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A Comparison of Eggs, Larvae and Pupae in Fourteen Species of Heliconiine Butterflies from Trinidad, W. I.^{1, 2}

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(Plates I-XVI; Text-figures 1-14)

[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. The 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, with an annual rainfall of 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." by William Beebe, *Zoologica*, 1952, Vol. 37, No. 13, pp. 157-184].

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I. INTRODUCTION

THIS contribution is one of a series on the biology and ecology of butterflies of the nymphalid subfamily Heliconiinae. The egg, larva and pupa of all of the 14 species recorded from Trinidad are described. It is for-

tunate that all except one genus in the subfamily are represented, as well as species from most groups composing the large genus *Heliconius*.

The study has a triple purpose. First, it aims to make available to taxonomic workers descriptions of the growth stages in a relatively homogeneous group of butterflies. Such descriptions occur in the literature for only a few heliconiines; without exception these accounts lack the detail necessary for comparative study, either interspecifically or of different populations. The second purpose is to provide a foundation for studies on the ethology and sensory physiology of the immature stages. Thirdly, the contribution is intended to serve as one of a series of basic studies leading to an understanding of the phylogeny of the group and of the evolution of its noteworthy adaptations.

Certain characteristics make the subfamily especially suitable for detailed investigation. The group is widely distributed throughout the tropics and subtropics of the western hemisphere. It includes numerous species, many having an extensive range, and sympatry is common. It has furnished classic examples illustrating the theories of aposematic coloration and Müllerian mimicry. Polymorphism is so prevalent in some localities that the systematic standing of many forms remains in question. Patterns of social behavior in both larvae and imagoes are proving to be surprisingly complex, with involved sensory bases. Finally, members of the family have shown themselves to be well adapted to life in tropical insectaries and, as larvae, in the laboratory; their behavior in all stages can, therefore, be studied by observation and experiment.

Six contributions in the series have already been published (Beebe, 1955; Crane & Fleming, 1953; Crane, 1954, 1955, 1957; Fleming, 1960).

In their most general characteristics, the life histories of all 14 species under consideration are similar and may be informally summarized as follows: The egg, which is laid on *Passiflora* spp., is characterized externally by a network of strong horizontal and vertical ridges. The larva has numerous, paired, branching spines, including one pair on the head and three pairs on most body segments; the body is otherwise almost smooth. The pupa varies from very rough, with tubercles, flanges and spines, to almost smooth; gold-colored spots and a pair of long cephalic appendages may be present or absent. The duration of the egg stage is four days or less; the five larval instars require a minimum total of 13 days for completion; the pupal stage lasts 9 or 10 days. Although the total minimum time of development from oviposition to emergence of the butterfly is accordingly 26 days, development often continues for three or four days longer.

The data in the present study have accumulated slowly since the opening of the Zoological Society's Trinidad Field Station in 1950, when the first egg of *Heliconius erato* was accidentally brought into the laboratory on a casually collected vine, and the larva reared by the senior author. Although most of the heliconiine butterflies known from Trinidad were soon discovered near the Station, the identification and description of the larvae and their respective food-plants proceeded erratically, through successive seasons, as a by-product of the work on imaginal behavior. Meanwhile, as our interest grew in the ethology and phylogeny of the group, it became essential to study the immature stages. Serious attempts to complete the data for the present contribution began in 1959, and it was not until May, 1960, that the last unknown larva, that of *H. numata*, was secured.

Since each of the 14 species has seven pre-imaginal stages (egg, five larval instars and pupa), 98 different forms are concerned. Each had to be described in life, studied in preservative, and variations established through comparisons of series. Whenever the life history of another species became known to us, revisions in our existing keys, descriptions, and phylogenetic hypotheses became necessary. Also available for study were the growth stages, living and preserved, of eight of the same species from Surinam, which served for preliminary geographic comparisons.

The study presented here deals only with major external characters and is still, therefore, far from complete. The most notable gaps are in the lack of work on setae and crochets in older larvae, although those of the first instar have been treated in detail by Fleming (1960), on detailed comparisons of spinules on the scoli and in the omission of mouthpart studies. It is expected that future studies of behavior and sensory physiology will contribute to the knowledge of these aspects.

For generic nomenclature, Michener's (1942) revision of the Heliconiinae is followed; the specific names are those of Kaye in "The Butterflies of Trinidad" (1921). The subspecies recognized by Kaye are as follows:

Dione juno juno (Cramer)

Agraulis vanillae vanillae (Linnaeus)

Dryadula phaetusa phaetusa (Linnaeus)

Dryas iulia iulia (Fabricius)

Philaethria dido dido (Clerck)

Heliconius isabella isabella (Cramer)

Heliconius aliphera aliphera (Godart)

Heliconius melpomene euryades Riffarth

Heliconius numata ethilla Godart

Heliconius erato hydara Hewitson

Heliconius ricini insulana Stichel

Heliconius sara thamar (Hübner)

Heliconius wallacei wallacei Reakirt

Heliconius doris doris (Linnaeus)

It will be noted that more than three-fifths of the species occurring on the island are referred to the mainland form originally described. In the general geographical region under consideration, infraspecific distinctions at present appear to be so much in need of revision that we have omitted subspecific names altogether from the body of the text.

To Fritz Müller we owe the beginning of a comparative study of heliconiine development. Working in Brazil, he described (1877, 1877-1878) morphological characters of eggs, larvae and pupae in seven species, in sufficient detail to be helpful today. Moreover, his attempt to trace phylogenetic relationships in the group, with reference both to ethological and morphological characters, is the only effort along these lines that has been made up to the present. Müller's work concerned the following species: *Dione juno*, *Agraulis vanillae*, *Dryas iulia*, *Phil-aethria dido*, *Heliconius eucrata* (*narcea*), *H. isabella* and *H. aliphera*; the foregoing generic nomenclature is that followed in the present paper.

A few years later, W. H. Edwards described and illustrated the immature stages of North American forms of *A. vanillae* (1880, p. 122) and of *H. charithonius* (1868-1897, Vol. 2, p. 884). His excellent work has been quoted, usually in condensed form, by many subsequent writers on American butterflies, starting with Scudder (1889).

Seitz (1913) in his introduction to the Heliconiinae and in the descriptions of the various genera, gave a general account of the larvae, with brief, sometimes inaccurate, descriptions. He included, however, a number of useful observations on food-plants and habits.

Characteristics of the Heliconiidae, treated as a family, were given by Fracker (1915, p. 131). His account was based on the characters of *H. charithonius*, with the statement that "they apply also to most of the known South American forms."

Kaye (1921) presented a note on the coloration of *A. vanillae*, the duration of the pupal period in *D. juno* and the food-plants in seven species. Bourquin (1949) described and illustrated the life history of two specimens of *H. phyllis* from Argentina. Comstock (1955) described and figured the egg of a Mexican subspecies, *H. charithonius vazquezae*, for comparison with that of the Florida form, *H. charithonius tuckeri*.

The illustrations are the painstaking work of

four people, each of whom it is our pleasure to thank: Julie C. Emsley for all drawings of eggs and larvae, except Text-figs. 5A, 5F, and 10-14; Frances Waite Gibson for the latter text-figures and for all drawings of pupae (Pls. XIV and XV); Russ Kinne for all the photographs in Pls. I-XIII; and Sam Dunton for Pl. XVI. We wish also to express our appreciation to the following who, through their patience and skill in rearing the larvae during various seasons, made this study possible: Susan Allan, Constance Carter, Frances Waite Gibson, Rosemary Kennedy, Jane S. Kinne, Ellen Ordway and Barbara Young.

Finally, special appreciation goes to a group of organizations and individuals who have contributed generously to the study: The National Science Foundation, the National Geographic Society, the Alcoa Steamship Company, Mrs. Mabel Ingalls and Mr. Kurt Reisinger.

II. MATERIALS AND METHODS

Throughout the seasons at the field station, several hundred individual heliconiines contributed directly to this study. Immature stages and food-plants were discovered in three ways. First, wild plants of *Passiflora* spp. were located and searched repeatedly; most lepidopteran eggs laid on species of this genus proved to be those of heliconiines. Second, imagos were followed which were flying in the neighborhood of known *Passiflora* vines, or in a special fashion often preceding oviposition. Third, wild-caught females were presented, in the Station's out-of-doors insectaries, with a selection of *Passiflora* spp.

Food-plants were not always the same in Trinidad and Surinam, or even in different parts of Trinidad. Some species were strict in their demand for a single species of *Passiflora*; others were tolerant of several. Table 2 gives the species and their preferred plants.

Nine of the fourteen species have now been induced to breed and lay eggs in the insectaries. During the study, eggs for rearing in the laboratory were collected daily and brought inside, to protect them from predacious ants.

Only five of the species are gregarious, and it was found that, when reared in numbers, all except these grew best when maintained in individual glass dishes. Even gregarious species, unless kept on long pieces of cut vine placed in water, or on large and thriving potted plants, developed best when no more than five to ten individuals were kept in a single dish or small aquarium. Attempts to rear the larvae out-of-doors, on wild or cultivated vines, through the use of netting "sleeves," were not successful; the

principal trouble was the high humidity, even during the dry season; the netting easily became saturated and mold rapidly developed both on leaves and, often, on the caterpillars. In a rain-forest climate, therefore, the method is impractical and troublesome to use for this group.

Except in the gregarious species, the single eggs were kept in individual dishes of a size suitable to serve the larva for several instars. Early isolation was necessary since, given the opportunity, a newly hatched, normally solitary caterpillar often eats an adjacent egg after dispatching its own shell. Low slender dishes, 60×28 mm., with fitted lids, proved the ideal size and type through the first three or four instars. The space was adequate, the dishes were easy to clean and even the smallest larvae could not escape. Early instars were also reared in 3×1 -inch vials, with the uncorked mouths pushed into a tray of moistened sand. In this method, changing of the leaf and cleaning were necessary only every three or more days, and less table space was occupied. The moisture, however, was difficult to control since small changes in the weather strongly affected humidity and condensation in the vial. Larvae passed the fourth and fifth instars very successfully in covered glass refrigerator dishes, measuring $4 \times 4 \times 2\frac{1}{4}$ inches. A piece of wire screening, cut to the size of the lid and placed beneath it at the proper time, served most larvae for pupation. Two species preferred plain glass (*Heliconius isabella* and *H. aliphera*).

In all containers, except vials over moist sand, it was essential to provide moisture. A small section cut from a cylindrical cotton wad, such as is used by dentists, was dampened and kept constantly in each container. The size and degree of saturation had to be carefully adjusted to the size of the larvae, and to the size and thickness of the current food leaf, since excess moisture and mold were as much to be avoided as dessication. The larvae also drank from drops of water left on the sprinkled leaves, as described in this group by A. J. Alexander (paper in preparation).

After pupation, the screen or glass was transferred to the open top of a pint or quart preserving jar, in which was placed a moistened dental wad, until emergence. Self-adhesive labels were transferred with the larvae, as containers were changed.

Through the above system, a maximum of 560 non-gregarious individuals, distributed throughout the growth stages, were accommodated at one time in a room measuring about 12 feet square and serviced by one to two workers, exclusive of a local leaf-gatherer. These especially large numbers occurred in connection

with a study on polymorphism in the heliconiines, which has been concomitantly in progress. Usually only a small fraction of that total was kept on hand at once.

The principal rearing problem was to insure a constant daily supply of leaves, freshly picked in the early morning, of the kinds and sizes suitable for the various instars of the different species. Great variations in requirements were shown by the larvae, as will be discussed in the subsequent report on behavior. During the dry season especially, the availability of leaves within practical distance of the Station placed a limit on the number of larvae that could be reared simultaneously. Leaves in excess of immediate requirements were sprinkled and placed in a plastic bag or covered dish in the refrigerator for later use. Some species of *Passiflora* keep well in this way for several days.

Larvae were cleaned daily except when molting. All disturbance was avoided during that time, although care was taken always to keep vibration of the floor and moving of dishes to a minimum. During periods of disease, dishes that had held sick larvae were sterilized and hands and instruments washed in alcohol; there has never been any evidence, however, that these precautions were helpful.

In the field, all of the species at one time or another were scarce or showed strong evidence of disease. Since parasites in the group are rare, and since most of the heliconiines are strongly aposematic, disease is doubtless an important natural method of control. After repeated efforts we have given up attempts to curb disease in the laboratory, and have found that by waiting a few weeks or months, healthy stock becomes once more available. The above remarks apply entirely to wild-caught young, so that possible effects of either inbreeding or laboratory conditions are not involved. Stocks bred in our insectaries, however, were subject to the same symptoms.

In the most common forms of disease, specimens show one or more of the following symptoms: bent or deformed scoli (exclusive of scoli mechanically damaged by leaf or dish pressure during molting), green or yellowish emissions from the mouth or anus, prolongation of instars, shrinking and refusal to eat. Recovery is rare and the resultant imagos are usually sickly. Except when even imperfect imagos were desired as simple genetic records of pattern inheritance, it proved advisable not to waste time tending unhealthy individuals.

The abnormalities mentioned above are distinct from growth difficulties more probably due

to hormone irregularities and involving molting and pupation.

The dry season seems to produce more disease than the wet, and it appears very likely that some of the troubles may be brought on by seasonal differences in the *Passiflora* leaves. Possibly the lack of rain leaves a poisonous deposit which in other seasons is washed away. Likely substances are secretions from certain ants that frequent the honey glands of *Passiflora*; it has been noted casually that at least some heliconiines avoid these leaves, both when egg-laying and as caterpillars. Possibly, too, a noxious substance from the plant itself is concerned. Finally, in both dry and rainy seasons, heavily mildewed leaves are avoided by the caterpillars when other leaves are available.

All color descriptions and all drawings of pigmentation patterns were made from living specimens.

All drawings of morphological characteristics were made from preserved specimens through the use of a binocular microscope equipped with a grid and micrometer scale, and with the aid of a slide rule.

The photographs were made with a Leica camera and, when the subjects were larvae, an electronic flash. A piece of wire, covered with white insulation and measuring 2 mm. in diameter, was used for the support of larvae in full-length views, in order to include a scale in each negative.

III. EGGS

(Text-figs. 1, 2; Pl. I)

Characteristics of the Subfamily.—Subcylindrical, flattened at the base, tapering in distal portion, often flattened distally, rarely almost semi-spherical. Surface covered with conspicuous reticulations bounded by vertical and horizontal ridges, the latter sometimes indistinct toward the base. Height .54 to 1.67 mm.; diameter, .54 to 1.30 mm. Number of vertical ridges 5 to 17 regular, plus 1 to 5 irregular and distal. Color: Greenish-white, buff-yellow, orange-yellow, pinkish-orange or dark red, sometimes mottled before hatching by the developing pigment of the embryo.

Characteristics of the Species.—Table 1 is the result of an examination of three to seven non-sibling individuals of each of the fourteen Trinidad species except *Dryadula phaetusa*. In this species only two eggs were examined.

Food-plants.—All of the heliconiines lay their eggs on the vines of the genus *Passiflora* (passion flowers). The species usually selected by the ovipositing females in Trinidad are given in

Table 2. *Dione juno* and *Heliconius doris* lay numerous eggs in a single-layered mass; *H. ricini*, *H. sara* and *H. wallacei* deposit small clusters; all the other species lay their eggs singly. The number of eggs laid and their position, whether single or many, on the vines are important species distinctions; they will be discussed in an ethological contribution now in preparation.

Duration of Egg Stage from Oviposition to Hatching.—Normally four days, occasionally three, rarely two.

IV. LARVAE

A. CHARACTERISTICS OF THE SUBFAMILY

First Instar

See Fleming, 1960.

