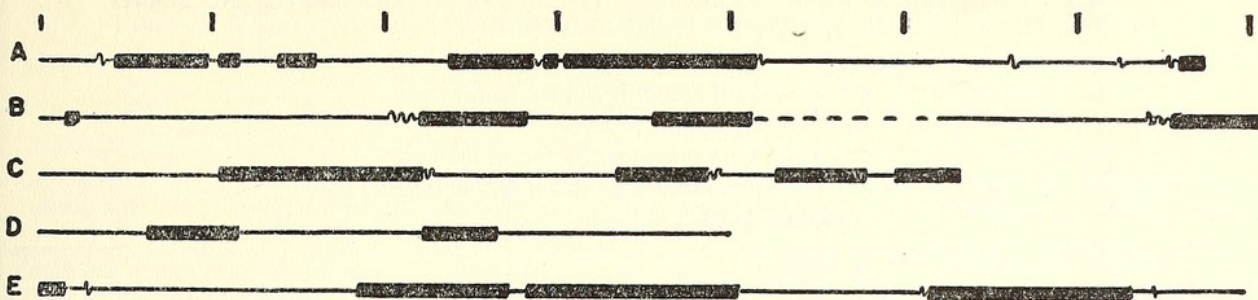
Late larval or prepupal behavior was watched outside the laboratory among rows of *Passiflora* vines planted by Simla staff. Where the host vine was not available in the vine rows, prepupal larvae were kept on extra large vines stuck into bottles in the laboratory. Observations of feeding patterns and choice of pupational site were also made in the field where possible. In no such case was any discrepancy found between these observations and those made under laboratory conditions.

At night caterpillars were watched beneath either a red or very dim white light. Individual animals were identified by peculiarities of anatomy or color or, in cases where they were very similar, by keeping them on separate vines. Numerous mirrors had to be used to render the activities of the caterpillars visible without disturbing them.

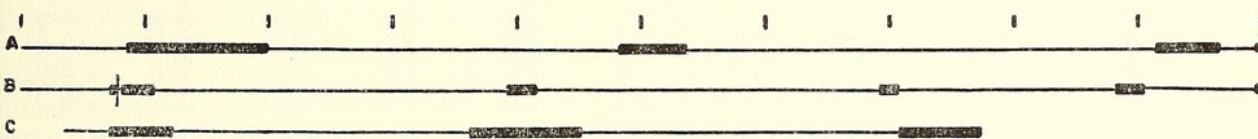
III. FEEDING RHYTHMS

It has generally been recognized that most, if not at all, lepidopterous larvae show rhythm in their behavior patterns. Thus Crowell (1943) reported that a large number of species have feeding periods of about 20-30 minutes alternating with rest periods of similar duration. The caterpillars of at least ten species of heliconiines from Trinidad are no exception (see Text-fig. 1 for examples).

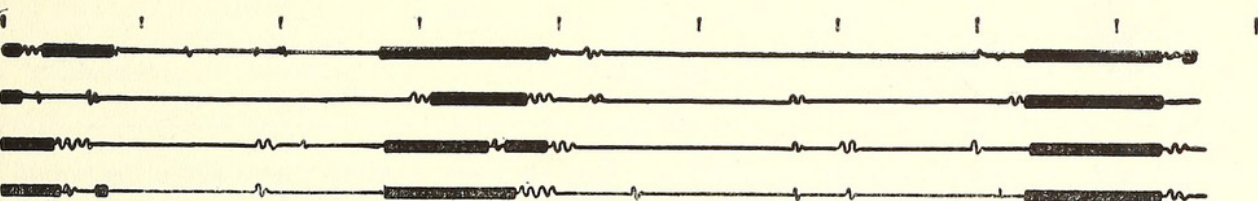
As Ford (1945) has recorded for caterpillars such as the Silver-studded Blue (*Plebejus argus*) and the Black Hairstreak (*Strymonidia pruni*), most of these species show rhythmic bursts of feeding evenly throughout both day and night. An examination of the activity patterns suggests that there are specific differences in the details of this rhythm, but the picture may be blurred by changes in the pattern during the course of an instar. Thus the duration of feeding periods immediately after a larval molt is shorter than of those immediately before (Text-fig. 2). Again, the rhythm differs between instars, while just before pupation there are long, almost uninterrupted periods of feeding.



TEXT-FIG. 1. Feeding rhythm in caterpillars the day after their fourth molt. Thick straight lines = feeding; thin straight lines = resting phases; thin wavy lines = walking or other movement. The time intervals on the upper line = 30 minutes. *a*, *D. iulia*; *b*, *H. isabella*; *c*, *H. aliphera*; *d*, *H. melpomene*; *e*, *H. erato*.



TEXT-FIG. 2. The feeding and resting periods in a caterpillar of *H. melpomene*: *a*, the day before the fourth molt; *b*, immediately after eating the cast fourth exuvium; *c*, the following morning. The convention used is as in Text-fig. 1. The line drawn down through the first feeding period of 2*b* indicates an interruption.



TEXT-FIG. 3. Synchronization of feeding and resting in a group of four *H. doris* caterpillars.

While the majority of the species feed throughout the 24 hours, *H. doris* does not normally feed at night, a habit which Ford (1945) records for the Dark Green Fritillary (*Argynnis aglaia*) and the Swallow-tail (*Papilio machaon*). Furthermore, two species, *D. iulia* and *H. melpomene*³, show a tendency, during their fifth instar, to rest throughout the day⁴.

Ford has recorded a similar change of feeding habit in the last larval stage of the Scotch Argus (*Erebia aethiops*) which feeds only during the night at this period, although earlier it was not so restricted.

³ From the laboratory notebook of Barbara Young (1957), it seems probable that *P. dido*, a species which I have not observed, is similar in this respect to *D. iulia* and *H. melpomene*. The characteristic may, however, appear earlier in the life of the caterpillar, possibly by the third instar.

⁴ Using the amount of dung deposited during a certain time as a measure of the intensity of feeding, it seems that, in these latter cases, light may be a direct inhibitory stimulus. Thus a caterpillar of *D. iulia*, if kept in darkness during the day, eats more than twice as much as it does in daylight, producing 2.4 pellets per hour, as opposed to 0.9.

In naturally gregarious species, such as *D. juno*, *H. doris*, *H. sara* and to a lesser extent *H. ricini*, the caterpillars synchronize their feeding and resting periods (Text-fig. 3). The beginning of the feeding period is somewhat less strictly coordinated than its end; this reflects the possibility that synchronization is controlled by at least two factors.

An internally controlled rhythm could initiate feeding periods. In caterpillars which have been deprived of food or for some other reason are not eating, *e. g.*, the nocturnal phase of *H. doris*, there are indications of a persistence of rhythmicity expressed as alternating periods of rest and locomotor activity. If indeed the locomotor activity corresponds to the feeding activity, it will follow that the onset of the activity period is determined not simply by a reflex due to lack of food, as suggested by Crowell (1943), but by some endogenous pattern. The rest periods are usually induced by factors which affect all the animals simultaneously, possibly such extraneous stimuli as a sudden wind, the passing of an ant or the touch of an observer. The last-mentioned stimulus has in fact been noticed to end the feeding periods in various

TABLE I. RELATIONSHIP BETWEEN LARVAE OF THE SUBFAMILY HELICONIINAE AND PLANTS OF THE FAMILY PASSIFLORACEAE IN TRINIDAD

Key: *—Host plant.
 +—Will accept if put on plant.
 —Refuses if put on.
 (*)—Very occasionally found on.
 (*—)—Eggs found on it but larvae refused it.
 (S.T)—South Trinidad.

Species	Species of <i>Passiflora</i>								
	<i>auriculata</i> HBK	<i>vespertilio</i> Linnaeus	<i>tuberosa</i> Jacquin	<i>rubra</i> Linnaeus	<i>quadriglandulosa</i> Rodschied	<i>serrato-digitata</i> Linnaeus	<i>laurifolia</i> Linnaeus	<i>lonchophora</i> Linnaeus	<i>foetida</i> Linnaeus
1. <i>Dione juno</i>	+—			+		*	(*—)		+
2. <i>Agraulis vanillae</i>	+			+			+	(*)	*
3. <i>Dryadula phaetusa</i>			+	(*)	+—				(*—)
4. <i>Dryas iulia</i>	+		*	+			—	—	—
5. <i>Philaethria dido</i>			—				*		
6. <i>Heliconius isabella</i>				+		*(S.T)	*		
7. <i>Heliconius aliphera</i>			+—	*	?*(S.T)		+	*	+
8. <i>Heliconius melpomene</i>	+		(*)+				*	+	
9. <i>Heliconius numata</i>								*	
10. <i>Heliconius erato</i>	+	*(S.T)	*				(*)+		
11. <i>Heliconius ricini</i>			—				*		
12. <i>Heliconius sara</i>	*						+	+	
13. <i>Heliconius wallacei</i>					*				
14. <i>Heliconius doris</i>						*	(*)		

species. If this stimulus is given early in the feeding period, it will have no effect or merely occasion a momentary halt. Towards the natural end of the period, however, it usually causes premature resting. These considerations may also apply to the habits of the non-gregarious caterpillars, for these tend to fall into a synchronized rhythm of eating and resting when

kept on the same or neighboring leaves—a phenomenon which has been observed especially in *H. aliphera* and *H. melpomene*.

Regardless of how such synchronous eating is controlled, any selective advantage of such behavior would surely come from the limit which it sets to the time during which any caterpillars are moving. Movement of the prey is

TABLE II. VEGETATIVE CHARACTERISTICS OF THE VINES ON WHICH THE CATERPILLARS FEED

Species	Vine Size	Texture of the Stem	Leaf Texture	Covering of Leaf	Abundance of Leaves	Leaf Shape
<i>Passiflora auriculata</i>	Slight, maximum 10', climbing	Slender, smooth	Tender-medium	Smooth	Fairly scarce	Simple, entire
<i>Passiflora rubra</i>	Medium, bushy, climbing	Medium, branches more than other vines	Medium	Medium	Abundant	Widely bi-lobed
<i>Passiflora tuberosa</i>	Slight, effervescent	Slender	Tender-medium	Mat	Scarce	Bi-lobed, narrow-wide
<i>Passiflora quadrigrandulosa</i>	Climbing, reaches height of 30'	Tough-medium	Tough-medium	Rough-mat	Fairly scarce	Bi-lobed, unequal
<i>Passiflora serrato-digitata</i>	Medium, sprawling	Smooth, sturdy	Tender-medium	Smooth	Fairly abundant	5-7-palmate
<i>Passiflora laurifolia</i>	Climbing, reaches up to 30'	Tough, frequent branching	Tough-medium	Smooth	Abundant	Simple, entire
<i>Passiflora foetida</i>	Sprawling, medium	Tough-medium, hairy	Medium	Hairy & glandular	Fairly abundant	Tri-foliolate
<i>Passiflora lonchophora</i>	Slender, climbing up to 40'	Tough	Tender-medium	Smooth	Fairly abundant	Tri-foliolate

important to insect and reptilian predators and, furthermore, would assist in calling the attention of any bird to a caterpillar. Thus with the exception of "agonistic" movements when disturbed, the caterpillars would do well to remain as motionless as possible during non-feeding periods. Without synchronization of feeding movements, some animals could always attract the attention of predators to the resting caterpillars, as well as to themselves.