Second through Fifth Instars

The larvae are characterized by close similarity in basic structure and variety in color patterns. Although setal differences are, as usual, the essential characters in the first instar, in the practical taxonomy of advanced larvae the most useful distinctions are the relative lengths of the scoli (branching spines), the shape of the head and the color pattern in life.

Terminology.—The structures and designations used in the descriptions to follow are indicated on Text-figs. 3 and 4. The terminology selected is that of Forbes (1910) and Fracker (1915).

The following list defines, for use in this contribution, certain terms for workers from other fields who are unfamiliar with the morphology of lepidopterous larvae. The definitions are after Fracker (*l.c.*, pp. 141-144).

Adfrontals. The narrow areas on the cephalic aspect of the head, adjoining the front on each side.

Anal plate. A chitinized area covering part of the last abdominal segment.

Annulet. One of the small rings into which a segment is divided by transverse constrictions.

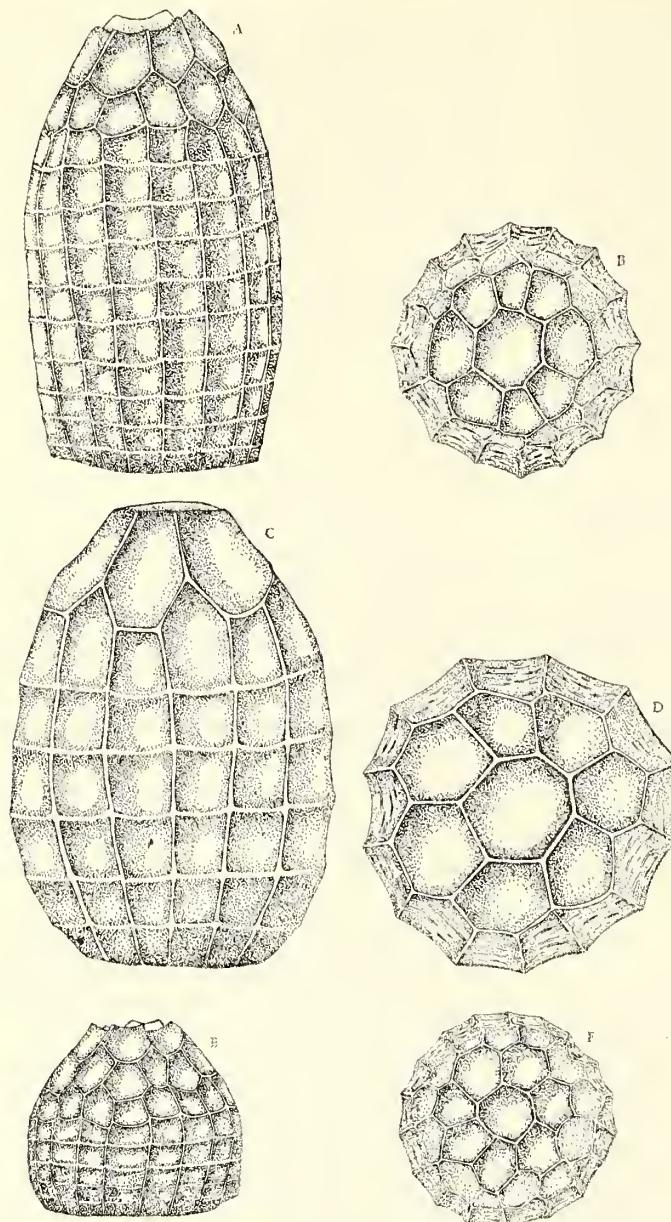
Biordinal. Said of crochets when they are arranged in two concentric rows.

Chalaza. A small chitinized projection bearing one to four setae on small, separate prominences.

Crochet. One of the series of chitinized, hook-like, cuticular structures on the distal surface of the prolegs.

Epicranium. The sclerite which constitutes the greater part of the head.

Front. The sclerite between the arms of the epicranial suture, triangular in shape.



TEXT-FIG. 1. Examples of eggs in the genus *Heliconius*. A, B, *H. erato*; C, D, *H. sara*; E, F, *H. aliphera*. Lateral and dorsal views of each, drawn to the same base diameter.

Proleg. A fleshy abdominal leg.

Prothoracic plate. A chitinized area covering part of the dorsal half of the first thoracic segment.

Scolus. A spinous projection of the body wall.

Seta. A chitinized, hair-like projection of cuticula arising from a single trichogen cell and surrounded at the base by a small cuticular ring.

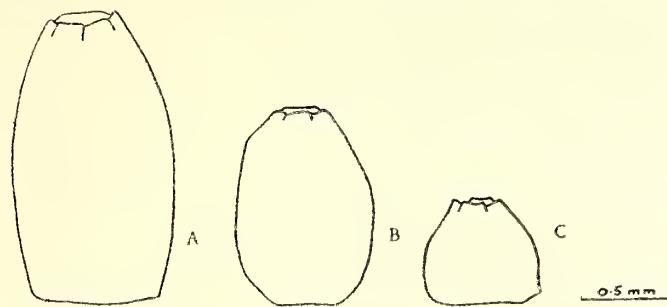
Spinule. One of the short lateral branches of a scolus.

Verruca. A definitely bounded, somewhat elevated portion of the cuticula, bearing several to many setae.

Abbreviations.—In Text-figs. 3 and 4 are given terminology and abbreviations used in the following pages in the descriptions of the larvae. It will be noted that the prothorax, mesothorax and metathorax are designated as "1 TH", "2 TH" and "3 TH". Similarly, the abdominal segments are written as "1 AB", "2 AB", etc. "10 AB" is also referred to in the text as the anal segment.

The names of scoli are capitalized and abbreviated, as follows:

Dorsals: The uppermost series of scoli, on the thorax and abdomen.



TEXT-FIG. 2. Eggs of *Heliconius erato*, *H. sara* and *H. aliphera*, drawn to the same scale. Lateral views.

Laterals: The lower series of scoli on the thorax.

Supralaterals: The median series of scoli on the abdomen.

Sublaterals: The lowest series of scoli on the abdomen.

2 TH Dorsal: The scolus nearest dorsal mid-

line on mesothorax (second thoracic segment).

5 AB Supralateral: The scolus in middle row on fifth abdominal segment.

3 AB Sublateral: The scolus nearest ventral mid-line of third abdominal segment.

Etc.

TABLE 1. CHARACTERISTICS OF EGGS IN THE HELICONIINAE OF TRINIDAD

| Species | Color | Height (mm.) | Diameter (mm.) | No. of Vertical Ridges | No. of Horizontal Ridges | Illustrations |
|--------------------------------|-------------------------------------|-----------------|-------------------|------------------------------|-------------------------------------|---------------------------------------|
| 1. <i>Dione juno</i> | Dark red. | 1.05-1.07 | 0.72-0.75 | 13 | 12-13 + 4-5 | Pl. I, Fig. 1 |
| 2. <i>Agraulis vanillae</i> | Buff yellow.* | 1.08-1.13 | 0.81-0.86 | 16-17 | 10-11 + 2-3 | Pl. I, Fig. 4 |
| 3. <i>Dryadula phaetusa</i> | Buff yellow.* | 1.67-1.72 | 1.08-1.10 | 17 | 16-17 + 3-4 | — |
| 4. <i>Dryas iulia</i> | Buff yellow.* | 1.13-1.17 | 0.97-1.10 | 18-21 | 10-11 + 2-3 | Pl. I, Figs. 8, 9 |
| 5. <i>Philaethria dido</i> | Buff yellow.* | 1.61-1.67 | 1.24-1.30 | 20-24 | 12-13 (series unbroken) | — |
| 6. <i>Heliconius isabella</i> | Pale greenish to pale yellowish. | 0.96-0.98 | 0.89-0.92 | 14-17 | 5-7 + 2-3 | Pl. I, Figs. 10, 11 |
| 7. <i>Heliconius aliphera</i> | Pale greenish to pale yellowish. | 0.54-0.59 | 0.54-0.63 | 18-20 | 5-7 (close set) + 2-3 (wide-spaced) | Text-figs. 1E, 1F, 2 |
| 8. <i>Heliconius melpomene</i> | Orangish-yellow. | 1.37-1.45 | 0.92-1.02 | 15-16 | 9-11 + 1-2 | Pl. I, Figs. 6, 7 |
| 9. <i>Heliconius numata</i> | Greenish-yellow to orangish-yellow. | 1.08-1.19 | 0.82-0.91 | 15-19 | 10-12 + 2-3 | — |
| 10. <i>Heliconius erato</i> | Greenish-yellow to orangish-yellow. | 1.40-1.57 | 0.81-0.85 | 15-17 | 8-10 + 2-3 | Text-figs. 1A, 1B, 2 |
| 11. <i>Heliconius ricini</i> | Buff yellow. | 1.13-1.17 | 0.70-0.73 | 17-18 | approx. 12-13 (ill-defined) + 2-3 | Pl. I, Figs. 2, 3 |
| 12. <i>Heliconius sara</i> | Pale yellow to orangish-yellow. | 0.96-1.18 | 0.65-0.75 | 12-14 | 5-6 + 1-2 | Text-figs. 1C, 1D, 2 Pl. I, Fig. 3 |
| 13. <i>Heliconius wallacei</i> | Pale greenish-yellow. | 1.08-1.13 | 0.86-0.97 | 17-20 | 6-9 + 3-4 | — |
| 14. <i>Heliconius doris</i> | Buff yellow to pinkish-orange. | 1.08-1.18 | 0.75-0.81 | approx. 23-25 (ill-defined) | 12-13 + 2-3 | — |

* Mottled with brown before hatching.

TABLE 2. FOOD PLANTS OF THE HELICONIINAE OF TRINIDAD

Key: *—Usual choice of ovipositing female.
X—Occasional choice of ovipositing female.

| Species | Species of Passiflora | | | | | | | | |
|--------------------------------|--------------------------|--------------------------------|---------------------------|---------------------------|--------------------------------------|------------------------------------|-------------------------------|--------------------------------|---------------------------|
| | <i>auriculata</i> HBK | <i>vespertilio</i> Linnaeus | <i>tuberosa</i> Jequin | <i>ripara</i> Linnaeus | <i>quadriglandulosa</i> Rödschied | <i>serato-digitata</i> Linnaeus | <i>laurifolia</i> Linnaeus | <i>lonchophora</i> Linnaeus | <i>cyannea</i> Masters |
| 1. <i>Dione juno</i> | | | | | * | | | | |
| 2. <i>Augraulis vanillae</i> | | | | | | | | | * |
| 3. <i>Dryadula phaetusa</i> | | * | | X | | | | | |
| 4. <i>Dryas iulia</i> | * | | | | | | | | |
| 5. <i>Philaethria dido</i> | | | | | | * | | X | |
| 6. <i>Heliconius isabella</i> | | | | | X | * | X | | |
| 7. <i>Heliconius aliphera</i> | | | | X | | | | | * |
| 8. <i>Heliconius melpomene</i> | | | | | | * | X | | X |
| 9. <i>Heliconius numata</i> | | | | | | | | | * |
| 10. <i>Heliconius erato</i> | * | * | | | | | | | |
| 11. <i>Heliconius ricini</i> | | | | | | | * | | |
| 12. <i>Heliconius sara</i> | * | | | | | | | | |
| 13. <i>Heliconius wallacei</i> | | | | | * | | | | |
| 14. <i>Heliconius doris</i> | | | | | | * | | | |

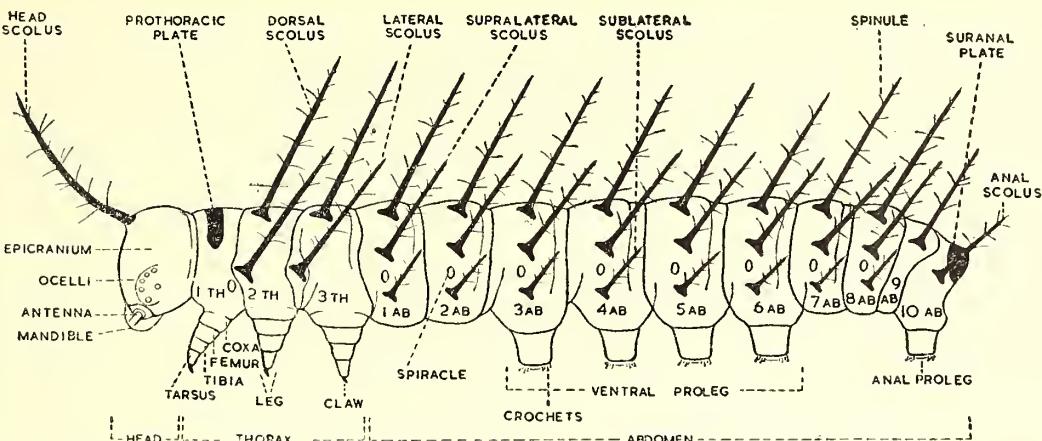
Measurements have been made as follows:

First instar. Length at hatching: Measured in life before egg shell is eaten. Length, maximum: Measured in life when larva is extended, usually just before defecation, about 36 hours after hatching, before molting begins.

Fifth Instar. Maximum length: Measured in life when larva is extended, usually before defecation, and at maximum length exclusive of

scoli. This condition is usually attained late on the third, or early on the fourth, day after the molt, before the beginning of shrinkage and other prepupal changes.

Head Height: Measured from posterior part of base of Head Scolus to tip of the moderately extended mandibles. The small size of the mandible minimizes, for present purposes, the inexactness of the word "moderately." It indicates



TEXT-FIG. 3. Diagram of a heliconiine larva, 5th instar, lateral view. Chelazae and setae omitted.

that the measurement was made with the mandible in the position usually found, or easily arranged, in preserved material; the distal tips of the members of the pair are neither touching nor maximally separated. This position was found to be best for comparisons among species and instars.

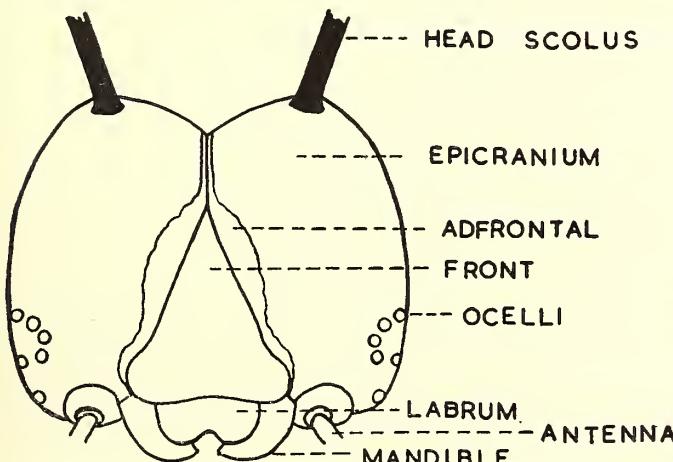
Lengths of Individual Scoli: From base to tip, in a straight line, exclusive of basal expansions and distal spinule.