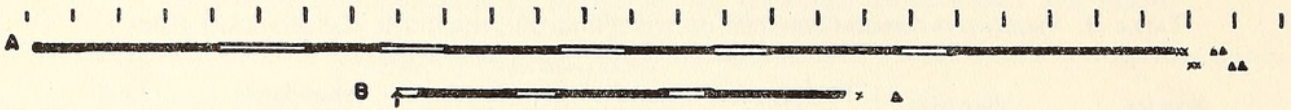
IV. FEEDING

Although heliconiine imagines feed on nectar from a variety of flowers, their larvae feed only on various species of passion vines (Family Passifloraceae). Usually feeding is confined to the leaves, but in some cases tendrils, stalks, flowers and hairs are also eaten. Ten species of vine growing in Trinidad have been found to support one or more of 14 species of heliconiine caterpillars (see Table I). These vines vary fairly widely in their vegetative characteristics (see Table II) and are, moreover, somewhat variable within each species.

One factor which determines which species of vine a caterpillar eats is, of course, the fairly high specificity in respect to oviposition site shown by the heliconiines; the eggs are almost invariably laid on the "natural" food-plant of the species. Occasional "mistakes" are, however, found in the field (see Table I).

Tolerance of an "unnatural" host vine may alter according to what a caterpillar has eaten previously, the stage and number of its instar and possibly its water load immediately before a test. Thus *H. alipha* raised to the fifth instar on *P. lonchophora* accepts *P. rubra* almost immediately and with no change of its previous patterns of eating and resting. The converse is not true. *H. alipha*, raised on *P. rubra* to the equivalent stage and then transferred to *P. lonchophora*, wanders and rests without eating for several hours before beginning to feed. In this species there is a tendency for later instars to show less specificity in their food preferences than the earlier ones. The matter has not been investigated in detail among other species, but tests made on the day before pupation indicate that host preference is then less strict.

Sometimes when a butterfly oviposits on an abnormal species of vine, the caterpillars refuse to eat altogether, e.g., *D. juno* laying on *P. laurifolia* (Table I). In other cases they may accept the abnormal food plant but their growth may be reduced and/or retarded. Text-fig. 4 shows the latter effect on a group of *D. juno* fed on leaves of *P. auriculata* and *P. rubra* as opposed to one fed on the natural food-plant (*P. serrato-digitata*). The number of instars is greater, molting is more protracted and most growth periods are longer. It has not been established whether they actually eat less in



TEXT-FIG. 4. The effect of food plant on instar number and length in *D. juno*. Growth and feeding are indicated by the black lines, molting by the white lines. Crosses indicate the time of hanging up and triangles the shedding of the last larval skin. Time interval = 24 hours, and the arrow indicates when the second group were collected as they molted into the second instar. **a**, Four caterpillars on *P. auriculata* and *P. rubra*; **b**, 13 caterpillars on *P. serrato-digitata*, their normal food plant. Information for the upper picture was kindly supplied by Jocelyn Crane.

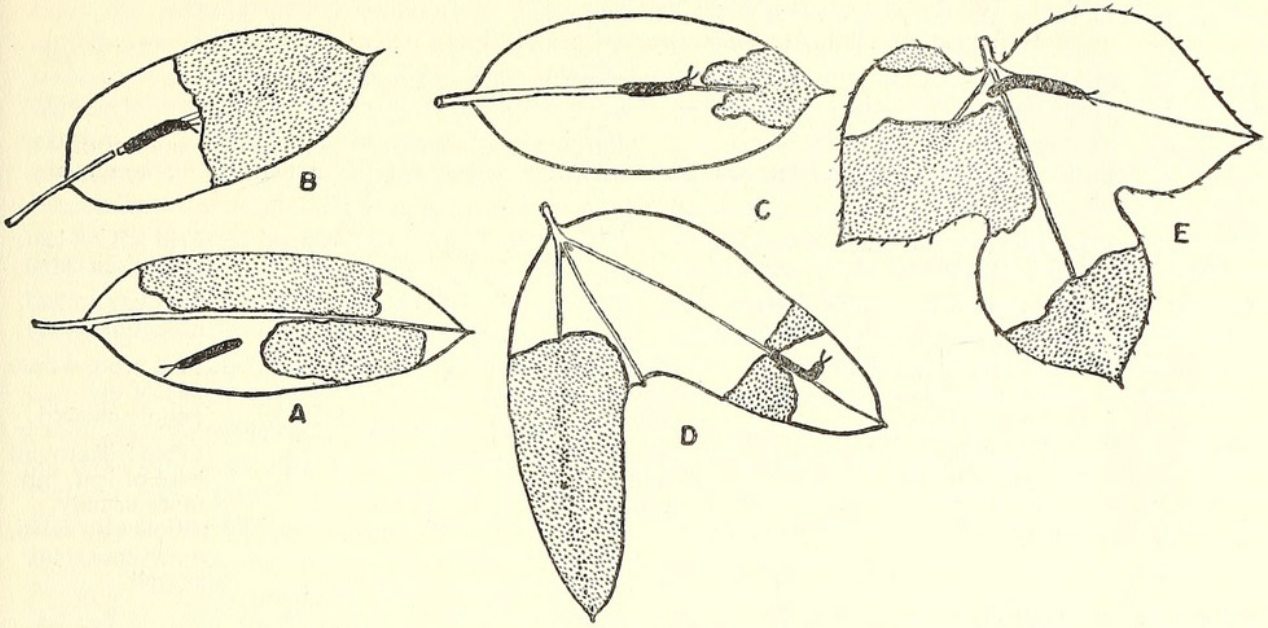
unit time under the unfavorable conditions. There are, moreover, behavioral changes in such cases; for instance the synchronization of feeding is lost. This may reflect a more basic physiological disturbance, for the synchronization of molting and pupation also disappears.

It is not clear how the caterpillars distinguish between a vine which they accept and one they reject. Some rejections occur after the material has actually been chewed. Thus *H. ricini* refused to eat *P. tuberosa* after tasting it and rejected an aqueous extract of *P. tuberosa* leaves, though it would drink similar extracts made from its food-plant *P. laurifolia*. In other cases caterpillars can certainly make a distinction

without having to taste the material. Thus neither *H. isabella* nor *D. iulia* will attempt to eat *P. foetida*; in fact the former cannot be persuaded to remain on this vine, commonly dropping off as soon as it is put on a *P. foetida* leaf. It seems possible therefore that in this species of caterpillar, behavior is controlled by more than one factor, in keeping with Dethier's (1937) findings on larvae of the gypsy moth. Such an effect might explain conclusions such as those of Merz (1959) who declares that among the larvae of monophagous species of Lepidoptera many are less specialized than had been previously supposed. The technique she used in testing the larvae was to present them

TABLE III. INFORMATION RELATING TO CROWDING OF EGGS AND THE SITE WHERE THEY ARE NORMALLY LAID BY THE HELICONIINE BUTTERFLY

Species	Gregariousness	Leaf Size	Leaf Surface	Tendrils
<i>Dione juno</i>	60/90 in raft almost touching	Medium (but tender)	Under	
<i>Agraulis vanillae</i>	Single	Leaves indiscriminately	Upper	
<i>Dryadula phaetusa</i>	Single	Medium		
<i>Dryas iulia</i>	Single	Medium	Upper	Fresh, dry
<i>Philaethria dido</i>	Single	?	?	Thick
<i>Heliconius isabella</i>	Single or few scattered	Medium-large	Under	
<i>Heliconius alipha</i>	Scattered 5/6 or single	Medium-large	Under	
<i>Heliconius melpomene</i>	Single	Subterminal leaflets, medium	Upper	Young
<i>Heliconius erato</i>	Single	Subterminal leaflets, medium leaves	Upper	
<i>Heliconius ricini</i>	4/12 loose cluster	Among leaf buds		
<i>Heliconius sara</i>	About 25 in tight cluster	Among leaf buds		
<i>Heliconius wallacei</i>	25/30 fairly loose cluster	Among leaf buds		
<i>Heliconius doris</i>	36/52 in raft almost touching	Medium leaf	Upper	



TEXT-FIG. 5. Patterns left on leaves by the feeding of caterpillars, the stippled part being that eaten. The caterpillars concerned are shown in their typical resting positions and postures on the appropriate leaves. **a**, *H. isabella* on *P. laurifolia*; **b**, *H. melpomene* on *P. laurifolia*; **c**, *H. ricini* on *P. laurifolia*, chewed to give the ragged effect rather than the straight across, shown for *H. melpomene* and often produced by *H. ricini*; **d**, *D. iulia* on *P. tuberosa*; **e**, *A. vanillae* on *P. foetida*.

with dried leaves moistened with sugar water. Regardless of additional complications of the possible attraction of sugar water itself, the physical properties of the leaf are vastly changed by desiccation.

a. Leaf Patterns

Since the butterflies further show consistent preferences for oviposition in particular sites on the vine (Table III), the food first accepted by the caterpillars will be affected by this choice, for the newly-hatched animals usually eat the food nearest to them. Thus *H. isabella* and *H. alipha* begin eating the undersurface of a leaf, although they will feed when placed on its upper surface, a position in which they are never found in the field. Again, a high percentage of *H. melpomene* start by eating a tendril. However, of a batch of 20 caterpillars from eggs laid on tendrils and offered a choice of tendrils and young leaves, 55% ate leaves, disregarding the tendrils after they had investigated them. Thus, in certain cases at least, the feeding sites of first instar larvae are determined simply by the normal oviposition site and where, as with *H. melpomene*, some selection might be exercised, this cannot find expression.

Besides showing specific preferences for a single or various species of vine, the larvae leave characteristic patterns (Text-fig. 5) on material which they have been eating, a phenomenon

which is well known in many phytophagous insects (see Hering, 1926).

The following features are among those distinguishing different patterns in the heliconiine species of this study.

1. The green cells alone may be scraped away from the surface of a leaf, leaving only a layer of transparent epidermal cells on the far side. This is in contrast to an actual hole being chewed in the leaf or its being eaten away from a margin so that bays or channels are left.

2. The midrib of the leaf or leaflet may remain when the caterpillar abandons the leaf, or it may be eaten together with the blade of the leaf or, in complex patterns, it may be ignored while the caterpillar eats most of the blade but is finally eaten before the leaf is abandoned.

3. Whether it is finally eaten or not, the midrib may also be the focus for other specific attentions. *H. melpomene*, *H. ricini* and, in special cases to be mentioned later, *H. erato*, will chew a small chunk out of the ventral midrib of the leaf on which they are feeding. Occasionally there may be two such "furrows" chewed across the same midrib but usually a single one is cut between the base of the leaf and the level at which the caterpillar rests between feeding periods. On the other hand the midrib may be involved in complicated channeling and

TABLE IV. FEEDING BEHAVIOR OF TEN SPECIES OF HELICONIINE CATERPILLARS
(Information relating to *Philaethria dido* supplied by Constance Carter)
Key: + — Eaten.