Color.—All color descriptions were made from series of healthy, non-anaesthetized specimens in the middle of an instar. Unfortunately, the colors and patterns, although of high taxonomic importance, are usually fugitive in preservative. Ridgway's "Color Standards and Nomenclature" was used in compiling the notes of the colors of the various growth stages and series of individuals. Since these series of notes continued to accumulate on most species for at least several seasons, the Ridgway system proved valuable in recording the range of variation and in

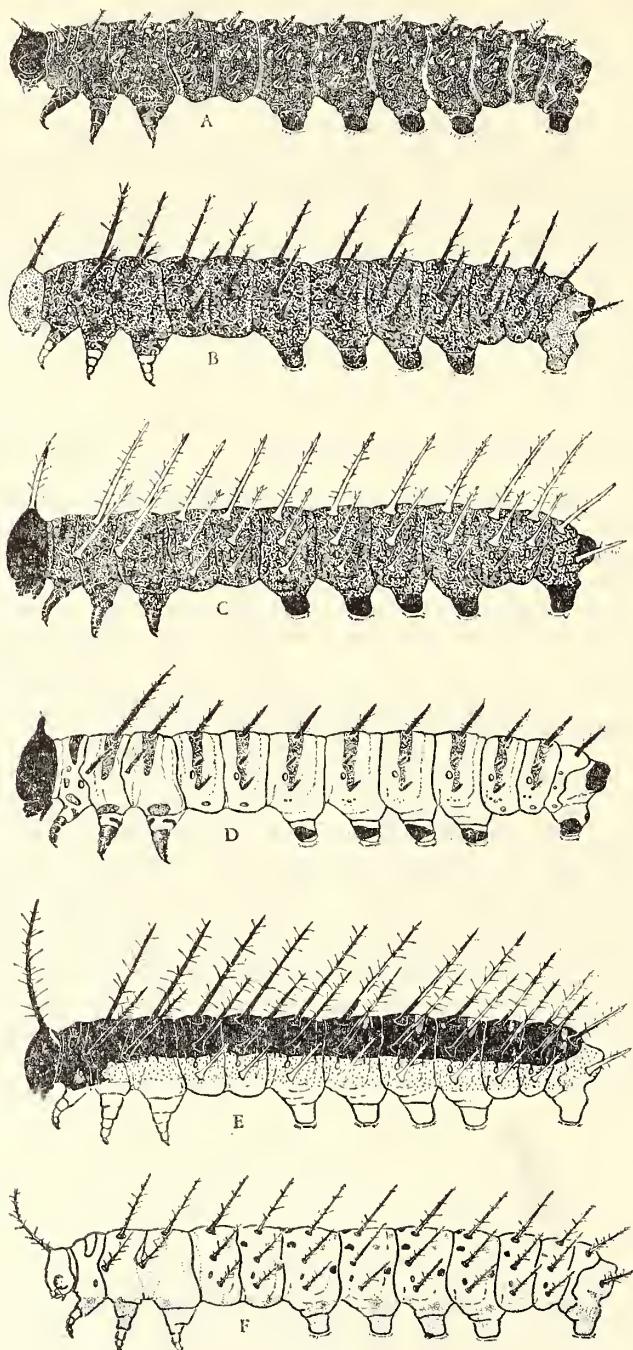
correlating the notes which have resulted in the descriptions to follow. It seemed preferable, because of the decreased availability of Ridgway, the uneven fading of color samples in extant copies and the lack of meaning of Ridgway's names for many modern workers, to reduce the indicated range of hues, shades and saturations into the simplest designations possible. Thus a preliminary summary of larval variation reading ". . . usually Maroon through Diamine Brown to Hessian Brown; sometimes Chaetura Drab or Fuscous" becomes in this paper "dark brown, usually tinged with reddish."

Color descriptions of complexly patterned or highly variable species, such as *Dryas iulia* and *Heliconius isabella*, respectively, are given in considerable detail for two reasons. First, indications are in this way apparent of possible affinities with other species. Second, valid comparisons with the same species in other localities will be, it is hoped, facilitated.

In the descriptions, "stripe" is used to desig-



TEXT-FIG. 4. Diagram of a heliconiine larva, head, frontal view. Setae and postero - ventral mouthparts omitted.



TEXT-FIG. 5. Examples of fully grown heliconiine larvae, 5th instar, drawn to same total length. Scoli drawn without perspective, to facilitate comparisons. Note differences in relative sizes of head, lengths of scoli and spinules, absence of anal scolus in *H. doris* and differences in amount and distribution of dark pigment indicated by depth of shading. Drawn from freshly preserved specimens; proportion of head length to body length and distribution and depth of pigment, however, are from measurements and notes made on living specimens. Chelazae and setae omitted. **A**, *Dione juno*; **B**, *Dryadula phaetusa*; **C**, *Heliconius wallacei*; **D**, *H. doris*; **E**, *H. aliphera*; **F**, *H. numata*.

nate any marking running antero-posteriorly along the larva, while "band" is reserved for a vertical marking (extending dorso-ventrally) regardless of its width.

Diagnosis.—Larvae with paired scoli on head and body, those on 1-8 AB in three rows on each side; unpaired scoli absent; fleshy filaments absent; setae short and few; chalazae and verrucae few, confined to lower parts of body; head moderate to large; body almost cylindrical throughout length; legs with coxa, femur, tibia, tarsus and simple tarsal claws; 5 pairs of prolegs, on 3, 4, 5, 6 and 10 AB; crochets biordinal, the circle incomplete.

Description.—**Head:** (Text-figs. 3, 4, 5, 6, 7). Length between 4 and 11% of extended length in full-grown larvae, distinctly bilobed; each half with a scolus surmounting epicranium. Scolus ranging from a large, pointed tubercle to a long process more than 2½ times height of head and up to one-eighth total length of full-grown and extended larva. The scolus varies also in the degree of abruptness with which it arises from the apex of the epicranium, and in the direction and degree of its curvature. Breadth of head varies, in accordance with the varying degrees of convexity of the epicranial lobes and the shape of the triangular frontal, which ranges from broadly equilateral to narrowly isosceles; frontals reaching at least halfway to epicranial apex. Setae few to moderate, never closely set.

Thorax and Abdomen: Prothoracic plate always divided by dorsal midline into two parts: rarely each half is again divided; setae on the plate range from 2 pairs to many. Anal plate well or poorly developed, its setae few and small.

Scoli: All scoli paired, their number and arrangement identical in all species except *Dione juno* and *Heliconius doris*; *D. juno* differs in having a small scolus arising from prothoracic plate, while *H. doris* lacks a scolus on 10 AB. With these exceptions, the scoli occur as follows: 1 TH, no scoli; 2 and 3 TH each with one dorsal and one lateral scolus; the Dorsals arise near the middle of each segment, the Laterals close to the anterior margin and just above level of prothoracic spiracle. 1-8 AB each with 3 scoli, forming a dorsal, supralateral and sublateral series. The Dorsals are continuous with the dorsal scoli of the thorax; the Supralaterals arise slightly above level of thoracic Laterals and only slightly farther forward than the Dorsals on each segment; the Sublaterals arise between the spiracles and the bases of the prolegs, almost directly beneath the Dorsals. 9 AB gives rise only to a Dorsal. 10 AB, the anal segment, has, except in *H. doris*, a single scolus well below dorsal midline.

The lengths of the scoli vary greatly among the species from less than vertical diameter of ocelli group to more than twice head height; the longest may be shorter or longer than the Head Scoli; 2 TH Dorsal is sometimes considerably longer than the remaining body scoli. Spinules always well developed, often elongate, especially in species with very long scoli.

Setae few in number, always small, often practically confined to the sublateral and ventral surfaces. A well-developed verruca or chalaza usually present above bases of legs. Small verrucae often present on 1, 2, 7 and 8 AB, at level of the bases of prolegs occurring on the remaining abdominal segments. Prolegs all well developed. Crochets biordinal, forming arcs which are scarcely more than semi-circles.

Color: The larvae show a great range of pigment and pattern, from yellow-green through yellows and oranges to red-orange, and from white through browns and grays to black; blue-green, blue, violet and red hues are, however, absent. The patterns include solid colors, stripes, bands and spots, as well as complex combinations resulting in disruptive coloration.

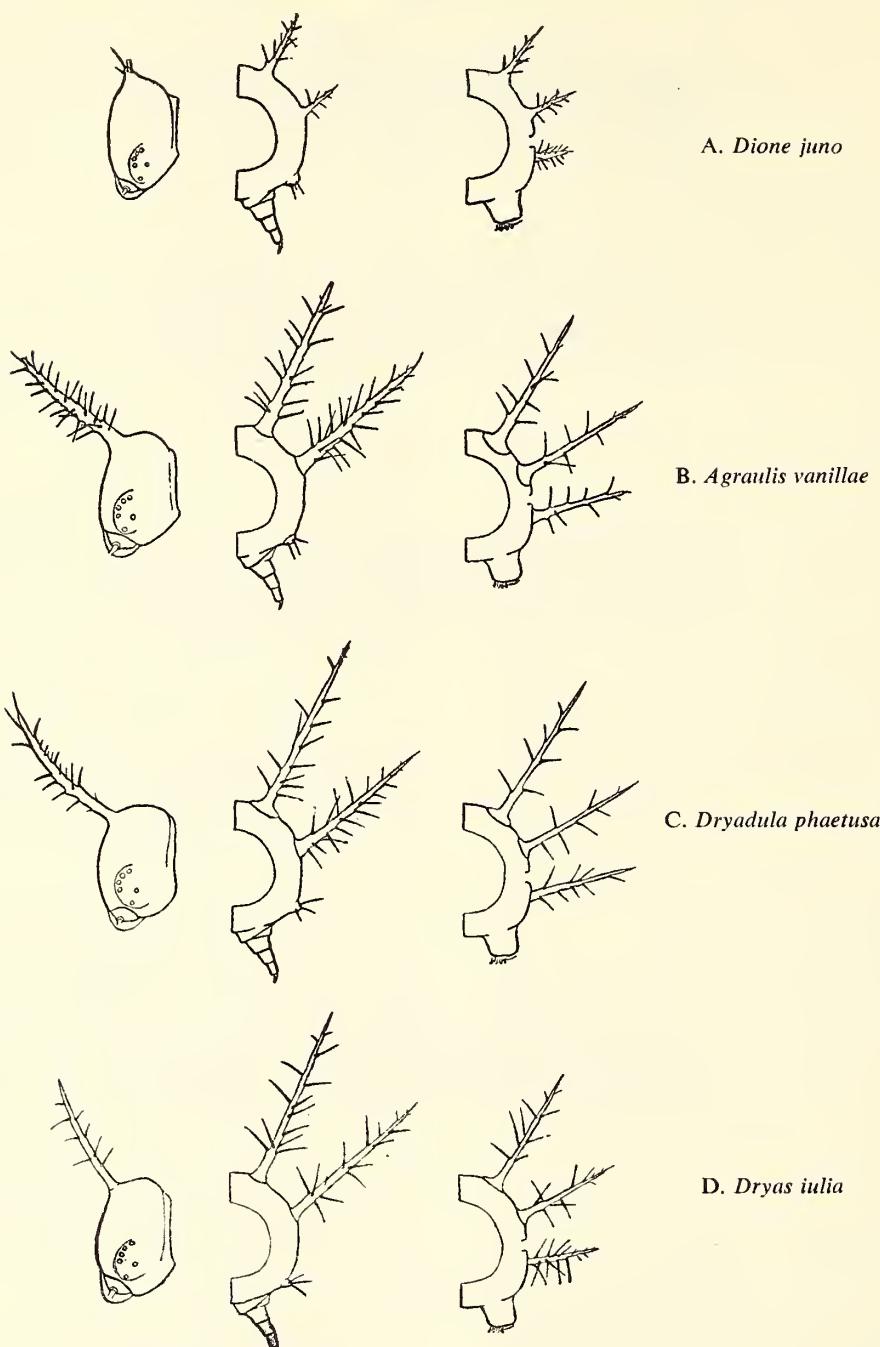
The colors and patterns in each of the fourteen species provide the most convenient diagnostic characters; unfortunately, they are highly evanescent in preservative, and hence are of practical taxonomic value only for students of the living larvae.

Although each species can be distinguished at a glance in life from every other species after it has reached the penultimate instar, there is often a great deal of intraspecific variation. These differences are usually dependent chiefly on the amount of dark brown or black pigment present in an individual. Since the pigments in this group have apparently not been analyzed, the term "melanin" will not be used.

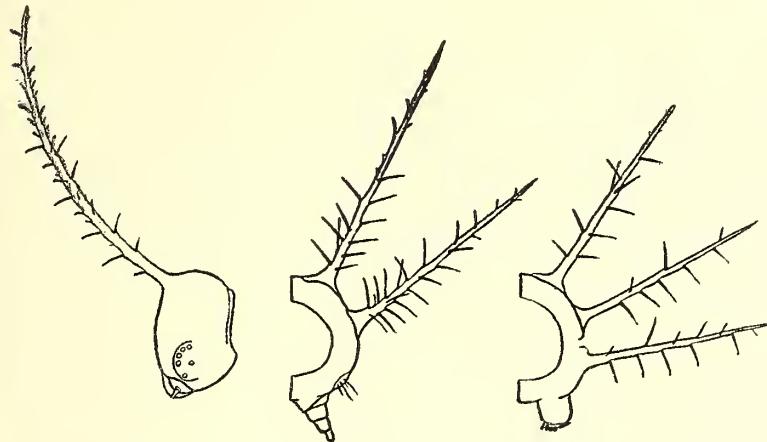
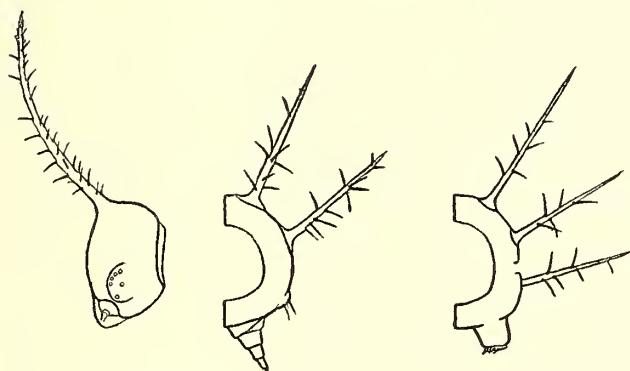
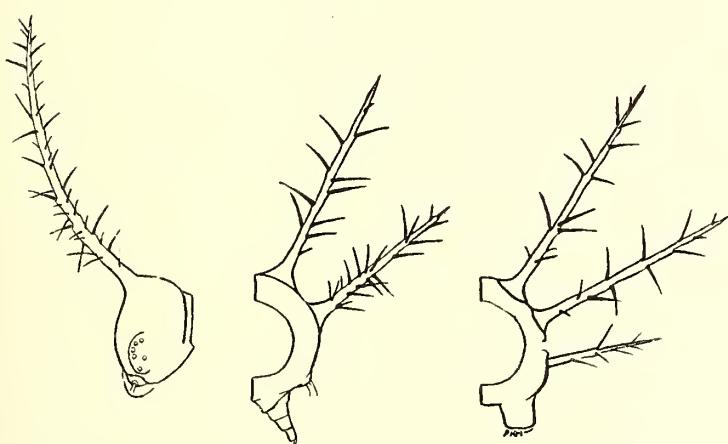
Because of the great variety in coloration, no characters of probable value in the definition of the subfamily have been detected. The following structures, however, are always black, and will not be mentioned in the descriptions of the species: ocelli, chalazae, verrucae, claws and crochets.

Remarks on basic pigment patterns are reserved for the discussion (p. 151).

Growth: All species in the group normally pass through five larval instars; occasionally sickly, crowded, or undernourished individuals complete six instars before pupation; more rarely, apparently healthy individuals also complete six. Bourquin (1946) reports four instars for a specimen of *Heliconius phyllis* in Argentina; this individual died after pupation.