Species	Scraping, holes, margin chewing	Midrib eaten, eaten later, or left	Midrib treatment	Leaf margins eaten	Leaf tips eaten	Amount of leaf abandoned
<i>Dione juno</i>	Scraping in first instar at least	Left	?	+	Dropped	Frill left on leaf, no petiole eaten
<i>Agraulis vanillae</i>	Holes chewed	Eaten later or ignored		+	+	Frill left on leaf, no petiole eaten
<i>Dryadula phaetusa</i>	1st instar, 2nd, chews channels in from margin	Eaten later	Channeling and bridging	+	+	Frill around base of leaf or petiole chewed
<i>Dryas iulia</i>	Chews channels in from margin even in first instar	Eaten later	Channeling and bridging	+	+	Often frill around base of leaf, but more usually petiole also eaten, sometimes stem as well
<i>Philaethria dido</i>	Chews channels in from margin even in first instar	?	?	?	?	?
<i>Heliconius isabella</i>	Scraping 1st, 2nd instar	Left, occasionally eaten later		+	Dropped	Base of leaf, midrib and tip are left
<i>Heliconius alipha</i>	Scraping 1st, 2nd instar	Sometimes eaten later, usually not		+	Sometimes definitely discarded	Always base of leaf is left
<i>Heliconius melpomene</i>	Very occasional scraping, usually channels or bays chewed from margin	Eaten together with blade	Chews furrows across under surface	+	+	1/2 leaf or frill around base is left
<i>Heliconius erato</i>	Never holes or scraping but channels or bays from margin	Eaten together with blade	May chew furrow in petiole	+	+	All leaf, and frequently petiole and often part of stem, is eaten
<i>Heliconius ricini</i>	Never scraping, but holes or channels and bays from margin	Eaten, often left by groups of larvae	May chew furrows across under surface	Often left, especially when eating as a group	+	About half leaf if larvae is solitary, if in group may eat even stem
<i>Heliconius sara</i>	As in <i>Heliconius ricini</i>	Eaten	May chew furrows across under surface			If larvae in a group, no leaf left; even stem chewed
<i>Heliconius doris</i>	Chewing from margin	?	?	?	?	?

bridging behavior shown by *D. iulia* and *D. phaetusa*.

4. The margins of a leaf may be left by *H. ricini* as tattered edges or they may be eaten with the rest of the leaf.

5. Leaf tips may be regularly eaten, as by *H. ricini* and *H. melpomene*; if the tips are not eaten they may be allowed either to fall to the ground or to remain with the midrib.

6. When a caterpillar moves over to a new leaf, as much as half the old leaf may be left,

only a small stub may remain or the caterpillar may have eaten it entirely. Some species (e. g., *D. iulia* and *H. erato*) normally eat the petiole, while *H. erato* eats the stem as well.

Table IV shows the distribution of these six characteristics among the species studied.

Many of these specific features appear to have no very obvious significance in the lives of the caterpillars. Some are extremely consistent and appear to be endogenously differentiated while others occur only under certain conditions and it seems that environmental fac-

tors are at least partly responsible for their appearance. The case of *H. aliphera* and *H. isabella* will be considered first. These scrape the cells from the surface of leaves instead of chewing through as do other larvae which eat the same host vines, *P. lonchophora* and *P. laurifolia* respectively. The scraping is seen only in the first, second and to some extent third instars of both species, which gives the impression that it occurs when the animals are too small to do otherwise. The same idea is also gained from the fact that *H. isabella* occurs on the tougher leaves of *P. laurifolia* while young *H. melpomene* and *H. ricini*, which feed on the same vine and do not use the scraping method, are limited to thin and tender leaves. Moreover, on several occasions a first instar *H. melpomene* did scrape for a short while when it was on a tougher leaf than is normal for this species. Finally, it is possible to induce a third instar *H. isabella*, which has been scraping at a tough leaf, to eat holes by putting it on a tender one, though it reverts to scraping when replaced on the tough leaf.

These observations suggest that the scraping habit of *H. isabella* is determined by purely mechanical considerations. This cannot be the full explanation, however, for the first and second instar *H. isabella* still scrape when put on tender leaves through which *H. melpomene* will chew. Further *H. aliphera* scrapes on the softest of *P. lonchophora* leaves. Nor can the effect be attributed in any simple way to the differences which occur in the sculpturing of the mandibles for *H. aliphera* and *H. isabella* are capable of chewing through both the upper and lower surface of a leaf at which they nevertheless only scrape if left on one side. Thus it does not seem that these caterpillars eat only the one epidermal layer because they are incapable of dealing with the other. Scraping would rather seem to be, at least in part, an inherited pattern in *H. aliphera* and *H. isabella*, although it is lost later and can be modified by external circumstances. It is probably present in the early instars of some species such as *H. melpomene* but is not expressed in the conditions in which these normally live.

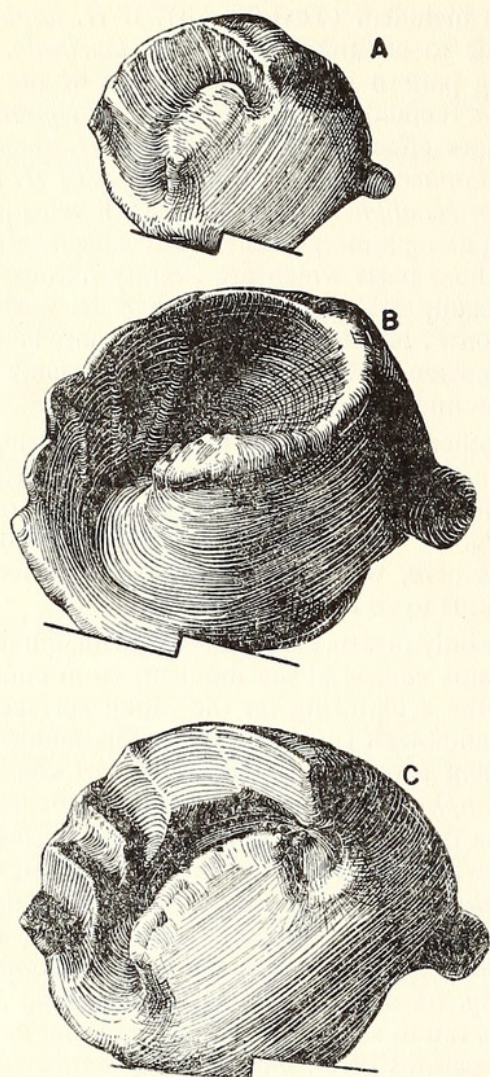
Eating or leaving the midrib is another characteristic for which there seems to be a simple, mechanical explanation. Although both *H. isabella* and *H. melpomene* feed on *P. laurifolia* leaves of similar texture, the appearances of the leaves left by the two species is quite different. *H. isabella* leaves the tip and the midrib entire and only the blade on either side is chewed away. (Text-fig. 5a). *H. melpomene* eats the tip of the leaf and straight across the blade,

midrib included. (Text-fig. 5b). If *H. aliphera* is made to eat the leaves of *P. laurifolia*, its feeding pattern is the same as that of the *H. isabella*. It could be suggested that *H. melpomene* has more effective mandibles than *H. isabella* or *H. aliphera*. Indeed, an individual of *H. isabella* or *H. aliphera* does leave small veins projecting along a margin where it has been eating, as if those parts which are slightly fibrous are less readily taken. Further, when *H. isabella* feeds on *P. serrato-digitata*, with a more succulent and tender leaf, it does not invariably reject the midribs.

Another species which rejects the midrib, at least in the third, fourth and early fifth instars, is *D. juno*. This caterpillar feeds on *P. serrato-digitata*. If the same mechanical explanation applies here, we would expect its mandibular apparatus to be still less efficient.

The only measure of efficiency of mandibular apparatus comes, at the moment, from considering the sculpturing on the biting surface of the mandibles (Text-fig. 6). On this factor the argument about the ineffectiveness of chewing in *H. aliphera* and *H. isabella* seems to be borne out, for these two possess none of the ridges and cusps which are clear on the maxillary edge of *H. melpomene* and *H. ricini* mandibles and the molar process is distinctly lower, flatter and smoother (cf. *H. aliphera* and *H. melpomene*, Text-fig. 6a and b). On the other hand, such studies fail to support the suggestion that chewing apparatus of *D. juno* is inefficient, for this caterpillar (Text-fig. 6c) has distinct cusps and ridges on the maxillary edges of its mandible although they are admittedly broader and less well formed for cutting than those of *H. melpomene*. The molar process, like that of *H. aliphera*, is well separated from the maxillary edge but is nevertheless somewhat cusped and there are small auxiliary cusps lying part way between molar and maxillary edges. Thus, arguments from simple considerations such as mandibular sculpturing do not throw light upon feeding differences, if indeed it is legitimate to expect them alone to serve as an index of chewing efficiency.

It is important, moreover, to recognize that the actual feeding patterns of these caterpillars are distinct. *H. melpomene* (and also *H. ricini*) eat across a leaf, taking both blade and midrib in a single action, whereas, if they accept the midrib, *H. aliphera* and *H. isabella* first eat the blade of a leaf and then, subsequently, the midrib which remains. Thus, whether or not mechanical factors determine whether the midrib can or cannot be eaten, these do not exert



TEXT-FIG. 6. Biting surface of the right mandible of a fifth instar caterpillar, showing the maxillary edge along the upper margin of the drawing and the molar process in the mid foreground. The projection on the lower right is the point of articulation. **a**, *H. aliphera*; **b**, *H. melpomene*; **c**, *D. juno*. Drawing by F. Waite Gibson.

an immediate influence over the pattern of feeding behavior.

b. Furrowing Behavior

H. melpomene and *H. ricini* share another very distinct behavior pattern in regard to the midrib. Caterpillars of either species will be found on the undersurface of *H. laurifolia* leaves, eating from the tip of a leaf back toward the base. Some time after a caterpillar has begun eating, it will turn around, walk a short way up the midrib and chew out the furrow mentioned earlier (Text-fig. 5b). At its deepest point this furrow is one-third of the depth of the midrib. It may be chewed out immediately after a bout of eating, during a rest period or just before the animal returns to the tip of the

leaf to eat. It seems improbable, therefore, that the material is eaten merely for its nutritive value.

Initially it seemed possible that such furrows might serve to control the flow of water into a leaf; perhaps when the water content of the leaf blade rises too high for a caterpillar, it chews furrows across the midrib, so reducing the water flow. Experiments do not support this hypothesis; desiccated caterpillars and those in normal water balance still chew furrows both in wilting and in normal leaves. Thus it seems improbable that the primary function of the activity is that of upsetting water transport in the leaf. Further, the furrow often does not go deep enough to injure the vascular bundles in the midrib.

A second possibility is that furrows represent a simple way of preventing other caterpillars' coming down the midrib and disturbing or even attacking the larva beyond the furrow; it may serve as a form of territory marker. No unequivocal evidence has been found for or against this theory. When an intruder has turned back and away after reaching a furrow, the response might have been mediated by movements made by the furrow-owner. Conversely, on one occasion when the owner had been removed, an intruder walked on down the midrib, crossing the furrow with scarcely any hesitation. This could be attributed to the intruder's being aware that there was no caterpillar beyond the furrow and that it could therefore ignore the "warning." Slight indications that this may be at least part of the explanation come from the fact that both *H. ricini* (semi-gregarious) and *H. sara* (gregarious) do not produce these furrows when they live together in a group but if individuals of either species are kept isolated they may do so.

Another point of interest in regard to this furrowing habit relates to *H. erato*. In many respects the behavior of this caterpillar is clearly related to that of *H. melpomene* and *H. ricini* and it might therefore be expected to show some signs of chewing furrows. Its normal food-plant is *P. tuberosa*, whose ventral midrib hardly protrudes at all, and on this vine it makes no attempt to chew furrows. Raised on *P. rubra* or *P. auriculata*, however, *H. erato* produces furrows indistinguishable from those of *H. melpomene*. This latter species will, however, attempt to chew furrows when kept on *P. lonchophora*, another vine with negligible midrib. These furrows are quite recognizable, although they may go rather deep and even be developed into a hole. Thus *H. erato* may, on an unusual host plant, make furrows if the midrib is

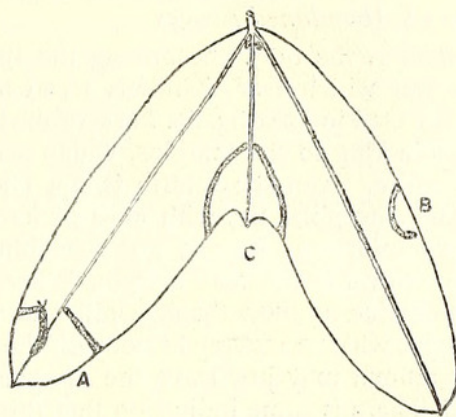
strongly developed while *H. melpomene* will retain its normal pattern on an unusual host even if the midrib is almost absent.