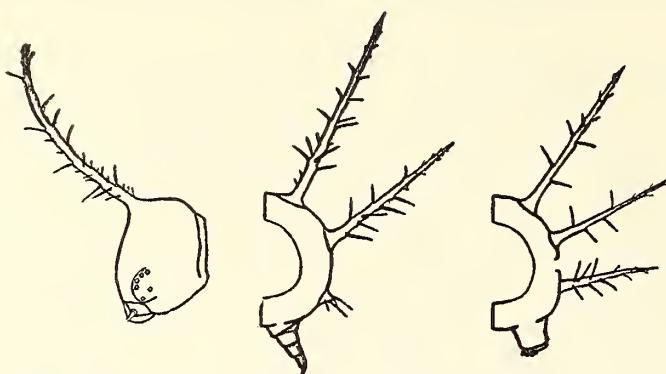


TEXT-FIG. 6. Heliconiine larvae, 5th instar. Diagrams illustrating relative lengths of scoli in 14 species. In each species, the diagram on left represents the head, lateral view; middle diagram, second thoracic segment (2 TH), right half of cross section, frontal view; right diagram, fourth abdominal segment (4 AB), right half of cross section, frontal view. The diagrams are all drawn with the head height as constant, measured from posterior base of head scolus to ventral tip of extended mandible. Labrum and labium omitted. The diameters of thoracic and abdominal body walls are in all cases drawn arbitrarily to same height as head, represented in reality by the condition temporarily reached in each species about the second day after molting. Labrum, labium, chelazae, except on lower thorax, and setae omitted; leg and proleg convention-

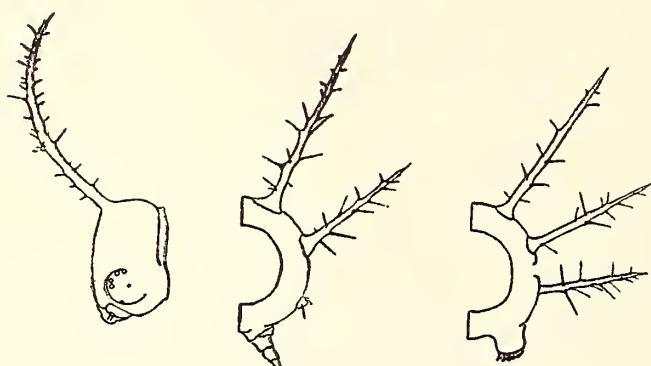
E. *Philaethria dido*F. *Heliconius isabella*G. *Heliconius aliphera*

TEXT-FIG. 6 (continued)

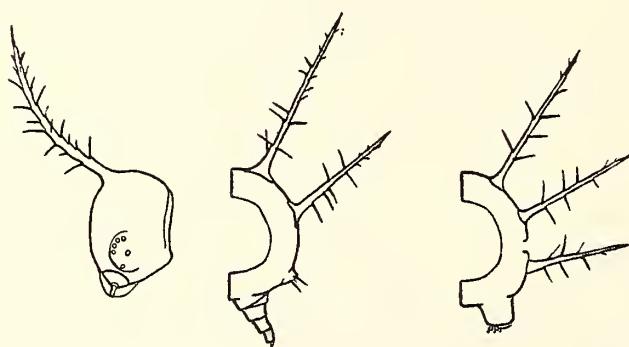
alized, scoli drawn on each cross section as if in the same plane, in order to facilitate comparison (cf. Text-fig. 3 for actual positions). Relative lengths of all scoli and of spinules on scoli, and of general arrangements of spinules exact; numbers of spinules only approximate, but approaching exactness in relation to one another. All scoli are drawn as if unpigmented, and all spinules as black. For realistic pigmentation, see text.



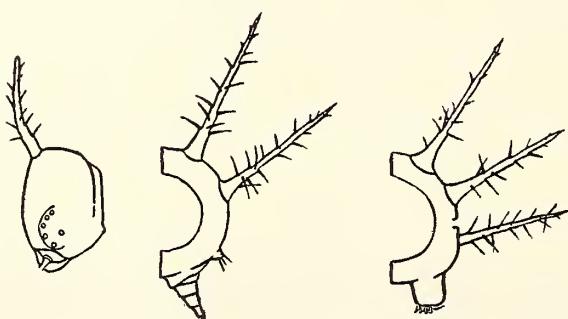
H. *Heliconius melpomene*



I. *Heliconius numata*

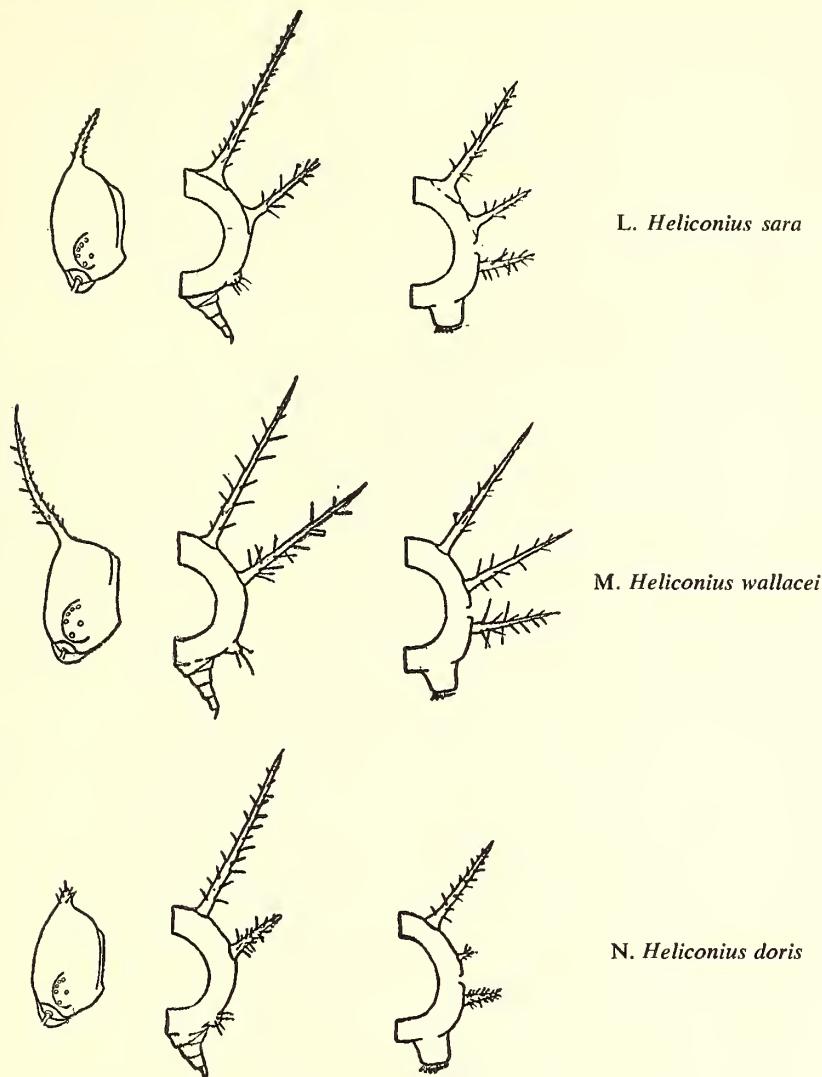


J. *Heliconius erato*



K. *Heliconius ricini*

TEXT-FIG. 6 (continued)



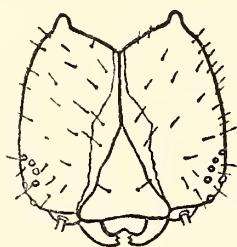
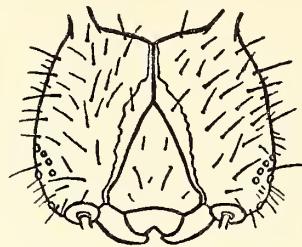
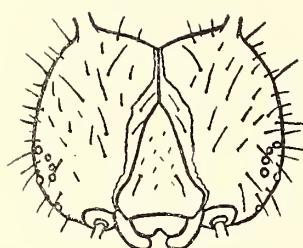
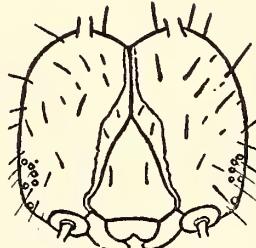
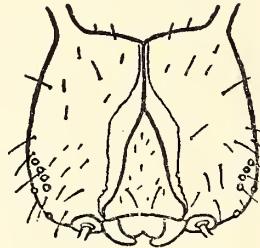
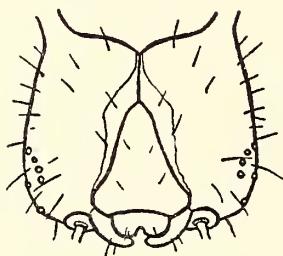
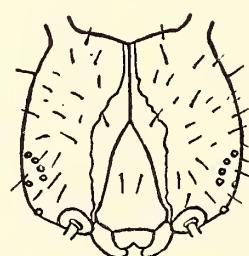
TEXT-FIG. 6 (continued)

The duration of the instars is almost constant throughout the group, although variation in unhealthy larvae, or among those maintained under unfavorable conditions, is very great. Minimum durations of the instars are apparently normal and are as follows: First instar, 2 days; second instar, 2 days; third instar, 2 or 3 days; fourth instar, 2 to 4 days; fifth instar, 5, rarely 4 or 6, days; minimum total, 12 days.

In larvae that eventually pupate successfully in the laboratory, prolonged instars rarely occur before the fourth instar, even when food is scarce and moisture insufficient. Abnormally prolonged stages often occur in the fourth, however, and may last up to 10 days in the fifth.

Similar delays, under the disadvantageous conditions often occurring in nature, must very frequently take place in wild populations.

The maximum length attained ranges from 23 mm. in *H. aliphera* to 48 mm. in *Philaethria dido*. These two species also represent the extremes of size in the imagoes. Since the course of linear growth agrees well with the usual expansion of molting larvae, only lengths for the first instar, and the maximum attained by any measured individual in the fifth, are given. Great variation occurred in the sizes of individual larvae which later emerged as healthy adults. The maximum length attained could be roughly controlled merely by the amount of moisture

A. *Dione juno*B. *Agraulis vanillae*C. *Dryadula phaetusa*D. *Dryas iulia*E. *Philaethria dido*F. *Heliconius isabella*G. *Heliconius aliphera*

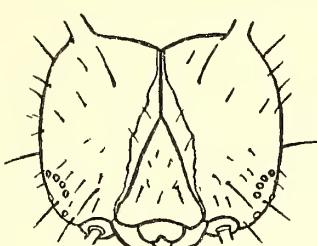
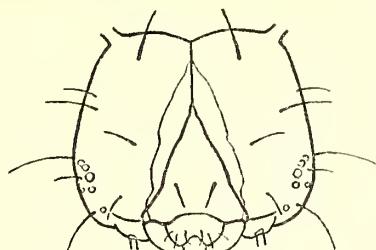
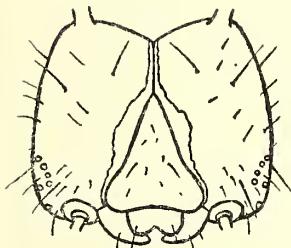
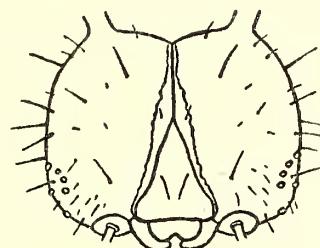
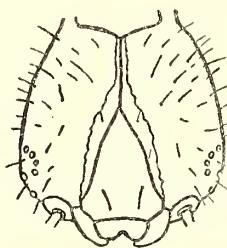
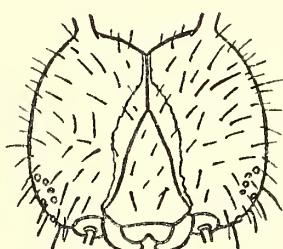
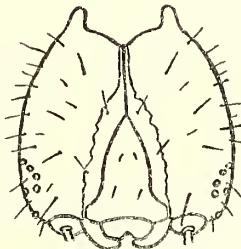
TEXT-FIG. 7. Heliconiine larvae, 5th Instar. Heads, frontal views of 14 species, drawn to same height, measured from base of scoli to ventral tip of mandible, which is comparably extended in each species. Numbers and position of setae roughly approximate, but relative numbers of setae on the species closely approximate reality.

kept in the dish, provided the larva had sufficient food and, especially, by the degree of "fleshiness" of the large leaves with which it was provided in the final instar; for example, healthy *H. melpomene* pupated at any length from 32 to 42 mm., although the usual length was about 38 mm.

The major changes with growth between the second and fifth instars involve proportions of the head and the relative length of the scoli in respect to the head height (Text-figs. 8, 9; Pls. VI, VII). As in most animals, the head is relatively longest in young larvae. In all species, the

head becomes narrower in respect to its height when viewed from the front, while the scoli become longer. The growth curve of the scoli, which appear abruptly in the second instar, is roughly in accordance with principles of heterogonic growth; in contrast to the head breadth, the development of the scoli is positively heterogonic with respect to the head height. If the constant selected for the frontal growth drawings (Text-fig. 8) were the head width rather than the head height, the elongation of the scoli at each molt would of course have been greater.

Remarks on the development of color are reserved for the discussion.

H. *Heliconius melpomene*I. *Heliconius numata*J. *Heliconius erato*K. *Heliconius ricini*L. *Heliconius sara*M. *Heliconius wallacei*N. *Heliconius doris*

TEXT-FIG. 7 (continued)

B. KEY TO FIFTH INSTAR LARVAE
(Unique characters in italics)

A. Scolus present on 1 TH, near lower margin of prothoracic plate; all scoli short, the longest less than half head height. Head black; body dark brown with small orange spots, silver speckles
Dione juno, p. 129

AA. Scolus absent on 1 TH; some scoli longer than half head height. Color not as above.

B. Scolus absent on anal segment (10 AB); Supralaterals shorter and thinner than Sublaterals. Head black; body greenish-yellow with dark transverse bands....*Heliconius doris*, p. 144

BB. Scolus present on anal segment; Supralaterals longer than Sublaterals. Body not greenish-yellow with dark bands.

C. Head Scolus no longer than head height and less than $\frac{3}{4}$ length of 2 TH Dorsal.

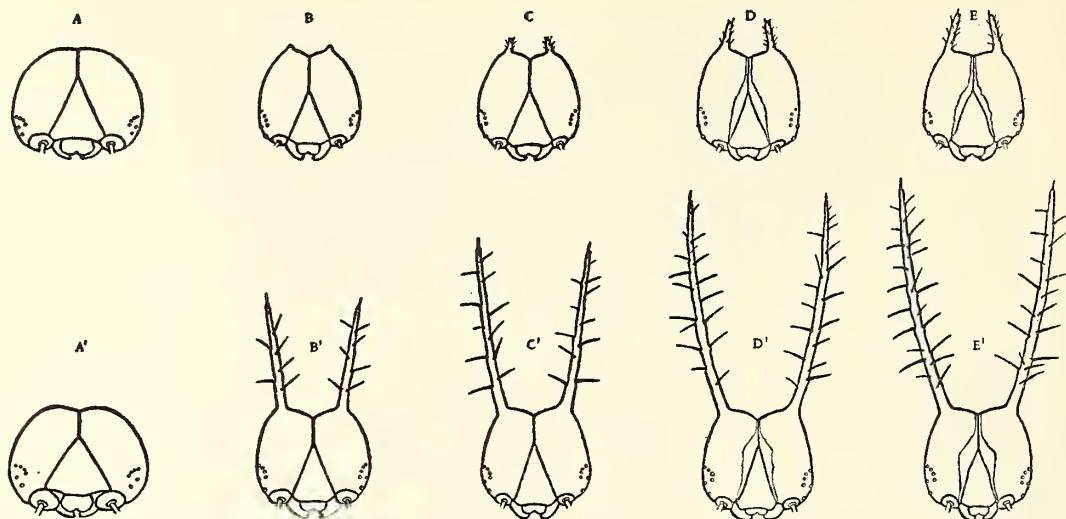
D. Head Scolus less than $\frac{1}{2} \times$ head height; 2 TH Dorsal more than $1\frac{1}{2} \times$ longer than any other scolus; 2 TH Lateral clearly shorter than 4 AB Dorsal. Head and scoli black; body reddish-black.

Heliconius sara, p. 143

DD. Head Scolus clearly more than half head height; 2 TH Dorsal clearly less than $1\frac{1}{2} \times$ next longest scolus; 2 TH Lateral at least as long as 4 AB Dorsal. Coloring various.

E. Sublaterals less than $\frac{1}{2} \times$ 2 TH Dorsal.

F. No spinules nearly as long as vertical diameter of ocelli group; prothoracic plate broadly triangular with more than 2 prs. of setae. Head black; body black to reddish-black; scoli bright yellow....*Heliconius wallacei*, p. 144



TEXT-FIG. 8. Heliconiine larvae. Heads of two species, frontal views, 1st through 5th instars. Drawn to same height, measured from base of scolus to ventral tip of mandible. To facilitate comparison, scoli have been drawn without allowance for perspective. Setae omitted. **A**, *Heliconius sara*, first instar; **B**, same, second instar; **C**, same, third instar; **D**, same, fourth instar; **E**, same, fifth instar. **A'-E'**, *H. aliphera*, corresponding growth stages.

FF. Some spinules longer than vertical diameter of eye group; prothoracic plate narrow with 2 prs. of long setae. Head marked with white, black and maroon; body buffy brown spotted and banded with white and dark red; scoli variably dusky.

Dryas iulia, p. 132

EE. Sublaterals clearly longer than $\frac{1}{2} \times$ 2 TH Dorsal.

G. Head Scolus clearly shorter than head height; Head black; body yellow with black spots.

Heliconius ricini, p. 143

GG. Head Scolus about as long as head height. Color not as above.

H. Head brown and white; body dark with narrow bronze-orange stripes above and a pale lateral stripe.

Agraulis vanillae, p. 130

HH. Head orange; body brownish-black...*Dryadula phaetusa*, p. 131

CC. Head Scolus much longer than head height, at least as long as 2 TH Dorsal.

I. 2 TH Lateral longer than 4 AB Dorsal; all spines very long, the Head Scolus up to $2\frac{1}{2} \times$ head height. Head orange; body white with black bands; tumid bases of scoli orange; prothoracic plate narrow with 2 prs. of long setae.

Philothria dido, p. 135

II. 2 TH Lateral clearly shorter than 4 AB Dorsal; Head Scolus at most slightly more than twice head height. Color not as above.

J. Head Scolus at least $1\frac{3}{4} \times$ head height. Head black with white; body dorsally black with white or yellow markings; lower sides yellow or white. Prothoracic plate broad, divided into 2 or 4 parts, with a total of 2 or 3 prs. of small setae.

K. Head Scolus about $1\frac{3}{4} \times$ head height; Sublaterals scarcely shorter than Supralaterals; AB Dorsals about $\frac{1}{6}$ longer than head height. 8 and 9 AB segments orange above.

Heliconius isabella, p. 137

KK. Head Scolus about twice head height; Sublaterals less than $\frac{3}{5}$ as long as Supralaterals; AB Dorsals almost twice head height. No orange on 8 and 9 AB segments.

Heliconius aliphera, p. 138

JJ. Head Scolus $1\frac{1}{2}$ or less \times head height. Prothoracic plate slender with 2 prs. of long setae. Body white with black spots.

L. Prothoracic plate unpigmented (except setae).

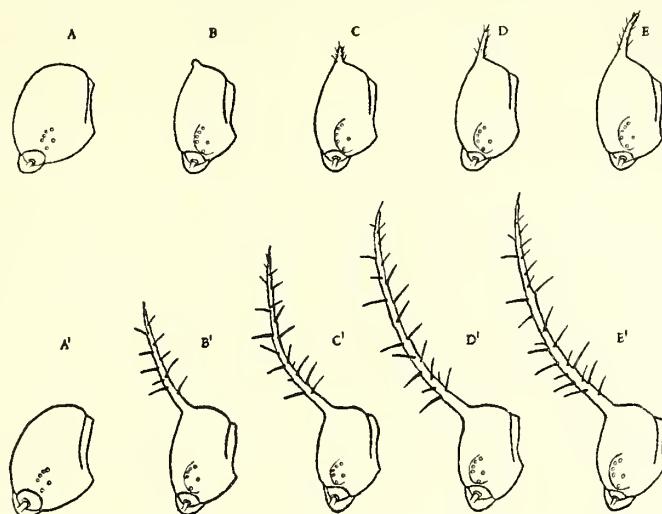
Heliconius numata, p. 140

LL. Prothoracic plate black.

M. Head and prolegs orange-yellow.
Heliconius melpomene, p. 139

MM. Head buff; prolegs with dusky patches externally.

Heliconius erato, p. 142



TEXT-FIG. 9. Heliconiine larvae. Heads of two species, lateral views, 1st through 5th instars. Arrangement and scaling as in Text-fig. 8. A-E *Heliconius sara*; A'-E', *H. aliphera*.

C. DESCRIPTION OF THE SPECIES

1. *Dione juno* (Cramer)

a. FIRST INSTAR. (Pl. II, Figs. 12, 13).

Setae and Crochets: Fleming, 1960, p. 91; Text-figs. 4, 5.

Color: Head, prothoracic plate, anal plate and bases of setae groups black. Body, legs and prolegs dull orangish-yellow.

Length: At hatching, 1.7 mm.; maximum, 2.5 mm.

b. FIFTH INSTAR. (Text-figs. 5A, 6A, 7A).

Diagnosis.—A scolus on 1 TH; all scoli extremely short, the longest (2 TH Dorsal) less than half head height. Body dark brown marked with small orange spots.

Description.—Scoli: Head Scolus short, its height less than distance between posterior and lowest ocelli. A slightly longer scolus, thick and with sparse spinules, arising from lower part of prothoracic plate; this character is unique among the 14 species under consideration. 2 TH Dorsal, although the longest scolus, measures less than half head height; 8 AB Dorsal slightly longer than remaining scoli; the latter show no striking differences in length, although the Supralaterals and Sublaterals are, progressively, slightly shorter than the corresponding Dorsals. Spinules short.

Head: In frontal view, higher than broad; lateral margins of epicranial lobes scarcely rounded; lobes in lateral profile behind scolus moderately rounded. Head length about 6% of maximum total length.

Prothoracic Plate: In addition to the scolus on 1 TH described above, each half of the broadly triangular, elevated plate gives rise to a long, strong seta on a tumid base near dorsal midline; a third seta, of moderate size, arises between it and the scolus, but behind both; many very small setae also are present.

Color: Head, prothoracic and anal plates, scoli, legs and external sides of prolegs all glossy black. Body velvety dark brown to almost black with small, paired spots, brownish-yellow to brown-orange. On middle part of body the arrangement is very regular, in three series as follows, from dorsal profile ventrally, on each segment: First series, 2 spots near dorsal midline (1 anterior, 1 posterior); second series, 3 larger spots at level of Dorsals (1 in front and 2 behind), the largest spot on any segment being always the one in front of the Dorsal; third series, 3 spots as in second series, but in front of and behind Supralaterals.

The second and third series may be viewed together on each segment as forming three faint vertical bands, although the elements are not joined. The pre-scolus spots continue dorsally with the anterior spot of the first series, and the first post-scolus spot with the posterior spot of the same series. Since they are all non-marginal, they may correspond to Bands 2, 3 and 4 of the five bands traceable in a number of species (p. 151). Occasionally a narrow silvery band is visible on the anterior margin of a segment, in a position corresponding to Band 1. The spots and indications of series are best developed on 1-7 AB, and missing altogether on 10 AB. There is

sometimes a scattering of small silvery speckles, especially dorsally.

Maximum Length: 37 mm.

c. SECOND, THIRD AND FOURTH INSTAR.

Scoli: Scolus on 1 TH distinguishable in second instar.

Color: Head black throughout all instars, as are prothoracic and anal plates. Body color progressively darker brown with each molt. The first spots appear in the fourth, the most conspicuous being those of the first series, near dorsal midline, although there are traces of others laterally; all are small and obscure, brownish-yellow, and mostly vertically oval in shape. Most scoli dusky in second, the least pigmented being the Sublaterals; all scoli completely black in the third and thereafter, except that a few posterior scoli sometimes remain partly translucent through the third. Legs and outer sides of prolegs fully black by third.

2. *Agraulis vanillae* (Linnaeus)

a. FIRST INSTAR. (Pl. II, Figs. 16, 17).

Setae and Crochets: Fleming, 1960, p. 91; Text-figs. 4, 5.

Color: Head, prothoracic plate, legs, anal plate and all setae black. General body color varying from translucent buffy to pale brown, with white spots and brown bands as follows: 2 rows of white spots, the upper larger, first, between dorsal and supralateral setae groups and, second, below supralateral setae groups; these spots occur on 2 and 3 TH and on 2, 4 and 6 AB; rarely present also on 1 TH. Brown bands, varying in intensity and width with the individual and its age, present on 1, 3, 5, 7 and 8 AB; bands on 7 and 8 AB sometimes coalesced and extending onto 9 AB during part of instar. Bases of setae faintly dusky in early part of instar. Prolegs variably dusky, sometimes black distally.

Length: At hatching, 2.6 mm.; maximum, 4.2 mm.

b. FIFTH INSTAR. (Text-figs. 6B, 7B, 11A; Pl. IV, Fig. 26; Pl. IX, Fig. 53; Pl. X, Fig. 62).

Diagnosis.—Head Scolus about as long as head height; no scolus remarkably elongated; Sublaterals clearly longer than half 2 TH Dorsal. Body with narrow orange or shining orange-brown stripes in upper half; a white stripe, continuous or broken, in lower half.

Description.—Scoli: Head Scolus almost straight, diverging from other member of pair, scarcely longer than head height. All Scoli moderately long with long, numerous spinules. 2 TH Dorsals longer than other Dorsals, slightly longer than Head Scolus, about 1.3 times head

height which about equals 4 AB Dorsal. Lateral, Supralaterals and Sublaterals well developed, progressively slightly shorter than the corresponding Dorsals on each segment. All Sublaterals clearly longer than half 2 TH Dorsal.

Head: In frontal view, broader than high; lateral margins of epicranial lobes little rounded; lobes in lateral profile behind scolus strongly rounded, notably setose. Head length about 6% of maximum total length.

Prothoracic Plate: Each half flat, broadly triangular, with 2 long setae, 1 moderate and many small ones.

Color: Head creamy white marked strongly with orange-brown, principally in vertical bands, as follows: 1, extending from inner margin of base of scolus to adfrontals, and coloring adfrontals, adjacent margin of epicranial lobes and labrum; 2, a medially broken band extending antero-laterally, from base of scolus ventrally through ocelli; 3, a band from posterior base of scolus to posterior margin of head.

Base color of body above level of Supralaterals, gray to black marked with 3 pairs of narrow stripes, variably orange to orange-brown, the latter usually with a metallic sheen. The first stripe is submedian, the second between Dorsals and Supralaterals; the third immediately below Supralaterals and running through spiracle level. All three run the entire length of thorax and abdomen, although they are irregularly and variably interrupted; submedian stripe often with a black division on each segment setting off a posterior spot from an anterior stripe; second stripe always more broken than first or third. At the levels of the Dorsals and Supralaterals are, sometimes, in the basic dark region, extra rows or irregular sprinklings of white or yellowish dots.

Below the third stripe is a fourth stripe of variable breadth and continuity, but immaculate white or buffy; it extends to the level of the Sublaterals. Ventral to the latter the body is black, with transverse rows of white or yellow dots on median abdominal segments; there is always one row on each segment from the Sublateral to the proleg base, and, often, two anterior and one posterior row in addition continuing around ventral surface. Finally, a row of 4 or 5 white dots usually surrounds proleg base externally.

Scoli brownish or dusky to black, the tips always darkest, sometimes completely black in dark individuals; scoli bases set in small black spots.

Maximum Length: 35 mm.

c. SECOND, THIRD AND FOURTH INSTARS.

Color: In second instar, head completely black as in first; a median pale frontal spot appears in third and persists in fourth; remaining cephalic markings do not appear until fifth.

On the body, the dark bands and pale spots of first instar persist through second; the basic body color darkens from buffy in the first through orangish-brown in the second to black in the third; the gray cast, if any, never apparent until the fifth.

The orange body stripes appear in the third, the submedian stripe being best developed, and usually in two sections as in many fifth instar individuals, the more posterior, smaller section yellow, the anterior orange. The second stripe is represented chiefly by an elongated white spot on even-numbered abdominal segments, below level of Dorsals; this series appears to be homologous with the similarly placed white spots of the first two instars in this and other species (p. 151). The third stripe, homogeneously dull orange, is broken but distinct. In some individuals, no white stripe or other pattern is found below this level; in others, sometimes two or three light spots occur on each segment, at level of Sublaterals, but these tend to appear only late in the instar; irregular yellowish speckles are sometimes sparsely present in third, especially anteriorly.

In the fourth, the chief developments are in the increased distinctness of the two lower orange stripes. The second stripe is still indistinct but partly yellow now, with no indication of the early white spots, and is more clearly a stripe; the third stripe is the most interesting since there are indications on each segment that it is composed of five separate spots, the first on each segment largest. One to three faintly yellow spots at level of sublateral scoli, usually behind spine, but a larger one sometimes in front. The rows of 4 or 5 small white dots usually found in fifth surrounding ventral proleg bases also appear in the fourth.

Prothoracic and anal plates, scoli, legs and prolegs black throughout the instars.

3. *Dryadula phaetusa* (Linnaeus)

a. FIRST INSTAR.

Setae and Crochets: Fleming, 1960, p. 91; Text-figs. 4, 5.

Color: Head translucent brown, margined posteriorly with black. Body dull yellow with dark brown bands on 1, 3, 5 and 7 AB and three series of white spots as follows: First series, between dorsal and supralateral setae groups on 2 and 3 TH, and on 2, 4, 6 and 8 AB. Second series, exactly as in *Agraulis vanillae*, between

supralateral and sublateral setae groups (p. 130). Third series, below sublateral setae groups, on 2, 4, 6 and 8 AB. Prothoracic plate, suranal plate and tumid bases of setae dark dusky, often almost black; legs black, prolegs variably dusky.

Length: At hatching, 3.1 mm.; maximum, 4.8 mm.

b. FIFTH INSTAR. (Text-figs. 5B, 6C, 7C).

Diagnosis.—Very similar in form to *Agraulis vanillae*, differing noticeably only in the distinctly curved Head Scolus; coloration very different, *Dryadula phaetusa* being black with an orange head, with no trace of the body stripes so characteristic of *vanillae*.

Description.—Scoli: All scoli slightly longer and more slender than in *A. vanillae*, but their proportions are very similar; 2 TH, the longest, is fully one and one-half times the head height instead of only about one and one-third; Head Scolus slightly but definitely curved, instead of practically straight.

Head: In both frontal and lateral views, epicanthal profiles more rounded than in *vanillae*, except for dorsal profile behind Head Scolus, which is arched in both species. Head strongly setose, as in *vanillae*. Head length about 6% of maximum total length.