Compared with *H. melpomene* and *H. ricini*, *H. erato* displays very aggressive behavior towards other caterpillars. This can be interpreted in terms of the suggestions made above that one function of furrowing is as a territory marker. Possibly *H. erato* lived previously on a *P. laurifolia*-like vine with its thick veins. After the change, furrowing was difficult and its role in territorial defence was replaced by the development of more aggressive behavior.

c. Channeling Behavior

The channeling behavior of *D. iulia* and *D. phaeusa* (possibly also *P. dido*) is in some respects reminiscent of the furrow-chewing of *H. melpomene*, *H. ricini*, *H. sara* and *H. erato*. Both *D. iulia* and *D. phaeusa* have been seen on *P. tuberosa* while the former has shown precisely the same pattern on *P. rubra* and on the simple-leafed *P. auriculata*. A larva walks down the midrib to the tip of the leaf or leaflet, then it turns and walks back a variable distance, often about one-third of the length. If its body is long enough to reach from the midrib to the margin of the leaf, the caterpillar stretches out and begins to chew a channel across from the margin to the midrib of the leaf. The channel usually slopes slightly towards the leaf base as it nears the midrib but sometimes is almost at right angles to the midrib. As soon as this first narrow channel reaches the midrib, the caterpillar stretches across to the other side and begins a second which will extend inwards as did the first. When it, too, has reached the midrib, the caterpillar is on a small island of leaf, bridged merely by the midrib of the leaflet (Text-figs. 5d and 7a). Usually the caterpillar then chews at the midrib and spins some silk across the bridge. Sometimes, though not invariably, the larva crosses back to the main part of the leaf, walks along the proximal margin of its channel and bites at it. This does not appear to remove any material but just dents the edges slightly. The caterpillar then returns to the distal side of the bridge and rests along the midrib or begins to eat the island.

Although it is usual for this channeling behavior to occur in relation to the midrib of a leaflet, it may also relate to the margin of a leaflet (Text-fig. 7b), especially in the early instars, or even to the central vein running down between the two leaflets (Text-fig. 7c). After the first island has been eaten away completely, midrib and all, the caterpillar walks further up the leaflet and repeats the procedure once or



TEXT-FIG. 7. *D. iulia* feeding on *P. tuberosa*. a, A caterpillar chewing the second of two channels which will cut the tip of the leaflet almost free of the base; b, channel chewed in relation to the margin; c, a channel chewed in relation to the vein between the two leaf lobes.

twice more before crossing over to the other leaflet.

Channeling is shown by caterpillars of *D. iulia* and *D. phaeusa* from the first to the fifth instar, although both the first and fifth tend to show it less distinctly. Immediately before pupation, larvae lose the channeling habit and eat leaves either from the tip or lateral margin, the pattern being very like that shown throughout life by *H. erato* on the same vine.

Channeling could serve the same function of territory-marking as has been postulated for the midrib furrows shown by *H. melpomene*, *H. ricini*, *H. erato* and *H. sara*. If a number of *D. iulia* caterpillars are put onto a stem with an abundance of leaves, they establish themselves, each one on a separate leaf, or at most one to each leaflet of a leaf. When a caterpillar is moved onto a leaf occupied by another animal, it walks down until it reaches the bridge and then turns back. This may be due to some movement on the part of the owner, who often crosses the bridge and swings at the intruder with its head. Two observations of a caterpillar turning back although the owner had been removed are offset by several in which it did not.

The question may finally be raised as to whether there is any direct relationship between furrowing and channeling. It seems unlikely, because *D. iulia*, though normally found on *P. tuberosa* which has only a slight midrib, will continue to channel and bridge when cultured on *P. rubra* and *P. auriculata*, both of which have thick midribs. It shows no tendency to furrow. It seems therefore more probable that the furrowing and channeling patterns have been independently evolved.

d. State of Abandoned Leaves

H. ricini is the only one among the species studied here which ever abandons a leaf in the state illustrated in Text-fig. 5c. Parts of the blade remain adhering to the margins, which are left almost entire. Even the midrib is not chewed level. The caterpillar lies with most of its body along the midrib as it eats, just stretching its head out towards the leaf margin. Where the leaf is too wide to allow the caterpillar to reach the margins without moving its body off the midrib, the animal may just leave the margins untouched. There is some indication that this particular pattern may be correlated with the gregariousness of *H. ricini*. When eggs are laid singly or larvae isolated by the experimenter, the feeding pattern of the caterpillars recalls the "straight across" action of *H. melpomene*. Several animals together produce a more ragged effect. Similarly *H. sara*, when part of its normal group, shows no clear-cut feeding pattern, though when a caterpillar is raised alone it eats in the typically *H. melpomene* fashion, straight across blade, midrib and margins and even chews furrows in the midrib.

The amount of leaf material left when a caterpillar abandons a leaf (Table IV) and moves to a new one is to some extent characteristic of the species, although external factors, such as whether or not there is more food available, do have some influence. There is also a tendency for earlier instars to abandon a leaf with a higher percentage of it remaining than in the case of later ones. Four species, *D. iulia*, *D. phaetusa*, *H. erato* and *H. sara*, habitually eat the petiole of their leaf and sometimes continue and eat the stem as well. The first three species eat *P. tuberosa* and it could be that the stem of this vine is more palatable than that of others. This seems somewhat improbable. Moreover, other caterpillars, e.g., *H. melpomene* and *H. aliphera*, eat neither petioles nor stems when they are fed on *P. tuberosa*.

It is possible to relate this habit to the vegetative characteristic of the vine on which the caterpillars normally live. Thus the natural food of *H. sara* is the small *P. auriculata* vine, while *P. tuberosa* is also slight and slender and its leaves are frequently very scanty (see Table II). Presumably there would be strong selective pressure for any animals living on such vines to practice economy as far as possible and this might explain this aspect of the behavior of *D. iulia*, *D. phaetusa*, *H. erato* and *H. sara*. It is relevant that, when *H. erato* is fed on *P. laurifolia* or *D. iulia* on *P. rubra*, they both still eat the petiole as well as the leaf. This facet of their feeding behavior is thus, at least to some

extent, independent of environmental control.

e. Feeding Positions

It has already been said that positions adopted by feeding caterpillars differ specifically. The most obvious difference in this respect is whether or not the midrib is used as an orienting feature. A caterpillar of *H. melpomene*, *H. erato*, *D. iulia* or *D. phaetusa* usually has at least part of its body along the midrib while it eats a leaf (Table V). If the leaf is so wide that the animal cannot stretch to the margin, it lies parallel to the midrib (see p. 16 for the exception in the case of *H. ricini*). This adherence to the midrib may possibly have some selective advantage in relation to camouflage from predators but whether this is so or not, it certainly gives the caterpillars a more secure hold on the leaf. It is much easier to dislodge an individual of *H. melpomene* placed on the blade of a leaf than one that has been allowed onto the midrib.

While *H. aliphera* and *H. isabella* occasionally orient themselves parallel to the midrib as they eat, they do not lie along it. Normally their orientation bears no relation to it. *D. juno*, *A. vanillae*, *H. doris* and *H. sara* appear sometimes to orient to it or along it but at other times to pay it no attention. *D. juno*, *H. doris* and *H. sara* are gregarious and the lack of a definite and consistent orientation in feeding may be correlated with this habit; certainly *H. sara* when isolated from its fellow caterpillars will lie along the midrib, while a group of *D. juno* walk only along the midribs of the leaflets when they search for a new feeding place. *A. vanillae*, however, shows no signs of any consistent orientation of its body with respect to the form of a leaf in feeding. Neither *D. juno* nor *H. doris* has been tested singly on a leaf.

In the field the caterpillars of most species feed on the under or abaxial surface of a leaf (Table V), which is almost invariably the ventral one. This is not necessarily so in the laboratory and it has been found that the different species tend to differ in their responses to a leaf whose position has been reversed (Table V). *H. aliphera* and *H. isabella* both return to the ventral position, even though this means that they will not be eating from the true upper surface. *D. iulia*, *H. melpomene*, *H. erato* and to a lesser extent *H. ricini* still choose the under surface though this is now dorsal. Thus *H. aliphera* and *H. isabella* seem to be using different criteria for their choice than the other four species.

Feeding in first instar *H. ricini* and *H. sara* is noteworthy in that the caterpillars are found on the upper surface of a tender leaf which is still young enough to be at least partly folded.

TABLE V. FURTHER INFORMATION RELATING TO FEEDING BEHAVIOR
Key: + - Behavior in column above does occur.
- - Behavior in column above does not occur.

Species	Oriented along midrib	Eats standing on petiole or stalk	Holds loose piece in forefeet and eats	Eats from upper or under leaf surface	
				Normal leaf	Leaf inverted
<i>Dione juno</i>	Sometimes	Only just before pupation	—	Both	Both
<i>Agraulis vanillae</i>	Sometimes	—	—	Both	Both
<i>Dryadula phaetusa</i>	Usually	+	?	Under	?
<i>Dryas iulia</i>	Usually	+	+	Under	Upper
<i>Heliconius isabella</i>	No	—	—	Under	Under
<i>Heliconius aliphera</i>	No	—	—	Under	Under
<i>Heliconius melpomene</i>	+	—	—	Under	Upper
<i>Heliconius erato</i>	+	+	+	Under	Upper
<i>Heliconius ricini</i>	+ Except when grouped together & when parallel to it	—	—	Upper in 1st instar, lower or both later	Upper
<i>Heliconius doris</i>	?	?	?	Both	Both
<i>Heliconius sara</i>	Sometimes	—	—	Both	Both

They congregate between the two blades of the leaf, chewing away from inside their cover. This habit, which in *H. ricini* may continue into the early part of the third instar, differs from the behavior of the older larvae, which remain as far as possible on the under surface of the leaf (Table V). In *H. ricini*, however, the attraction does not lie in the upper surface of the leaves as such but in the fact that the blades provide a cover. If a young leaf is bent in the opposite way from normal (*i. e.*, with two under surfaces together), young *H. ricini* still collect between the two folded blades, although they are now on the under surface.

The surface of a leaf on which a caterpillar feeds may in some cases determine the feeding pattern adopted. When *H. melpomene* is placed on the under surface of a *P. lonchophora* leaf, it orients along the midrib of one of the leaflets, starts from the tip and eats straight across, midrib and all. If, however, it is placed on the upper surface it orients as *H. aliphera* and *H. isabella*, and eats from the margin of the leaflet, tending to leave the midrib. Thus the straight-across type of feeding is probably dependent to a large extent on the larva's having the midrib for orientation and this feeding pattern may be a specialization of one not dependent on the presence of a marked midrib.

f. Eating Actions

The third column of Table V shows that only two species, *D. iulia* and *H. erato*, are known to

use their legs for holding a loose fragment of leaf while they eat it, though it is possible that *D. phaetusa* may also behave in this way. *D. iulia* and *H. erato* are the two species which normally eat even the petioles of their leaves, so it is not surprising that they have evolved a behavior pattern allowing them to make use of small fragments which are lost to other species. On the other hand, when it is the exuvia cast after a molt that are being eaten, all species which have been watched use their first legs and usually their second in manipulating the empty skin and its scoli. This is perhaps explicable if the exuvia-eating pattern is an old and stable one within the subfamily, uninfluenced by evolutionary adaptations relating to new food plants.