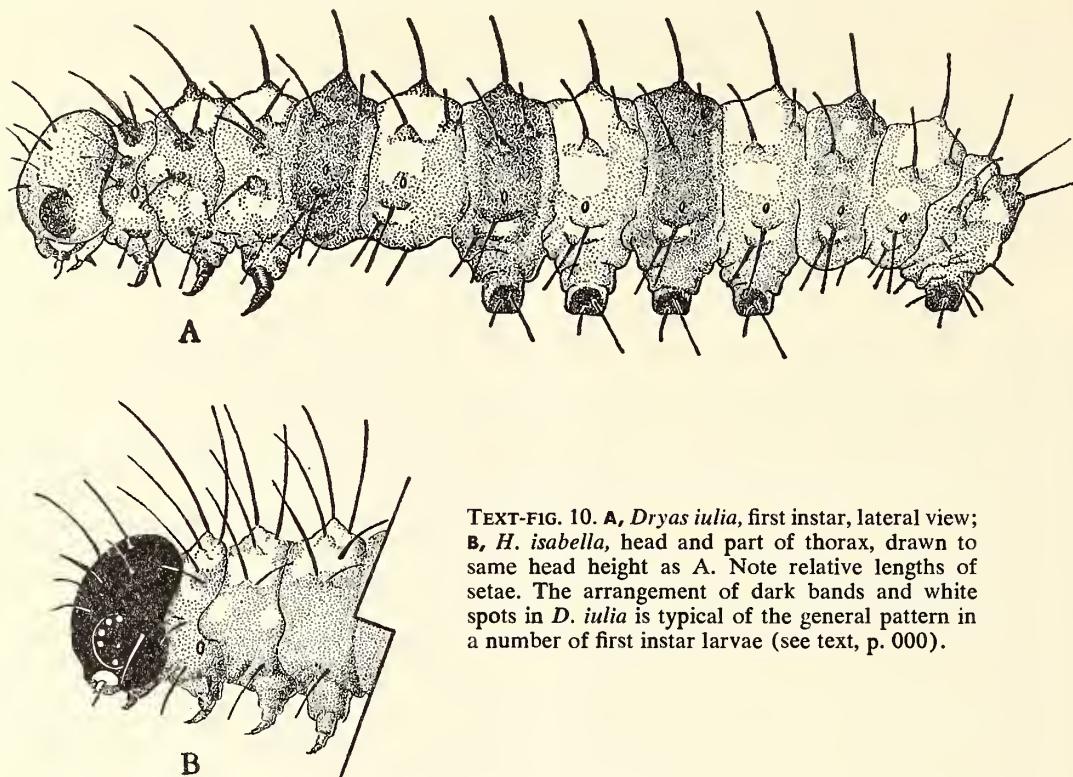
Prothoracic Plate: As in *vanillae*.

Color: Head pale to vivid orange. Body velvety dark brownish-black, except for strongly chitinized scoli bases which are so glossy black that in direct lighting they resemble silver spots. Intersegmental membranes, anal segment and anal prolegs lighter brown, washed with black. Legs orange, like head. Ventral prolegs as dark as general body color. Prothoracic plate and scoli all black.

Maximum Total Length: 40 mm.

c. SECOND, THIRD AND FOURTH INSTARS.

Head orange-brown, increasingly orange with each molt. Body, in second instar, homogeneous medium brown, darkening to successively deeper browns in third and fourth. In second only are vestiges of the white spots of the first instar apparent; they are represented by three white semicircles, one beneath each scolus and half-ring its base on 2, 4 and 6 AB; in addition, there are small clusters of white dots on all three thoracic segments below level of lowest scoli. The over-all brown color obscures the vestiges, if any, of the first instar's dark bands. Anal segment, in third and fourth, orange-brown to orange, like head, while 8 and 9 preceding it are the same color but washed with dusky. Scoli and legs black throughout the instars; ventral prolegs darker brown than body color, darkening



TEXT-FIG. 10. A, *Dryas iulia*, first instar, lateral view; B, *H. isabella*, head and part of thorax, drawn to same head height as A. Note relative lengths of setae. The arrangement of dark bands and white spots in *D. iulia* is typical of the general pattern in a number of first instar larvae (see text, p. 000).

with each instar; anal prolegs lighter, about same shade as body, but darker than anal segment.

4. *Dryas iulia* (Fabricius)

a. FIRST INSTAR. (Text-fig. 10A; Plate II, Figs. 14, 15).

Setae and Crochets: Fleming, 1960, p. 91; Text-figs. 4, 5.

Color: Head brownish; body yellow-brown with white spots alternating with brown bands; prothoracic and anal plates, setae and legs dark. The details of coloration, more complex and variable than usual in first instar larvae in this group, are as follows:

Head translucent orange-brown edged posteriorly with black. General body color similar but more yellowish. Dark brown bands present on dorsal half of 1, 3, 5, 7 and 9 AB, the first four stronger than the last. The pigment band passes through the antero-median part of the segment, always including the bases of the setae groups, but the anterior and posterior extension of the bands on each segment is various. White spots are present in three series along each side as follows: First series, on 2 and 3 TH and 2, 4, 6 and 8 AB, between dorsal and supralateral

setae groups; second series, on same segments, plus, sometimes, 1 TH between supralateral and sublateral setae groups; third series, present at least on 2, 4 and 6 AB, between bases of the two setae in sublateral group. This latter series is the most variable, being usually but not always discernible, and sometimes very strong; a roughly corresponding spot also usually present on 1 TH, sometimes faint or absent; it is sometimes present also on 2 and 3 TH, and, finally, usually present but very faint on 9 and 10 AB.

As indicated, there is great variation in the development of both dark and white pigment, particularly the latter, which may reach abnormally high expansion under chloroform and shortly after immersion in formalin. At these times the two upper rows of white spots may coalesce completely in front of the setae groups on each of the affected segments and the spots of the third series become far more prominent than usual; finally, traces of white spots appear even above the proleg bases, as in older larvae.

Prothoracic and suranal plates dark. All setae black, with slightly tumid, usually dark bases. Legs and prolegs dark brown.

Length: At hatching, 2.9 mm.; maximum 4.0 mm.

b. FIFTH INSTAR. (Text-figs. 6D, 7D, 11A, B; Pl. IV, Fig. 27; Pl. IX, Fig. 54; Pl. X, Fig. 63).

Diagnosis.—Head Scolus clearly shorter than head and Sublaterals, less than half 2 TH Dorsal; scoli otherwise long; 2 TH Dorsal about 1.3 times longer than either head or 4 AB, 2 TH Lateral scarcely shorter. Body buffy brown, spotted and banded with white, black and dark red.

Description.—Scoli: Head Scolus slightly less than height of head, slender, almost straight and directed more upward than in *Agraulis vanillae* or *Dryadula phaetusa*. Dorsals, Laterals and Supralaterals about as in *vanillae* (2 TH Dorsal being about one and one-third times head height, while 4 AB Dorsal and the other scoli are in proportion). The Sublaterals, however, are clearly shorter than one-half 2 TH Dorsal, and all the scoli are more slender. In the general form and proportions of all scoli, the greatest similarity is to the otherwise dissimilar *H. wallacei*, the most notable difference being only in the lengths of the spinules on the Head Scolus, Dorsals and Laterals, which are exceedingly long (sometimes surpassing the vertical diameter of the ocelli group) in *Dryas iulia*, as in *vanillae* and *phaetusa*, and unusually short in *H. wallacei* (see Text-fig. 6M).

Head: Epicranial profiles in both frontal and lateral views more rounded than in *vanillae*, less than in *phaetusa* or *wallacei*; setae less numerous than in any of those three species. Head length about 6% of total length in full-grown larva.

Prothoracic Plate: Each half very slender, non-triangular, with only two setae, each long and strong, the upper close to dorsal midline, the lower near ventral edge of plate. Among the species under consideration, similar plates are found only in *Philaethria dido*, *Heliconius numata*, *H. melpomene* and *H. erato*.

Color: The coloration of this species is more complex than in any others in the study; it is also moderately variable, especially on head and thorax.

General Appearance: A buffy brown caterpillar, spotted and banded with lighter and darker, head creamy white with strong black and dark red markings, of highly variable extent. Thorax with three transverse dark bands, visible when larva is extended; abdomen with black spots and speckles dorsally and, laterally, four oblique white bands alternating with dark ones, above a white, broken, lateral stripe running the length of the body. The distinctiveness of the markings varies considerably with the position of the caterpillar and the length of time

before pupation; there is also extensive individual variation.

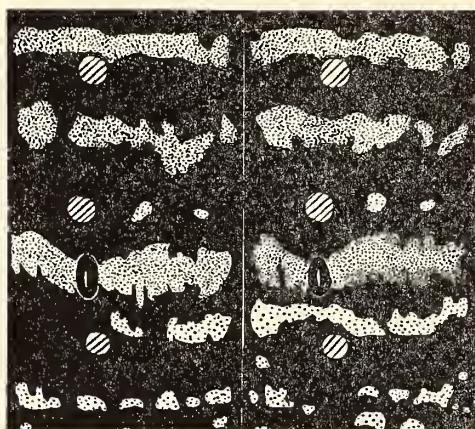
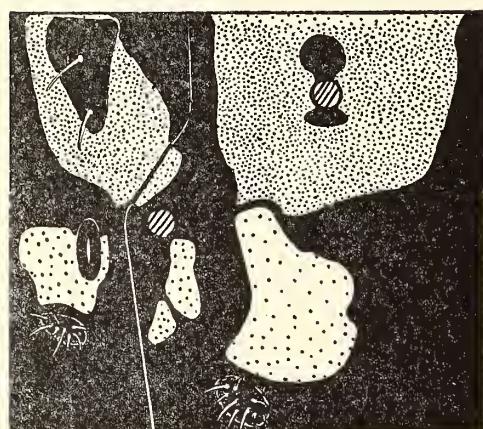
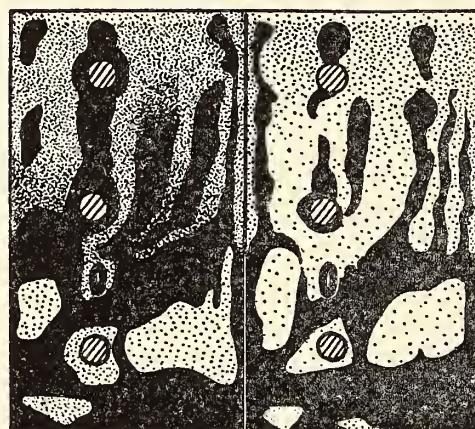
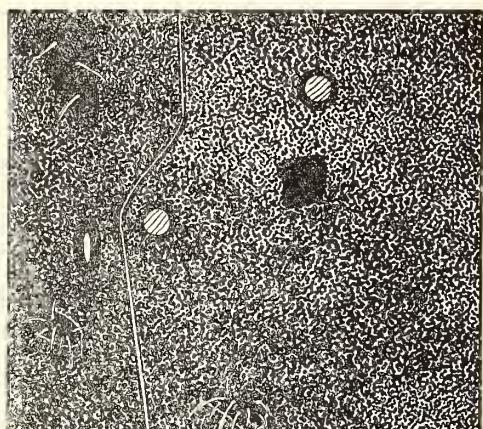
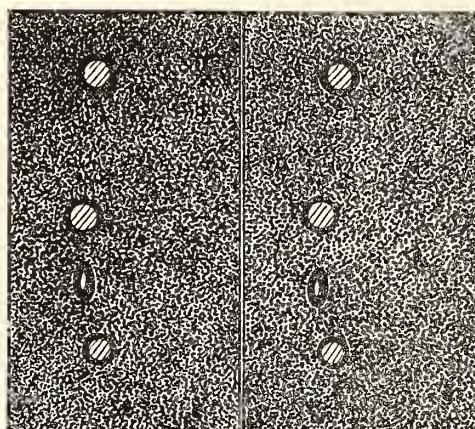
Head: Creamy white with black blotches and, posteriorly, a dull orangish-red or dark red border, of varying width, sometimes scalloped anteriorly, sometimes practically coalescing with the anterior black marking so that the basic white is largely superseded. There are five black blotches, all visible from the front, although variable in form; they are always discernible separately and in constant locations. One pair passes through Head Scoli, extending antero-ventrally; one pair lies below and lateral to the preceding, extending to edge of head immediately behind antennae; the fifth blotch is formed by the front which is normally wholly black; adfrontals creamy white, unpigmented.

Thorax: Anterior and posterior margins dark brown; median part of each segment buffy. At level of dorso-lateral scoli, invaginations of the brown marginal bands extend backward and forward on each segment, forming a reddish-brown lateral stripe; these characteristics, however, are extremely variable; in some specimens the marginal invaginations are practically absent; in others they almost cover the segment.

Abdomen: Dorso-laterally, to immediately below level of spiracles, the abdomen is brownish, with four obliquely transverse, dorso-lateral white bands on 2, 4, 6 and 8 AB, respectively, extending from antero-laterally to postero-dorsally. The alternating segments, namely 1, 3, 5 and 7 AB, are washed in the same areas with darker pigment than the general color of the segment, giving the effect of alternating dark and white oblique bands. The basic similarity of this pigmentation with that of a number of first instar larvae, including *Dryas*, is obvious (see p. 151).

On each abdominal segment are 5 transverse rows of highly variable dark spots and bars. The first, on anterior margin, is often composed of two large spots, subdorsal and lateral; on 1, 3, 5 and 7 AB is a third lower spot; the second row is composed of two spots, sometimes fused, through bases of the Dorsals and Supralaterals; they are largest on 1, 3, 5 and 7 AB, where the spots extend both above and below the scoli, further darkening these segments; on the remaining segments they are above the scoli only. The third, fourth and fifth rows are formed of narrow interrupted bands which are reduced to two irregular bands on the last several segments. On each segment these posterior rows are thicker and confluent basally, that is, at about the level of the spiracles.

Sides, from spiracle level to below level of

**A****B****C****D****E****F**

TEXT-FIG. 11. Heliconiine larvae: Pigment patterns in fifth instar from dorsal midline to base of legs and prolegs. Diagrams on left: 1 TH and 2 TH. Diagrams on right: 3 AB and 4 AB. **A, B**, *Agraulis vanillae*; a dark individual (cf. light individual in Pl. IV, Fig. 26); **C, D**, *Dryas iulia*; **E, F**, *Heliconius sara*.

Sublaterals, buffy white; on each segment a dark red band crosses the white diagonally upward, from front to back, merging posteriorly with the confluent margin of the three posterior transverse rows of black. Markings on last three segments progressively irregular and obscure.

Sublateral surface mottled dark brown and buffy gray; a prominent pale spot above anterior side of base of each proleg and a more posterior buffy spot behind base of each proleg.

Prothoracic plate black; suranal plate reddish-brown. Scoli variably pigmented, darkest distally; spinules black. Legs and prolegs reddish-brown.

Maximum Length: 32 mm.

c. SECOND, THIRD AND FOURTH INSTARS. (Plate VI, Figs. 36, 37, 38).

Color: The head remains translucent brown, without markings, through the third instar; very faint darker brown markings become visible in fourth; no cream or reddish markings are apparent before fifth. General body color brown throughout second, third and fourth, darkening with the successive molts; the dark bands and white spots of first instar are all traceable in all the later stages, more so than in any other species. In the third, the condition is almost perfectly intermediate between the similar state of the first and the complex pattern of the fifth. No red pigment on lower sides of prolegs is, however, developed before fifth. As in the fifth, in each of the instars the white markings are most clearly marked on the middle abdominal segments. The oblique bands of the lower sides are not distinct until the fourth, and the vertical narrow bands of the fifth are not usually clear before that stage on most segments.