H. erato, *D. iulia* and *D. phaetusa* also share what seems to be a related behavior pattern, in which they sit near the base of a leaf, on the petiole or even the stem, and chew at the distal end of the leaf, holding it with their legs and bending it back towards themselves. This habit of "pulling up" the leaf would also seem to be associated with the particular vine on which these species normally feed. *P. tuberosa* is one of the few species with medium-sized leaves still flexible enough to allow such bending. The behavior occurs when the larvae are in the fourth or fifth instar and are already beginning to become heavy for the thin and flexible leaves.

H. erato and *D. iulia* appear to twist their

heads more freely in eating than do the other species, while *H. melpomene* and *H. ricini* seem more flexible in this respect than *H. aliphera* and *H. isabella*. These differences are also reflected in the fact that, when they rest between a series of bites, *H. erato* and *D. iulia*, and to a lesser extent *H. melpomene* and *H. ricini*, have their heads overlapping the margin where they have been chewing.

There is no indication of "right-handed" or "left-handed" caterpillars, in that the head is never twisted to one side more than another. It goes to whichever side is the more convenient, considering the surface to be eaten and the disposition of the caterpillar's body as a whole.

Eating movements of all these species are alike in that the caterpillar extends and twists its neck. The mandibles then bite into the leaf. The head is drawn a little closer to the body and the jaws bite a second time. This is repeated until the head is against the body or the edge of the food is reached. The number of bites made during this movement of the head varies from 3 to 15, depending upon the length of material available for eating and its nature—more than one bite is given at a point where the material is tougher, such as a leaf vein.

While the head is being brought in from the extended position, the legs in all species are usually involved to some extent in shifting the thorax backwards. Sometimes all three pairs move but usually only the first two. There is a suggestion that the hind legs of *A. vanillae* are more active in this backward movement than those of other species. This may flatten the numerous glandular hairs with which *P. foetida* is covered. As will be seen later, this species shows a locomotory specialization which may also have evolved in relation to the problem of the thick, sticky hairs on this plant.

In eating, *H. isabella* and *H. aliphera* move their legs somewhat differently from the other species studied. A front leg, the one on the side to which the head is turned, beats rhythmically as the caterpillar makes its series of bites. The beats are generally made in the air but occasionally the foot will touch the leaf surface. No suggestion can be made concerning the significance of this movement and it is mentioned merely as a pattern shared by *H. aliphera* and *H. isabella* and appearing in no other species observed.

g. Eating of Egg-shells

Recently emerged larvae of the solitary *H. melpomene* and *H. erato* eat their own egg-shells within 10 to 20 minutes of leaving them. If they come across remnants of the egg-shells

of other caterpillars, they chew these too. When they find an egg which still has an embryo within, they show no inhibitions about eating into the shell and devouring the embryo. Were such behavior present in gregarious species such as *H. doris*, *H. sara*, *D. juno* or *H. ricini*, a whole batch of eggs might be destroyed by the first few larvae to emerge.

If, however, those caterpillars which are gregarious are less attracted to egg-shells they would be less likely to eat their fellow-larvae. This should be reflected in the absence of a tendency to eat their own empty egg-shells. Twelve *H. sara* eggs have been investigated in this respect and it was found that they had not been chewed other than at the emergence holes. *H. wallacei* has apparently a similar inhibition about eating its own or other egg-shells. This does not, however, hold for *D. juno* nor *H. ricini*, so that either a different method of preventing cannibalism has evolved here or inhibition of egg-shell eating is in no way associated with protecting developing embryos from predation by other caterpillars.

h. Eating of Cast Skins

The only question relating to the eating of cast skins that has been investigated, is whether or not foreign skins were acceptable and for how long. The answer is that any one species will accept the skins of any other if they are fresh and from first to fourth instar animals. Skins more than 24 hours old may still be eaten but they are often rejected. Similarly the skins cast by larvae molting out of the fifth instar and into a pupa are occasionally eaten (with the exception of the head capsule) but are usually rejected.

In testing the edibility of these various skins, the practice was to tie a piece of cotton thread tightly around the skin to be tested and then tie or tape the thread to the stem or leaf at the point from which the test animal's own skin had been removed. It was often the thread which the caterpillar ate when it moved to investigate the skin. Part of the attraction to the skin might lie in the spikiness of the spinules of the scoli, for the cotton threads had numerous minute threads attached to them, projecting like the spinules on the skin.

i. Drinking

Caterpillars of 10 species have been seen to drink water from small droplets on their leaves and there is little doubt that the other species also do this. The mouth is applied to the water, the mouthparts move and then remain still for the rest of the time. There is no indication that the drinking pattern is derived from that of eating or vice versa.

In the field even during the dry season there is abundant dew at night so that caterpillars have opportunity to drink adventitious water even when there has been no recent rain. They appear to thrive better in captivity when given free water to drink than when they are kept at a very high humidity but given no free water.

A pattern which is most noticeable in *H. aliphera* and *H. sara*, although it occurs in caterpillars of other species as well, is that of regurgitating a drop of green fluid when severely disturbed. After the effect of the disturbance has passed, the caterpillar takes up the fluid again, using the same pattern as when drinking water.

V. DEFECATION

Caterpillars all defecate at intervals throughout their periods of eating and resting and during locomotion. The rate of defecation varies, as measured by the time between the production of two fecal pellets, rising during any one instar with the increase in the duration of feeding periods. On the other hand the size of the pellets increases from one instar to the next, so that the range over which the defecation rate changes is roughly the same for the different instars of any species. As Nagasawa (1957) reported for the larvae of the gypsy moth, *Lymantria dispar* Linnaeus, there is no stepwise increase in the size of the fecal pellets as there is in head capsule size.

A fecal pellet is extruded as a small green cylinder, the form being very similar in all species. It dries and darkens to a brownish-black mass over a period of 2 to 3 hours. The defecatory behavior patterns of the species of heliconiine caterpillars studied here are all alike; the anal prolegs release their hold of leaf or stem, the hind end is raised into the air and the pellet expelled with more or less force from the anus. The rectal opening then closes and opens several times, moving rhythmically with the pads of the anal prolegs. Finally the hind end is once more lowered. *H. isabella* is the only species in which there is a noticeable waggle of the hind end immediately after defecation and even in this species it does not always occur. A caterpillar of any of the ten species watched (*H. doris*, *H. numata*, *H. wallacei* and *P. dido* have not been observed), will turn its head to its anus and with its jaws remove a pellet which has become stuck. Sometimes even after the pellet has been thrown free, the caterpillar turns and chews in the region of its anus, presumably at particles which remain.

When caterpillars are on a vine in a natural

position, the fecal pellets are either shot off or roll free of the leaf. Raised in dishes in the laboratory, however, the caterpillars frequently come across their own cast pellets. In these conditions a larva picks up the pellet with its mandibles, lifts its head and releases the pellet so that it may fall off the leaf or roll away. There is a slight tendency to jerk the head as the pellet is released so that it is actually thrown. In a dish in the laboratory a caterpillar invariably comes across the same or another pellet within a few minutes. It continues to reject pellets for a variable length of time and then apparently accommodates to the situation, ignoring pellets which are right beside its head. Constance Carter, who has raised large broods of *H. melpomene* for genetical work, reports that her caterpillars finally ceased to show the pellet-throwing behavior.

H. aliphera and *H. isabella*, when presented with fecal pellets, may attempt to throw them as do the other species. They may, however, show a variation which is peculiar to them. Instead of picking the material up in its mouth, a caterpillar bobs its head several times in the direction of the pellet, knocking it with the long head scoli. If the pellet is merely caught on some irregularity on the leaf, this treatment sometimes frees it and it falls away. In laboratory rearing dishes it is of course not usually effective. What is of interest is that the head bobbing or beating with the head scoli is also a response which both *H. isabella* and *H. aliphera* give to other more general disturbances.

D. juno is the only caterpillar in which an activity takes place that might be called "social defecation." Instead of a caterpillar turning and pulling a pellet free of its own anus, *D. juno* may have the pellet removed and rejected by another larva which is passing at the time. Usually the second caterpillar assists when the pellet is almost free, but sometimes it is almost dragged out of the defecating animal. It is not known how early in larval life this habit appears, but it persists into the late fourth instar before disappearing in the fifth. During the period over which the behavior occurs, a caterpillar is perfectly capable of ejecting pellets alone or of turning round and freeing a pellet from its own anus.

VI. RESTING

After an interval of feeding, caterpillars stop eating, turn away or walk backwards a short distance, and go into a resting phase. Both the position of a caterpillar relative to the leaf and its posture are, to a large extent, specific characters.

TABLE VI. RESTING BEHAVIOR OF TEN SPECIES OF HELICONIINE CATERPILLARS

Species	Main /general larval pattern of resting position in relation to leaf	Any change in resting position with prepupal stage	Posture of body
<i>Dione juno</i>	No definite orientation except to each other		Either straightened out or with thorax elevated
<i>Agraulis vanillae</i>	No definite orientation	Tends strongly to rest on stem or petiole	In "J" during early instars, later straight and extended on stem
<i>Dryadula phaetusa</i>	Along midrib		Usually "J" but straighter in later instars
<i>Dryas iulia</i>	Along midrib	Some tendency to rest on stem	Occasionally straight especially late 5th instar. Usually in "J"
<i>Heliconius isabella</i>	As in eating or facing opposite direction		Invariably straight, or with very slight curve
<i>Heliconius aliphera</i>	As in eating or facing opposite direction		Thorax usually curved to side. "J" less acute
<i>Heliconius melpomene</i>	Along midrib	None except coming off stem onto bottle in morning	Straight but usually thorax just out of line in front
<i>Heliconius erato</i>	Along midrib or stem	Strongly tends to rest on stem	Straight
<i>Heliconius ricini</i>	Along midrib, parallel to midrib or an oblique position		Straight but often thorax just out of line in front
<i>Heliconius sara</i>	No definite orientation except to each other		Straight, sometimes thorax elevated
<i>Heliconius doris</i>	?	?	?

a. Resting Position

Resting positions on a leaf are indicated in Text-fig. 5 and the last column of Table VI. In the same way that many behavior patterns change during the larval period, so does the choice of resting position. These positions can be divided into three main categories:

1. Those in which the caterpillars (*H. aliphera* and *H. isabella*) are oriented neither to the midrib or margin of the leaf nor to gravity. The only describable regularity is that in the resting position a caterpillar's body is oriented along the same line (or one parallel to it) as that taken during the previous period of feeding. The hind end may be pointing directly to or away from the site where the caterpillar finished eating.
2. Those (e. g., *D. iulia*, *D. phaetusa*, *H. melpomene*, *H. ricini* and to a lesser extent *H. erato*) which rest with the main part of their body along the midrib, irrespective of their last feeding position. After two individuals of *H. melpomene* have been eating side by side on a *P. laurifolia* leaf, they both crawl up and rest on the midrib, one behind the other.
3. The final group contains those species whose resting position shows no consistent rela-

tionship to the form of leaf. The details vary from species to species. Thus *A. vanillae* sometimes rests along the midrib, sometimes faces its feeding place, sometimes faces the opposite direction and often lies with its body having no particular orientation to anything at all. In later instars, however, this species most frequently rests on the petiole or stem of its plant.

In social resting among those species which are to some extent gregarious, the caterpillars usually lie side by side, frequently but not invariably facing in the same direction. In natural conditions the orientation of *D. juno* is in relation to the other caterpillars of the group rather than to environmental markers. The same would appear to be true of *H. doris* and also *H. sara*. If there has ever been a tendency to orient their bodies to the leaf in a particular way during the resting phase, it seems to have been lost in these gregarious species. The same explanation might apply to the slight tendency which the semi-gregarious species *H. ricini* shows away from the *H. melpomene*-type orientation, for it does not invariably rest along the midrib, but may lie obliquely or parallel to it.

Part of the pattern of resting during the day, or at least in the morning, shown by fifth instar *H. melpomene* and *D. iulia*, has been the selec-

tion of a particular resting position, away from the leaf on which they were eating. In many cases it has been a large leaf near the base of the vine but in the laboratory caterpillars have frequently chosen to rest on the bottle in which their vine was stuck. The same position was selected day after day.

b. Resting Posture (see Table VI).

The posture adopted by these various species of heliconiines during their resting phase must also be considered. A resting pose which may well be basic to the subfamily Heliconiinae is one in which the greater part of the caterpillar's body shows a particular orientation on the leaf but the head and thorax are turned to one side, giving what may be called the "J" position. This is shown in its most extreme form in *D. iulia* and *D. phaetusa* (Text-fig. 5d). *H. alipha* usually has a far less acute bend on the "J" and *H. isabella* such a gentle curve (when it is present at all) that it hardly resembles a "J" (Text-fig. 5a). *H. melpomene* and *H. ricini* rest in a "J" position in which there is no suggestion of a hook at the base of the "J", only a slight deviation from the straight line of the body, (Text-fig. 5b, c). When a number of *H. ricini* are kept together as a group, the "J" tends to straighten further.

Those species which show distinctly gregarious tendencies, *H. sara*, *H. doris* and *D. juno*, all rest with their bodies straight out or with the head and thorax arched up, the latter habit being especially marked in *D. juno*. This would seem to be merely a modification of the straightened position, allowing more crowding while preventing the animals' heads being buried. *H. erato* is somewhat anomalous for, although a solitary species, it rests with its body not only in a straight line but also extended; all the other species when they rest have their bodies contracted to some extent. *A. vanillae* in its fourth and fifth instars does, however, extend its body in resting on the stem.

The contraction of its body is most marked in a second anomalous case, that of *D. iulia* (Plate I). Here the whole thorax is drawn in towards the abdomen and this results in a marked humping of the first and second abdominal segments. Consequently the scoli borne on this region do not keep their normal orientation but all point forward along with those of the meso- and meta-thoracic segments, giving the animal a hunched appearance. The dorsal scoli of the second and third thoracic segments mingle with those of the first and second abdominal. The first lateral scoli, that belonging to the second thoracic segment, is always quite distinct

in the resting pose, but the lateral scoli of the metathoracic segment lie with the supralateral ones of the first two abdominal segments. This rest position is highly characteristic of *D. iulia* and has not been seen in other species. It is interesting in that it is extremely like the position taken up when the caterpillar is disturbed by a blast of air (not a touch), the only difference being that a disturbed caterpillar contracts so that the first lateral scoli also lies in the bunch of scoli, instead of being separate as it is in the rest position.

VII. WEAVING

When caterpillars are kept on fresh vines which are acceptable to them as food, they do not walk about very much. Between eating and resting a caterpillar may turn and walk away but often *H. melpomene*, *H. erato* and *H. isabella* just shuffle slightly backwards. Characteristic of even this brief walking, however, is behavior which may be called "weaving." The head is swung regularly from side to side and the spinneret behind the mouth spins a silk thread, touching it down to the surface so that figure-of-8 tracks are left behind the caterpillar.

Even when a caterpillar walks as fast as it may, it still trails a silk thread behind it, though in such conditions it is not attached as frequently.

This spinning of silk throughout the entire larval stage is undoubtedly of value to the caterpillar in that it always has a safety line attaching it to the leaf or stem and there is thus less danger of its being swept away from its vine. If a caterpillar falls, it hangs suspended on its thread of silk and subsequently climbs up this and back onto the point where it was attached.

A mat of silk threads is also spun over the surface of a leaf and this provides a secure footing for the claws and for the crochets of the prolegs. By watching the individual movements of a caterpillar's feet in walking, it is clear that the claws rely to a great extent on the silk trail to provide a foothold. A limb may make several movements and only when its claws make contact with the silk does it grasp. The effect can also be demonstrated by comparing the footholds of caterpillars on surfaces upon which they have been allowed to weave. Parts of a glass plate and of a smooth leaf (*P. lonchophora*) were covered by the weaving of *H. alipha*. A caterpillar was then dropped gently onto one surface or the other and as soon as it was on its feet, the glass or leaf was turned upside down. Occasionally the animal on the glass hung down for a short time,

its prolegs not grasping the surface immediately, but there was never any risk of its actually falling off. On the silk-covered leaf even the prolegs were attached quickly enough to prevent the hind end from hanging loosely. Conversely the caterpillar fell off clean glass, although occasionally it managed to remain for some time on the clean leaf. During this time it would rapidly weave on the under-surface of the leaf and as soon as its claws and crochets came in contact with the silk attachments, risk of their slipping decreased. An ability to remain on glass plates when these are reversed may have little value in the natural life of a caterpillar of *H. aliphera*, yet it is a fact that *H. aliphera* and *H. isabella* are the two species which weave most markedly and are also the animals which rest under the smooth blades of their leaves. It has already been suggested that part of the advantage of resting on the midrib is that it allows a more secure foothold, so a species living on smooth leaves and not utilizing the purchase of the midrib might well increase the extent of its weaving so that silk could be used in place of the midrib.

A caterpillar of *H. aliphera* or *H. isabella* will touch its spinneret to the substratum, then stretch its head back and then finally forward and down again. This behavior may be called "yawning" and though all species do yawn during the construction of the silk pad just before pupation, only *H. aliphera* and *H. isabella* have been seen to do it during earlier larval life. In spinning the pupational pad, yawning draws the silk so that a loop is formed. *H. aliphera* and *H. isabella* yawn predominantly when they return to their resting positions after feeding and it seems that these two species rest on a mat of somewhat looped silk instead of one with plain attachments like the other species. This would presumably provide them with a more secure foothold.

Weaving may be expected to occur whenever the foothold of a caterpillar is precarious. In fact, it seems to be elicited by any surface which is strange to the caterpillar—even if it has already been covered with silk by another animal. There are exceptions to this rule, the ambulatory phase immediately before a larva hangs up to pupate being a clear example. During this period the caterpillar walks onto many strange surfaces but will not begin to weave until it reaches a potential site.

Another example of the weaving behavior was first noticed in the laboratory dishes. Fresh leaves were put in for the caterpillars each day and frequently when those of the previous day were being removed they were found to be tied

firmly onto the dish and/or each other with silk threads. If there were a remnant of the petiole left it was almost invariably this part which was attached to the dish, though sometimes another projection might be used. This phenomenon is explicable in terms of what has already been said about weaving. The caterpillars remain on their leaves for most of the time, refusing to abandon a leaf in order to walk onto the glass. When they encounter the glass, however, there is a bout of weaving as they touch the strange surface; thus at this point the stem and glass become attached by a series of silk threads. The species on which these observations were initially made comes onto or deserts a leaf, walking along the midrib, so that caterpillars in the dishes would usually have come into contact with the glass from one or the other end of the midrib. Thus it was here, the petiole or sometimes the tip of the leaf, where the silk attachment was formed.

There are observations which suggest that such "tying-up" behavior is not unnatural and that it occurs in the field. In a number of instances caterpillars, living freely on large pieces of vine, have been seen to weave steadily between the petiole and the stem to which it is attached, thus reinforcing the natural junction. The behavior has been particularly noticed in *H. melpomene* but also occurs in other species. The same or a very closely related pattern is sometimes observed in *H. sara*, where a group of caterpillars will tie two or several leaves together with silk. Bell (1920) records how the larvae of the oriental lycaenids, *Vivachola isocrates* and *V. perse*, bind the stalk of the fruit on which they are feeding onto the branch with silk, and such behavior doubtless occurs among many other lepidopterous larvae.

Tying the whole leaf onto the stem would seem a possible safeguard against the leaf's becoming detached while the caterpillar eats from it—an event which has in fact been seen on two occasions in Trinidad. The same explanation could be true of the behavior of gregarious *H. sara*, for *P. auriculata* leaves will sometimes drop off while still green and while being chewed by the caterpillar. It is also an advantage when the leaf concerned is chewed loose by animals proximal to it. Any caterpillars which are feeding distally are then still able to cross by the silk bridge onto another leaf and so back to the vine. This also has been observed in the laboratory.

Even if its leaf comes loose or another animal chews away the link between leaf and vine, there is still a possibility that a caterpillar may be able to climb up and regain its place. This

cannot be said for a pupa in the same circumstances, because its power of movement is so limited. It is therefore not surprising that a caterpillar, preparing to pupate on a leaf petiole, old flower stalk, tendril or even a leaf, should frequently weave between the object on which it will pupate and the main body of the vine. Such behavior would certainly be selectively advantageous and has been recorded in many lepidopterous larvae (see Ford, 1945, and Hinton, 1955). Indeed, in the present study there have been four instances in *D. iulia*, one in *A. vanillae* and one in *H. melpomene* in which the slight silk attachment alone was holding the pupal support on the vine. The consequences of one of these pupae falling to the ground will be considered later.

The final point about weaving is that it may occur in situations in which the caterpillar seems merely to be generally disturbed. *H. aliphera* is especially prone to weave very actively on the surface of its leaf if it is poked, blown on, shaken or if another caterpillar comes near it. This could perhaps be regarded as an example of a displacement activity, though it may also be argued that a behavior pattern which ensures a more secure attachment to the substratum would be appropriate in a situation in which the animal is being attacked in any way. It seems very similar to behavior described by Dethier (1943) in lepidopterous larvae removed from their plant food and which he interprets as a "visual searching movement."

VIII. LOCOMOTION

Locomotion which occurs between feeding periods is normally of short duration. Nevertheless some specific differences are apparent. *H. aliphera*, *H. isabella*, *H. ricini*, *H. melpomene*, *H. sara*, *D. juno* and *D. phaetusa* make practically no movement at all, sometimes just walking slightly backwards, sometimes turning and walking a few centimeters. *H. erato*, *D. iulia* and *A. vanillae* often walk an appreciable distance, up the leaf, onto and along the stem. *D. iulia* walks very much more quickly than the others, directly and without stops. Conversely *H. erato* barely seems to be moving at all and frequently stops altogether. *A. vanillae* walks slowly, eating the hairs from the leaf, petiole and stem as it goes.

Both *A. vanillae* and *D. iulia* have peculiarities in their mode of walking but these do not always appear. *A. vanillae* has a strange, jerky stride; the anal prolegs are raised, carried forward and then oscillated back and forth just above the stem several times before they are finally put down in the new position. The head

and legs also show this jerky motion but not as strongly as the hind end. It is possible that the action normally results in flattening down the glandular hairs with which *P. foetida* is liberally covered, thus producing a clear area for attachment of the anal prolegs. These caterpillars seem rarely to leave their vines, even pupating on them; this might explain why they sometimes walk in this jerky way even in situations where there are no hairs to flatten, as when walking down a piece of wire. The peculiarity in walking of *D. iulia* also consists of a movement of the hind part. In this case the last segment with the anal prolegs is lifted and lowered sharply several times during each short burst of forward locomotion. No explanation is offered for this pattern.