Prothoracic plate and scoli jet black in the younger larvae; by the fourth some of the AB Dorsals are less fully pigmented, a trend which is often carried further in the fifth (see under Fifth Instar). Legs, prolegs and last two segments approximately same color as head, the legs sometimes darker, the last segments usually lighter; by the fourth instar only the area of the suranal plate is still light.

5. *Philaethria dido* (Clerck)

a. FIRST INSTAR.

Setae and Crochets: Fleming, 1960, p. 91; Text-figs. 4, 5.

Color: Head translucent orange-brown, its posterior margin dark. General body color buffy yellow with white spots and dark bands, similar to *Dryas* and others, but differing in details: Dark bands present on 1, 3, 5, 7 and 9 AB, sometimes on upper half of segment only, re-

stricted to middle portion, and sometimes extending ventrally to base of prolegs and covering much of the segment. White spots are in three series: First series, between dorsal and supralateral setae groups, on 2 and 3 TH and 2, 4, 6 and 8 AB; second series, between supralateral and sublateral setae groups on all segments in the first series and on anal segment in addition; third series, above bases of legs and prolegs and below the sublateral setae groups, on 1 TH and on 2, 4, 6, 8 and 10 AB. As usual, both white spots and dark bands are of variable extent. Setae black, legs and prolegs dusky.

Length: At hatching, 3.7 mm.; maximum, 6.0 mm.

b. FIFTH INSTAR (Text-figs. 6E, 7E; Pl. IV, Fig. 28; Pl. IX, Fig. 55).

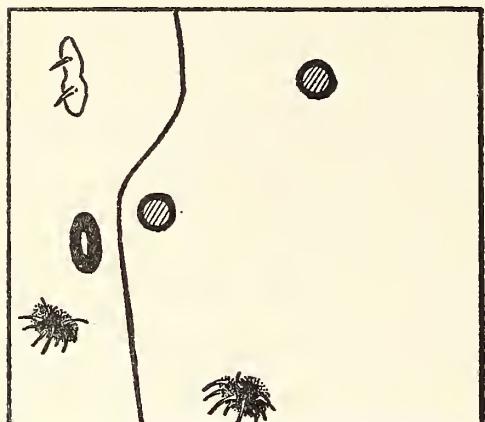
Diagnosis. All scoli exceptionally long, Head Scolus and 2 TH Dorsal being more than twice head height, bases of Dorsals and Supralaterals greatly expanded, tending to coalesce, bright orange-red in color; body otherwise banded with black and white, head orange.

Description. Scoli: Head Scolus about two and one-third times head height, moderately curving, members of the pair little divergent. 2 TH Dorsal slightly more than twice head height, 2 TH Lateral almost as long as 2 TH Dorsal and only slightly longer than 4 AB Dorsal. Supralaterals and Sublaterals exceptionally long, very slightly, and progressively, shorter than corresponding Dorsals; 4 AB Sublateral fully one and one-half times head height.

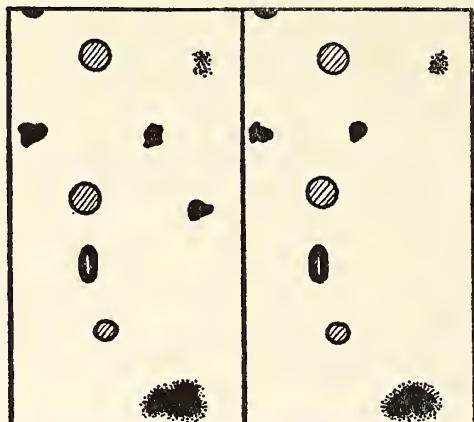
Head: Resembling *Agraulis*, with the epicranial profile in frontal view even less convex in upper portion, and with the front conspicuously narrower. In lateral view, the epicranial profiles most resemble *Dryadula* with even convexity both dorsally and anteriorly. Head length about 6% of maximum total length.

Prothoracic Plate: As in *Dryas* (p. 133), *H. numata*, *melpomene* and *erato*, each half very slender with only two setae.

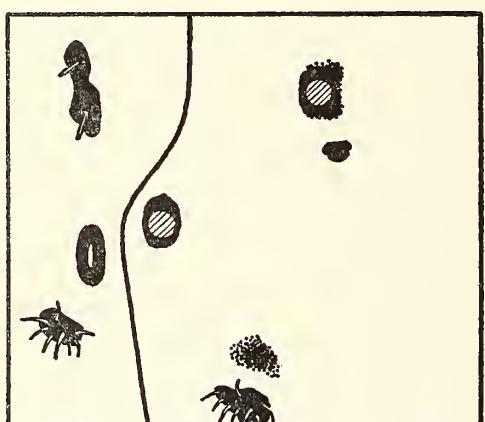
Color: Head bright orange. Body with all segments banded narrowly and more or less distinctly with black and white; when pigment is fully developed there are five white bands alternating with four dark on each segment; they show most clearly in the dorsal midline; in the areas of the Dorsals and Supralaterals they are obscured by the greatly tumid bases giving rise to these scoli. The bases are brilliant orange-red, and, on 1, 3, 5 and 7 AB, are so enlarged that the bases of the Dorsals coalesce with those of the corresponding Supralaterals, giving the effect of orange-red bands. The less tumid bases of all the other scoli also show some orange,



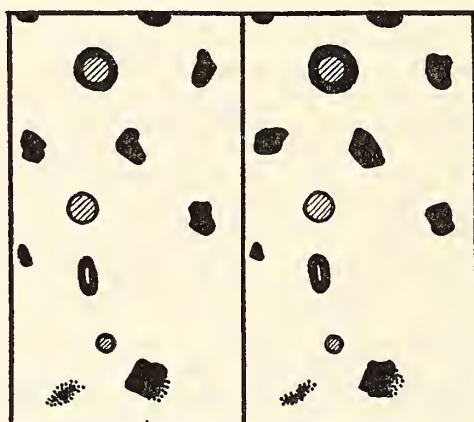
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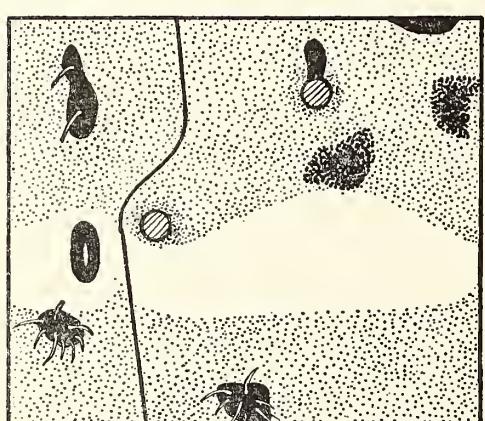
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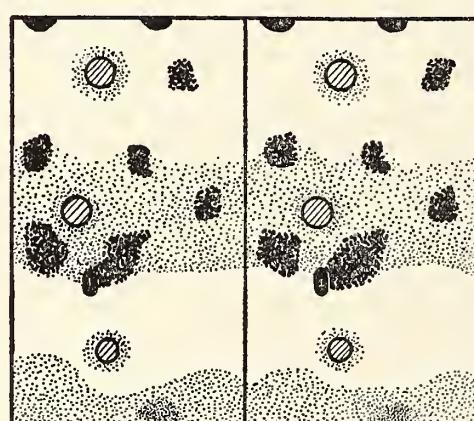
C



D

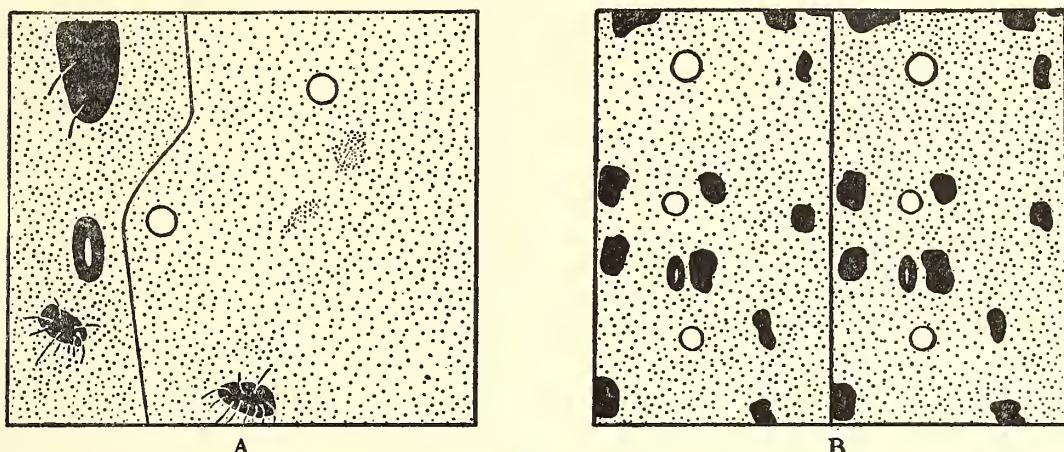


E



F

TEXT-FIG. 12. Heliconiine larvae: Pigment patterns in fifth instar from dorsal midline to bases of legs and prolegs. Diagrams on left: 1 TH and 2 TH; diagrams on right: 3 AB and 4 AB. **A, B**, *Heliconius numata*, **C, D**, *H. melpomene*, **E, F**, *H. erato*.



TEXT-FIG. 13. *Heliconius ricini*: Pigment pattern in fifth instar, from dorsal midline to bases of legs and prolegs. A, 1 TH and 2 TH; B, 3 AB and 4 AB.

except the Sublaterals. The Dorsals and Supralaterals themselves are also orange-red, except for black tips. Head Scolus, 2 TH Dorsal, 2 TH Lateral and Anal Scolus all black. Sublaterals white in basal half, orange-red medially, black distally. A purple-red stripe runs along sides below Sublaterals, and an oblique stripe of the same color on each proleg segment, diverging posteriorly to pass above base of proleg.

Prothoracic and anal plates black. Legs and prolegs unpigmented.

Maximum Length: 48 mm., the largest larva in the group under consideration.

c. SECOND, THIRD AND FOURTH INSTARS.

Color: The head becomes less brown and more orange with each molt. General body color dusky, banded with pale gray in second and third, black with pale gray in fourth; the pure white and narrow, distinct black bands do not become clear until fifth instar. The orange on thorax and abdomen appears first in the third, much grayed, and becomes bright and pure orange in the fourth; it does not become orange-red, nor does it extend into the scoli themselves, until the fifth. Prothoracic and suranal plates black throughout development. Scoli also black throughout, until fifth, except Sublaterals, which are medially pale in the fourth instar only, in the sections which become orange-red in the fifth. Legs black through fourth; prolegs dark through third; even in fourth they are still faintly dusky externally.

6. *Heliconius isabella* (Cramer)

a. FIRST INSTAR. (Text-fig. 10B; Pl. III, Figs. 18, 19).

Setae and Crochets: Fleming, 1960, p. 91; Text-figs. 4, 5.

Color: Head black. General color, dorsally and dorso-laterally, greenish-white with dusky, vertical bands on abdomen; these are strong on 1, 3, 5 and 7 AB, faint on 2, 4 and 6 AB. Last three segments (8-10 AB), as well as lower sides, ventral surface, feet and legs, entirely yellowish-white. On all segments, except those bearing the pronounced dusky bands (1, 3, 5, and 7 AB), the tumid bases of the two upper setae groups are white, not greenish-white. All setae black.

Length: At hatching, approximately 2.2 mm.; maximum, 3.3 mm.

b. FIFTH INSTAR. (Text-figs. 6F, 7F; Pl. IV, Fig. 29; Pl. IX, Fig. 57; Pl. X, Fig. 64).

Diagnosis.—Head Scolus about 1.75 times head height; none of Dorsals strikingly lower than remaining body scoli; 2 TH Dorsal and 4 AB Dorsal subequal, the latter the longer, about 1.25 times head height. Tumid bases of Dorsals and Supralaterals on 8 and 9 AB much enlarged, coalescent on each segment, bright orange; color otherwise black above, variably marked with lighter; a yellow stripe along sides, lower parts colorless.

Description.—**Scoli:** Head Scolus longer than in any other species in this study except *Philae-thria dido* and *H. aliphera*; it usually measures about 1.75 times head height although, as in all species with elongate scoli, there is considerable variation. It is strongly curved, in both lateral and frontal views. The body scoli are moderately long, and remarkable chiefly for their lack of striking differences in length, although as usual the Dorsals, Supralaterals and Sublaterals show some progressive diminution in size proceeding ventrally on each segment. AB Dorsals longest, much shorter than Head Scolus, about 1.2 times longer than head height; scarcely longer than

TH Dorsals. Sublaterals scarcely shorter than corresponding Supralaterals. Bases of 8 and 9 Dorsals and 8 and 9 Supralaterals greatly tumid and expanded, coalescent on each segment. Spinules on body scoli notably sparse and long.

Head: In frontal view, very similar to *P. dido*, the epicranial profiles scarcely rounded; lateral profiles also similar. Head length about 8.5% of maximum total length.

Prothoracic Plate: Divided into four parts, that is, two sections on each side of dorsal midline; each part broad and roughly quadrilateral, although there is variation in size, degree of distinctness and shape. Only one small seta on each of the four sections.

Color: This species, along with the very similar *H. aliphera*, is the most variable in larval coloration of all fourteen species under consideration. In both species there are very pale and very dark phases and an excellent range between. In neither species was a correlation found between a larval color phase and imaginal color, sex or health.

General Color: Head black with white markings anteriorly or largely white with black markings. Body black above, usually with narrow, transverse gray or white bands; upper part of 8 and 9 AB orange; anal segment (10 AB) yellow to white; a yellow lateral stripe running the length of the body above greenish-white, translucent legs, prolegs, lower sides and underparts. Prothoracic plate black; anal plate pale; scoli varying from pale to black.

Details of coloration on typical, dark individuals are as follows: head black with white anterior markings poorly developed, consisting only of divergent, interrupted, slender crescents on epicrania and as a spot extending across apex of front. Thorax and 1-7 AB entirely black as far down as level of Supralaterals, except for white on prothorax outlining the two paired black elements of prothoracic plate; 8 and 9 AB bright orange above; 10 AB white or yellow. A broad stripe, clear yellow, extending from 1 TH through 9 AB, from level of Supralaterals to Sublaterals. Spiracles outlined strongly in black; from their upper edge a narrow bar of black runs upward to the black area; a similar black bar occurs behind each spiracle. Below the Sublaterals, underparts, legs and prolegs translucent and colorless except for a faint greenish tinge.

Head Scolus completely black; Dorsals and Supralaterals black with pale tips except for those on 8 and 9 AB, which have the distal third to half pale; Sublaterals, including Anal Scolus, all translucent and colorless throughout.

In contrast, very pale individuals differ notably

in having far more white on the head, and in the presence of up to 5 transverse bands, white or gray, breaking the dorsal black area on each segment from 1 TH through 7 AB; these pale bands may be as wide as the alternating black bands. Pale individuals differ also in the paler orange of 8 and 9 AB, in the paleness of the yellow lateral stripe, and in the larger unpigmented areas on the Dorsals and Supralaterals. Head Scolus often with middle section unpigmented, while scoli on thorax and, especially, abdomen, tend to be unpigmented in distal half.

In a common intermediate phase the head is predominantly black, with strong anterior white markings on front and epicranial lobes and, posteriorly, a white stripe extending from the base of each scolus to posterior margin of head; in addition, there are three or four irregular dorsal, white transverse bands on each thoracic segment and three narrow bands on each segment of 1-5 or 1-6 AB, including submarginally, on anterior and posterior part of each segment.