The locomotor stage which frequently occurs just before pupation will be considered more fully later. Suffice it to say here that in most species it starts very sharply and that it may last as long as three hours, during which time the animal may cover as much as 50 meters of ground. With the exception of *A. vanillae* and occasionally *D. iulia*, the walking motion is smooth. *H. aliphera*, *H. isabella*, *H. erato* and *D. phaetusa* will seldom walk as far as a meter without stopping for one or more short rests. During this walking stage the animals show no obvious photopositive or photonegative orientation. There is, however, slight evidence of a negative geotaxis, at least in *H. aliphera*, *H. isabella* and *D. iulia*.

IX. SOCIAL BEHAVIOR

Information which allows an estimate of the degree of social behavior among larvae is available for only 10 of the 14 species of Heliconiinae in Trinidad. Of *D. phaetusa*, *P. dido*, *H. numata* and *H. wallacei* it can be said only that the last-mentioned alone among them is gregarious.

The other 10 species can be arranged in a series from the typically aggressive, asocial caterpillars of *H. erato* to those of *D. juno* which are not only gregarious but show signs of actual social behavior. As has already been said (Table III), the eggs of some of the species are laid together in a group so that the larvae of these species, *D. juno*, *H. ricini*, *H. sara* and *H. doris*, start living communally. The eggs of *H. isabella* and *H. aliphera* are never laid in a group but the female is not averse to laying more than one egg—up to six in the case of *H. aliphera*—on a single leaf. This contrasts strongly with the behavior of the female *H. erato* which flies away to another vine rather than lay an egg on a set of leaflets where one is already glued.

The degree of intolerance of one caterpillar

for others, either of its own or another species, is greatest in *H. erato*, which is never found sharing a leaf without fighting. *D. iulia*, *H. aliphera* and *H. isabella* also remain solitary on their leaves but when more than one caterpillar are together, they do not bite at each other as *H. erato* would do. A specimen of either of these three species will swing its head and thorax at an intruder or will shake the whole of its anterior half but there is very seldom any contact at all between such caterpillars. Two individuals of *H. aliphera*, for instance, may try for several hours to share the same leaf and it seems to be only their mutual disturbance which eventually results in their separation. Further, newly-emerged larvae of *H. erato* will attack and eat other larvae or eggs, while such behavior is comparatively rare in *D. iulia*, *H. aliphera* and *H. isabella*.

H. melpomene, while it eats eggs and newly-emerged larvae during its first instar, appears later to become more tolerant and will share a leaf with another caterpillar of approximately its own size even when there is an ample amount of leaves available. *A. vanillae* shows no violent reaction to sharing its leaf with others of its own or other species and has, furthermore, never yet been found to eat eggs or newly-emerged larvae. *H. ricini* shows even less response to other caterpillars than does *A. vanillae*, not even swinging its head at them as a rule. There is nevertheless no great attraction evident between *H. ricini* caterpillars. Although they may eat, rest and molt together as a group, one or two will frequently remain separate from the others, an occurrence which is almost never seen in *H. sara*, *H. doris* or *D. juno*.

Except in cases of food shortage, there is never any aggression between caterpillars of *H. sara*, *H. doris* and *D. juno*. In fact, individuals of the last-mentioned species seem distinctly unsettled when separated from others of their group. Even small groups of three or four caterpillars do not remain discrete in the presence of a larger collection, but join it. One specimen of *D. juno* appeared less unsettled when allowed to share a leaf with *H. ricini* than when it was alone.

Molting has not been watched in conditions approaching normal for *H. doris*. In glass dishes, however, they clearly orient to each other. Groups of *H. sara* and *D. juno* molt on the stem of their vine and are oriented to each other. *D. juno* form a double ring around the stem, bodies parallel to each other and to the stem, most with their heads pointing to the center. *H. sara* shows a far less strict orientation although the bodies of the larvae are parallel to each other.

As has been said in the section on feeding, gregarious species and in fact those which are not normally gregarious but are kept in groups by the experimenter, establish synchronization of feeding and resting. The degree of coordination varies from the strict effect in *H. doris* and *D. juno* to the more ragged one typical of *H. ricini* and the naturally solitary species. Similarly the synchronization of molting and pupation is more marked in the truly gregarious species.

Finally, *D. juno* alone has been seen to practice what has been termed social defecation, one larva discarding a fecal pellet from the anus of another. It has not been established whether *D. juno* will remove pellets from the anus of a species other than its own, nor is it clear whether or not there is any selective advantage to be had from social defecation. Certainly it would appear an easy habit to acquire in that all species of heliconiines have been seen to throw free pellets which they come across.

X. DEFENSIVE BEHAVIOR

Study of these caterpillars was started with a view to using their defensive reactions as clues in physiological work on their sense organs. It soon appeared that such responses are very variable and probably depend on the basic activity of the larva at the time. It was therefore necessary to expand the project so as to get some idea of these "basic activities." The caterpillars were disturbed as little as possible by the observer, the result being the information presented in sections I and II of this study. A further result was that defensive behavior was seldom elicited except in encounters between the caterpillars themselves or in fights with insects such as ants or mantids. It should therefore be held in mind that caterpillars may be capable of far more drastic and clear-cut defense responses than are described for them here.

The stock response is that of turning from side to side or banging the head and thorax continually towards the side that was stimulated.

In *H. isabella* alone the caterpillar may loosen the hold of its anal and posterior prolegs and thump its tail end up and down when disturbed. It is noticeable that this species is alone in having its posterior segments a bright contrasting color (see Beebe, Crane & Fleming, 1960). Two apparently otherwise unrelated species, *H. sara* and *H. aliphera*, are both prone to regurgitate contents of the gut, though such behavior can be elicited in other species as well. *H. aliphera* and *H. isabella* both beat at an object or intruder with their long head scoli, a habit already mentioned in the section on defecation.

Although *H. melpomene* and *D. iulia* also have long scoli on their head capsules, they have never been seen to use them as do *H. isabella* and *H. aliphera*.

XI. PHYLOGENETIC DISCUSSION

The observations recorded here were part of what was essentially a preliminary study, an attempt to expose problems which allow experimental analysis, and consequently any phylogenetic conclusions must necessarily be extremely tentative. It would appear that they are worth discussing, nevertheless, if only because they define more clearly what further information is needed.

The activity patterns have not revealed any striking similarities or differences between the species. While it would obviously be of great interest to investigate the control of these, it seems improbable that information on this score will contribute to knowledge of relationships. The nocturnal feeding in *D. iulia* and *H. melpomene* has probably been acquired independently—it is clearly a later specialization, taking effect only in the fifth instar. It certainly seems worth discovering whether the method of control is the same in both.

On the basis of feeding behavior, the 10 species studied fall into three major groups. This is true of patterns in the first instar larvae as well as later on and may be further correlated with the resting position and posture taken up between feeding. Within these three there are other, closer associations of species.

The first group is that comprising *A. vanillae*, *D. juno*, *H. aliphera* and *H. isabella*. None of these habitually orient their bodies along the midrib of a leaf or leaflet, either during feeding or rest. It is not known for certain how the first instar *A. vanillae* eat but certainly some individuals have been seen to chew holes in their leaves. The other three species all scrape the green cells from the surface of leaves, and it seems probable that this pattern is fairly generally present among heliconiines even though it is not in all cases the one naturally shown. If a leaf is thin enough, the caterpillar is likely to produce small holes where it has scraped and it seems possible that this is what occurs in the case of *A. vanillae*.

While *A. vanillae* and *D. juno* do not orient in relation to the midrib, *H. aliphera* and *H. isabella* never lie along or on it and appear to orient away from it. Their feeding patterns, especially that of *H. isabella*, result in the midrib's being left on an abandoned leaf. This tendency is perhaps reflected in two other charac-

teristics shared by *H. aliphera* and *H. isabella*. First, these two show a greater development of weaving behavior than any other species. This would be of importance when the foothold provided by a midrib is unavailable (see p. 18). Second, there is the trend seen in *H. aliphera* and characteristic of *H. isabella* towards attaching the pupa to the smooth blade of a leaf rather than the midrib of some other vein or protrusion (see section II).

H. aliphera and *H. isabella* both wave a single foreleg rhythmically during their feeding, a further indication of the sharing of behavior patterns.

The second group consists of *H. melpomene*, *H. ricini*, *H. erato* and *H. sara* (possibly *H. doris* as well). When these caterpillars are solitary their feeding position is sharply oriented towards the midrib, in that they lie along it during the rests between chewing as well as during feeding. When alone, all of these species eat straight across the leaf, cutting through the midrib as well as the blade. When raised in a group *H. ricini* and *H. sara* both become inconsistent in their patterns but this is to be expected, for the animals now tend to orient in relation to each other rather than to the leaf.

Furrowing across the midrib occurs in some circumstances in all of these four species. Until its function has been established, too much emphasis should not perhaps be laid on this. Yet it is suggestive of a fairly close relationship among the species, especially as it is in *H. erato*, at least, what might be called "vestigial behavior"—a pattern elicited only when the caterpillar is in somewhat abnormal conditions.

It seems possible that *H. erato* comes from a stock which lived on *P. laurifolia*, as do *H. melpomene* and *H. ricini*. When it migrated to the slender *P. tuberosa* vine, *H. erato* lost the sharp orientation to the midrib from its natural repertoire of behavior patterns and this only reappears now if it is fed on *P. laurifolia*. On *P. tuberosa* feeding and resting are still relative to the midrib but the habit of midrib furrowing is not displayed. Chewing straight across the blade and midrib is replaced to some extent by behavior such as the "pulling-up" technique. This enables *H. erato* to utilize even the tips of slender leaves onto which it is too heavy to climb. The flimsiness of many *P. tuberosa* leaves may also have led up to the evolution of the practice of resting on the stem instead of the leaf.

H. sara and *H. ricini* share the characteristic of eating holes or channels in subterminal leaflets while these are still folded together. This might be taken to indicate a close relationship.

Another explanation is, however, possible. Their eggs are laid in batches and are smaller than those of *H. melpomene* or *H. erato*; the maximal diameters of the eggs of *H. sara* and *H. ricini* are 0.65 and 0.70 mm. respectively; corresponding minimal diameters are 0.92 mm. for *H. melpomene* and 0.81 mm. for *H. erato*. Correlated with the smaller eggs are smaller first instar larvae and it is possible that their size allows the caterpillars of these species to pass between the folded blades of the young leaves. The significance of egg size is not clear. It might be related to the habit of laying eggs in batches, *i. e.*, laying a large number at once instead of a few each day. If this is indeed the case, the similar early larval habits may be more a reflection of adult behavior and physiology than a simple case of larval similarity.

The third group contains *D. iulia*, *D. phaetusa* and almost certainly *P. dido*. Feeding and resting orientation, as in the second group, are in relation to the midrib. Bridging and channeling behavior, however, is quite distinct from furrowing. In *D. iulia* such behavior is very consistently present and occurs on *P. auriculata* and *P. rubra* exactly as it does on *P. tuberosa*. The leaves of these two vines are furrowed by *H. erato* and *H. sara*, however, so that there is no question of channeling behavior being distinct from the furrowing simply because they occur on different plants.

Here again the feeding of first instar larvae is fairly distinct from that of the other two groups. *D. iulia*, *P. dido* and almost certainly *D. phaetusa* chew long channels, starting at the margin. This pattern is in fact clearly related to their channeling and bridging behavior which occurs later.

Despite the fact that *D. iulia* and *H. erato* have been relegated to separate groups here, there are nevertheless a number of similarities in their feeding patterns; both will bend a leaf back and chew it, both eat the last remnant of leaf, then the petiole and often even the stem. The sculpturing of the mandibles is superficially very alike in *H. erato*, *D. iulia* and *D. phaetusa*, the large cusps on the mesial end of the maxillary edge being especially well developed (see Text-fig. 8a, b, c). All these seem to be adaptations that might well be produced in species living on vines with few, flimsy leaves and where behavior and chewing apparatus were evolved in relation to minimal wastage of plant material.

The feeding pattern of the larvae of the first group, and especially *A. vanillae*, is considered to be more primitive than those of the others. This view is based on two facts. First, an individ-

idual from the second or third group, when forced to feed without the orienting signal of a midrib, shows a pattern which could easily have been produced by a caterpillar of the first group. Thus *H. melpomene* placed on the upper surface of a *P. lonchophora* leaf eats the margin instead of the tip of the leaf, frequently leaves the midrib and between periods of feeding orients relative to the place where it has been chewing, not the central part of the leaf. Second, *P. laurifolia* has a very well-developed midrib. This feature or the smoothness of the blade might influence a caterpillar towards orienting on the midrib; both together should be more effective. *A. vanillae* will indeed orient its body along the midrib of a *P. laurifolia* leaf. However, it neither eats in the specialized straight-across manner of *H. melpomene*, isolated *H. ricini* and *H. sara*, nor does it normally orient to the midribs of other vines.

Resting positions on the leaf have already been discussed. The basic pose of the body during rest seems to be a curve or bend and, with the exception of *H. erato* and larvae living in groups, the caterpillars of all species show this at some stage. *H. isabella* is less inclined to do so than *H. aliphera*, another fact indicating that it is somewhat further along a line of specialization than *H. aliphera*.

There are clear differences between the postures of *D. iulia* or *D. phaetusa*, that of *H. aliphera* and that of *H. melpomene* or the solitary *H. ricini*. The first two take up a distinct "J" position, with only the head and thorax twisted to one side. The bend in a resting caterpillar of *H. aliphera* is approximately at its second abdominal segment, while *H. melpomene* lies in a straight line with only its head and thorax slightly to one side (see Text-fig. 5b).

All species which rest along the midrib, *H. erato* and in their later stages *D. iulia* and *A. vanillae*, hold their bodies straightened out but this seems to have no more significance than that most stems or midribs are straight. *H. erato* and the later stages of *A. vanillae* rest in an extended position, but the fact that young *A. vanillae* rest in a contracted and bent posture suggests that this is more probably a case of convergence than relationship. *D. iulia* alone produces its peculiar humped-up rest pose, with its characteristically bunched spines, and no sign of this has been seen elsewhere, not even in *D. phaetusa*.

The gregarious species, *D. juno*, *H. doris*, *H. sara* and to some extent *H. ricini*, usually rest with their bodies laid straight along the substratum though this is less marked the fewer

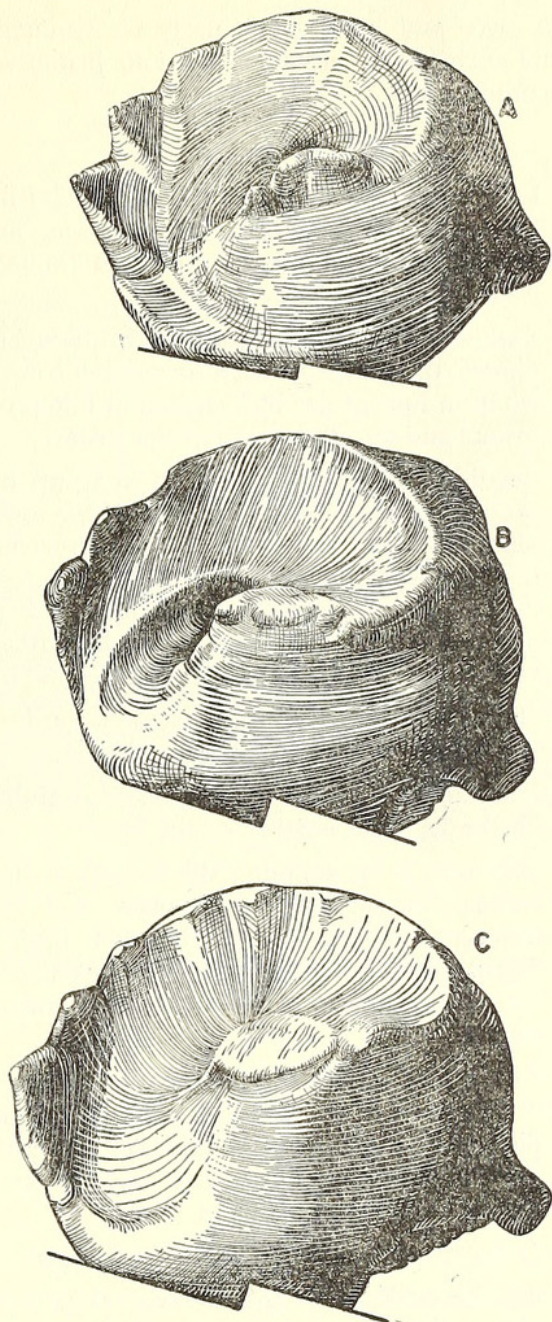
animals there are in the group. In some instances the caterpillars rest with their thoraxes elevated. This usually occurs when animals would otherwise overlap each other. It may appear even when there is no suggestion of crowding and occasionally occurs when a caterpillar rests alone.

It seems clear that the resting heliconiine caterpillar has its body bent laterally and that those species which rest in a straight line are the exceptions. However, there is no suggestion concerning the control of the behavior in each individual, for *D. iulia* will occasionally be found in a "J" pose even when sitting on a straight stem. The anterior part is in this case free in the air. Nor is there any indication of a possible selective advantage of such a bend to the larvae.

The range of social behavior does not at all reflect the groupings suggested on the basis of feeding and resting. *H. erato* is fairly distinct in its sharp intolerance for other caterpillars of any species. On the other hand the remaining species of the group in which *H. erato* has primarily been classified vary between vague tolerance on the part of *H. melpomene* to the distinct gregariousness of *H. ricini*, *H. sara* and *H. doris*. The question of social behavior in *D. phaetusa* and *P. dido* is largely an open one; if they are at all like *D. iulia*, they show neither violent aggressiveness nor any signs of gregariousness. The third group varies from slight intolerance shown by *H. aliphera* and *H. isabella* through the tolerance of *A. vanillae* to very distinct gregariousness in *D. juno*.

On the information available here there is nothing to distinguish the trends towards social behavior seen in *H. ricini*, *H. sara*, *H. doris* and *D. juno*. There is no indication that these have been independently achieved although this would be inevitable on evidence from feeding and resting. The matter of eating egg-shells (p. 14) has not been taken far enough to serve as more than a pointer to the need for further information.

In conclusion, larval behavior as estimated from feeding, defecation, locomotion, resting and weaving is specifically distinct. It seems likely that the differences reflect phylogenetic relationships within the group. If this be so, the present study suggests that *H. isabella* and *H. aliphera* are closely related to each other, *H. aliphera* being nearer the other species of *Heliconius*. Of these other *Heliconius*, *H. erato* is specialized away from *H. melpomene*, *H. ricini* and *H. sara* but shows indications of relationship nevertheless.



TEXT-FIG. 8. The biting surfaces of the right mandible of **a**, *H. erato*; **b**, *D. iulia*; and **c**, *D. phaetusa*, showing the common development of the first maxillary cusp and the separation of the maxillary and molar parts. Drawings by F. Waite Gibson.

D. iulia, *D. phaetusa* and almost certainly *P. dido* form a group which in many ways parallels that of *H. melpomene*. Of these *D. phaetusa* is less specialized in behavior patterns and shares to a lesser extent similarities which seem to have been independently evolved in *H. erato* and *D. iulia*.

D. juno and *A. vanillae* are less alike but on the whole they resemble each other more than they do any other species. In most respects

these two, and more particularly *A. vanillae*, would seem fairly closely related to primitive heliconiine stock.

XII. SUMMARY

1. Larval behavior of 11 of the 14 species of heliconiine butterflies of Trinidad was observed in the laboratory and to a limited extent in the field.
2. Periods of feeding alternate with quiescent phases, the extent of each depending somewhat on the species but varying in different instars and during any particular instar.
3. Feeding behavior is described in terms of preference for particular species of the food plant, vines of the Family Passifloraceae, the pattern left on the leaves and the movements made during eating. The first two differ from species to species but the last is very similar in all species examined.
4. Observations are recorded on how the larvae eat egg-shells, drink and defecate.
5. Resting is described in relation to position on the leaf and posture of the body.
6. The activity of spinning silk threads is described, its significance discussed and the different emphasis on such behavior in different species pointed out. Slight peculiarities of locomotion in some species are mentioned.
7. The extent to which a caterpillar will tolerate others of the same or other species is discussed, together with evidence for gregarious behavior in regard to feeding, resting, molting and defecation.
8. Defensive behavior is briefly mentioned.
9. On the evidence of the behavior described above, the grouping of species is discussed. It does not agree fully with that of the present taxonomy although it is itself consistent within its limits.

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EXPLANATION OF THE PLATE

PLATE I

- FIG. 1. Resting posture of *D. iulia*, showing the contracted state of the first abdominal and last two thoracic segments and the consequent bunching of the anterior scoli. Photograph by Russ Kinne.

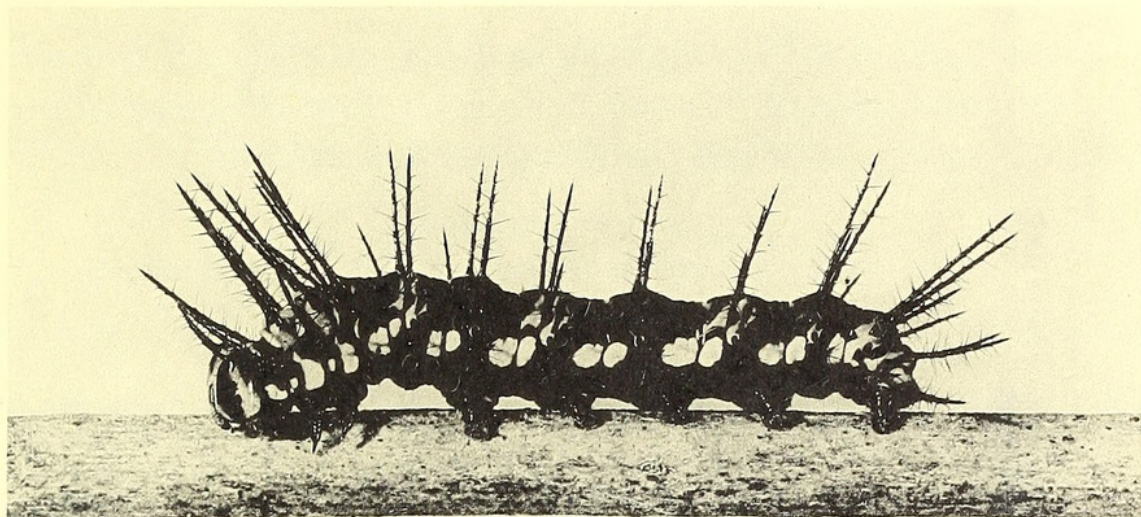


FIG. 1

A STUDY OF THE BIOLOGY AND BEHAVIOR OF THE CATERpillARS, PUPAE
AND EMERGING BUTTERFLIES OF THE SUBFAMILY HELICONIINAE IN TRINIDAD, W. I.



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