Maximum Total Length: 31 mm.

c. SECOND, THIRD AND FOURTH INSTARS. (Pl. VIII, Figs. 49, 50).

Color: Head entirely black in second instar as in first; thereafter with varying amounts of white; some individuals with more white on head in fourth than in fifth. Thorax with all elements of prothoracic plate black throughout; in fourth instar some individuals have the plate divided into two, not four, sections; 1 TH around plate always unpigmented in early instars, later white. Dorsal area increasingly dark brown, not black, through fourth, with traces of the darker bands of first instar apparent through the third. The first trace of yellow-orange on the tumid bases of 8 and 9 AB Dorsal are apparent in third. Lateral yellow may be visible in third, but usually not until fourth; it forms in several distinct areas on each segment, which later coalesce. The black bars running between the dark upper surface and the spiracles and post-spiracular areas appear in the fourth.

All scoli and spinules more or less dusky during second and third; middle section of Head Scolus at this time generally unpigmented; Sublaterals lose their pigment in the fourth and fifth instars. Underparts, legs and prolegs translucent and colorless, or with greenish tinge, throughout the instars.

7. *Heliconius aliphera* (Godart)

a. FIRST INSTAR. (Text-fig. 8A; Pl. III, Fig. 20).

Setae and Crochets: Fleming, 1960, p. 91; Text-figs. 4, 5.

Color: Head capsule pale translucent and colorless or slightly buffy; body pale translucent

yellowish except for dusky tumid bases of setae groups; setae black. No trace of dark bands or white spots.

Length: At hatching, 1.3 mm.; maximum, 2.4 mm.

b. FIFTH INSTAR. (Text-figs. 5E, 6G, 7G, 8E; Pl. IV, Fig. 30; Pl. IX, Fig. 56; Pl. X, Fig. 65).

Diagnosis.—Head Scolus about 2.25 times head height; 2 TH Dorsal and 4 AB Dorsal subequal, the latter the longer, about 1.8 times head height; 2 TH Lateral notably shorter than 4 AB Dorsal; Sublaterals at most slightly more than half length of Supralaterals. 8 and 9 AB Dorsals and Supralaterals without orange pigment; color otherwise similar to *H. isabella* in having upper portions dark with light markings, a pigmented white or buffy stripe midlaterally, and colorless ventral parts.

Description.—Scoli: Longer than in any other species in this study in relation to total maximum length of body, and longer than any of the species except *Philaethria dido* in relation to head height. Head Scolus variable, but usually at least 2.25 times head height, and between 20 and 30 per cent. of the highly variable maximum total length; moderately curved. Dorsals all about equally long through 7 AB, their spinules very long; the longest AB Dorsals very slightly longer than 2 and 3 TH. Dorsals about 1.8 times head height; 2 TH Lateral notably shorter than the Dorsals, about 1.5 times head height. Supralaterals of first several AB segments notably longer than thoracic Laterals; Sublaterals, although well developed, relatively shorter than in *H. isabella* or *P. dido*, measuring at most slightly more than half length of corresponding Supralaterals. Spinules on body scoli few in number but very long and, except on Sublaterals, stout at their bases. This larva appears more spinous and bristling than does that of any other species in this study.

Head: Similar to *isabella*, from which it differs in frontal view in the slightly more convex epicranial profiles and the narrower front.

Prothoracic Plate: Divided into two broad portions by dorsal midline; each half with three setae.

Color: Similar to *isabella*, with black, white-marked head, black or parti-colored dorsal and dorso-lateral areas, light-colored sides and posterior segments, colorless underparts, legs and prolegs, parti-colored scoli and high variability.

It differs conspicuously and unvarying as follows: There is no orange on 8 and 9 AB; the lateral stripe is often white, never as yellow as in *isabella*; finally, in *aliphera*, the light dorsal markings, when present, are yellow, not white,

and take the form of spots rather than narrow bands; often there is one anterior and one posterior spot on each segment.

The extremely pale forms of *aliphera* are relatively paler than corresponding *isabella*, with even the dorsal dark areas so weak in pigment that they appear gray. In *aliphera*, the distal, not basal, portions of parti-colored scoli are dark. As in *isabella*, no correlation whatever was found between larval color phases and imaginal pigmentation, sex or health.

Length: This is the smallest species in the study, with a maximum length of 24 mm.

c. SECOND, THIRD AND FOURTH INSTARS. (Text-figs. 8B', 8C', 8D'; Pl. VIII, Figs. 45, 46, 47, 48, 51, 52).

Color: Development of the pattern proceeds much as in *H. isabella*; its even greater variability makes details of its development in individuals or the species as a whole of little value. The head pigment appears first in the third instar, the white or yellowish pigment of the lateral stripe in the fourth.

8. *Heliconius melpomene* (Linnaeus)

a. FIRST INSTAR. (Pl. III, Fig. 24).

Setae and Crochets: Fleming, 1960, p. 91; Text-figs. 1-5.

Color: Head capsule dull orange buff, apparently always without posterior margin. General color, dull yellowish-orange with faint dark bands on 1, 3, 5 and 7 AB, apparent for a few hours only in the later middle part of the instar. Bases of all setae slightly tumid, brownish; setae dark except for pale tips; legs dark; prolegs dusky externally, at least in later middle part of instar. No trace of white spots.

Length: At hatching, 2.9 mm.; maximum, 4.9 mm.

b. FIFTH INSTAR. (Text-figs. 6H, 7H, 12C, D; Pl. V, Fig. 31; Pl. IX, Fig. 58; Pl. XI, Fig. 66).

Diagnosis.—Head Scolus about 1.5 times head height; 2 TH Dorsal slightly longer than others in dorsal series, less than 1.5 times head height; Sublaterals about 4/5 head height; prothoracic plate slender with 2 pairs of long setae, pigmented black; head and prolegs orange-yellow; body white with black spots.

Description.—In *H. melpomene*, *numata* and *erato*, the larvae are so similar that they can only be surely told apart by details of the pigment patterns in life.

Scoli: All moderately long, but without exceptional characteristics. Head Scolus moderately curved, slightly longer than any other, usually about 1.5 times head height, about as

long as 2 TH Dorsal; the latter is more than a third longer than either 4 AB Dorsal or 2 TH Lateral; 2 TH Lateral about a fourth longer than head height; Sublaterals about 4/5 head height, the Dorsals, Supralaterals and Sublaterals on the segments forming well-graduated series.

Head: In frontal view with epicranial profiles moderately convex in upper portions; from the side, the anterior profile below the Head Scolus is flattened. Head length 6.5% or less of maximum total length.

Prothoracic Plate: As in *Dryas iulia*, *Phil-aethria dido*, *H. numata* and *H. ricini*, slender, divided into halves at the dorsal midline, each half giving rise to two long setae.

Color: Head orange-yellow to yellow-orange-yellow, without dusky posterior margin; prothoracic plate black. Body altogether white with black spots except for posterior part of anal segment which is like head. Ventral surface dusky. Scoli black. Feet and prolegs, like head, without dark pigment.

The arrangement of the black spots is very constant in this species, as well as in *numata*, *erato* and *ricini*, as follows; not all spots, however, are present in full-grown *numata* larvae. Viewed casually, two series of quincunxes are apparent on each of the segments except in the anterior and posterior regions; they are placed one above the other, and share several spots. In detail, the spots are placed as follows:

1. A mid-dorsal series of 1 anterior and 1 median spot on all segments except 1 TH and 9 and 10 AB.
2. A series of one spot at levels of Dorsals in posterior part of segment on each of the same segments as in 1.
3. A series of 1 anterior and 1 median spot between Dorsals and Supralaterals.
4. A series of 1 anterior and 1 posterior spot at level of Supralaterals or slightly below them.
5. A series of 1 median spot immediately above level of Sublaterals on all abdominal segments except 9 and 10 AB.
6. A dark, dusky crescent (distinct from regular ventral pigment) above bases of legs, ventral prolegs and in corresponding positions on 1 and 2 AB.

Viewed as vertical series of spots, instead of horizontally, Series 1-5 inclusive show similarities to vertically-banded species, notably *Phil-aethria dido*.

Maximum Total Length: 42 mm.

c. SECOND, THIRD AND FOURTH INSTARS.

Color: Second instar, head orange-buff to

orange-yellow throughout development, as in first and fifth, but margined posteriorly with black; prothoracic plate dusky to black throughout; scoli and legs black throughout, suranal plate unpigmented. Body color in second instar still buffy and translucent, but all spots of full-grown larvae are discernible, faintly dusky; 9 and 10 AB as yellow as head; 7 and 8 AB yellower than more anterior segments, with spots extremely faint; white pigment starting development in more dorsal regions on 2 and 3 TH and 1 AB. Ventral prolegs with large dusky patch externally on each; anal proleg orangish-yellow, like posterior segments and head, immaculate except for dark secondary setae.

By the third instar, both the white pigment and black spots are well developed and the dark pigment of ventral prolegs usually reduced to a slight duskiness; 8, 9 and 10 AB yellow, immaculate, like head, with yellow tinge on 7 AB and also on lower sides from level of Sublaterals ventrally; all scoli bases of two upper series, except on posterior yellow segments, set in very small black spots.

Fourth instar like fifth except that entire anal segment is still orange-yellow, with traces of the same color on the two preceding segments (8 and 9 AB), and that the ventral prolegs still show traces of dusky patches externally.

9. *Heliconius numata* (Cramer)

a. FIRST INSTAR.

Setae and Crochets: Fleming, 1960, p. 91; Text-figs. 4, 5.

Color: Head translucent buffy, bordered posteriorly with black. Thorax and last abdominal segment translucent, paler buff than head; 5 AB darkest; 9 and 10 AB streaked with dusky. Bases of setae slightly enlarged with minute dark speckles; setae and legs dusky; prolegs dusky externally. No trace of white spots. Differs from *H. melpomene* and *erato* in the unbroken brown tinge on most of abdomen; at no time is there a banded phase.

Length: Maximum, 4.7 mm.

b. FIFTH INSTAR. (Text-figs. 5F, 6I, 7I, 12A, B).

Diagnosis.—Very similar to *H. melpomene*, from which it differs notably in having the prothoracic plate unpigmented, a difference which persists well in preservative. In life, the black spots are fewer and smaller than in the majority of *melpomene*, being almost always absent at least from the mid-dorsal line. Head Scolus usually about 1.5 times head height; 2 TH Dorsal slightly longer than others in dorsal series, less than 1.5 times head height; 2 TH Lateral about as long as head.

Description.—*Scoli*: In comparison with *melpomene*, the small differences in relative scoli length are too slight to be of practical taxonomic value without recourse to serial treatment, since as usual in species with long scoli there is considerable individual variation. The clearest differences are in the Laterals, which are shorter than in *melpomene* (2 TH Lateral about as long as head, instead of about a fourth longer). The Head Scolus is more curved than in *melpomene*, although there is great variation in this respect in both species; and all scoli in *numata* are slightly more slender.

Head: In frontal view, *numata* resembles *Philaethria dido* more than *H. melpomene*, with upper epicranial profile scarcely convex; anterior profile of epicranium in lateral view also notably straight. Head length less than 6% of maximum total length.

Prothoracic Plate: Slender, with two long setae, as in *Dryas iulia*, *Philaethria dido*, *H. melpomene* and *H. erato*.

Color: Head same orange-yellow as in *melpomene*. Thorax and abdomen: Pure white, including prothoracic plate, with black spots only as follows: Thorax none, except for black outlining spiracle and, in some specimens, a faint irregular dusting of dusky on lower sides and one spot (dusky or black) above base of each leg (see 6, below); occasionally a dusky spot on 3 TH between dorsal and lateral scoli. Abdomen with spots as follows in comparison with *melpomene*:

1. (Mid-dorsal series absent).
2. (Series at level of Dorsals absent).

3. Series of 2 spots on each segment—one anterior, one median—between Dorsals and Supralaterals, as in *melpomene*, but only on 3, 4, 5 and 6 AB, and, faintly, on 7 AB.

4. This long and important *melpomene* series is represented in *numata* only by single spots, not two, usually present on 3 and 4 AB, sometimes additionally on 5 AB, in posterior part of segment only, near level of Supralaterals; the spot may, however, be slightly above or below level of scolus.

5. (Series of 1 median spot above Sublaterals absent).

6. A spot as in *melpomene*, but not crescentic, above bases of legs, ventral prolegs and intervening segments.

In summary, spots in *numata* are practically confined to the dorso-lateral region of the abdomen. They show great variation, are almost always smaller than in *melpomene*, and are sometimes practically lacking. Text-figs. 12A, B diagram them at their most extensive.

In some specimens there is a faint irregular dusting of dusky on lower sides. Spiracles always rimmed noticeably with black; ventral surface translucent whitish. As in *melpomene*, the yellow on anal segment is confined to the region around anus.

Maximum Total Length: 39 mm.

c. SECOND, THIRD AND FOURTH INSTARS.

Color: Second instar distinguished from all others by having the prothoracic plate dusky to black; head and last two segments pale buffy, the head as in first instar margined posteriorly with black; thorax and abdomen still brownish-yellow, semi-translucent, immaculate throughout instar; scoli and spinules black, or almost so, for entire length; legs black, prolegs dusky to black externally except for unpigmented anal prolegs.

Third instar with head, prothorax and last three segments clear orange-yellow; prothoracic plate now unpigmented in some individuals, as in later instars; in others it is still very dark. General color dark brown with white pigment developing on 1-6 AB, surrounding locations of future spots; these are left brown as in younger larvae, with dusky speckles developing increasingly through the instar; no white pigment in dorsal midline; white developed chiefly on posterior part of each segment and around scoli bases; sometimes it forms a strong lateral stripe through Supralaterals. Dark spotting much more complete than in fifth instar, usually corresponding perfectly to that found in fully grown *melpomene* and *erato*, although the spots are relatively larger and less pigmented than in full-grown larvae of either of the latter species.

In addition to the generally quincunxial arrangement of the groups, the spots show clear evidence of three vertical rows of spots on each segment—a row of large spots before scoli, a second row of faint spots between and slightly behind scoli, and a third of large spots behind scoli. The two mid-dorsal spots belong to the anterior and middle rows. Traces are shown in this third instar also of a pigment spot on outer side of anal proleg.

Fourth Instar: Little or no reduction in number of spots described in third instar, which are also characteristic of *melpomene* and *erato*. The only reliable specific difference occurs in the pigmentation of the prothoracic plate, which is now unpigmented, as in fifth, except for black pigment which usually occurs immediately around base of the lower setae on each half of the plate, and for an occasional, subsurface dusky tinge.

In summary, while in color the second instar

is distinguishable from corresponding stages of *melpomene* and *erato*, the third cannot be differentiated and the fourth only by a single, slightly variable character.

10. *Heliconius erato* (Linnaeus)

a. FIRST INSTAR. (Pl. III, Fig. 25).

Setae and Crochets: Fleming, 1960, p. 91; Text-figs. 4, 5.

Color: We have been unable to find a reliable color difference distinguishing *erato* from *melpomene*.

Length: At hatching, 2.6 mm.; maximum 4.8 mm.

b. FIFTH INSTAR. (Text-figs. 6J, 7J, 12E, F; Pl. V, Fig. 32; Pl. IX, Fig. 59; Pl. XI, Fig. 68).

Diagnosis.—Very similar to *H. melpomene* and *numata*, from both of which it differs conspicuously only in details of color, as follows: Head buff, not orange-yellow; legs and prolegs with dusky pigment, instead of being immaculate; bases of some scoli orange. Prothoracic plate black, as in *melpomene*. The chief differences in non-color characters are confined to slightly shorter scoli, the head scolis being usually only about a quarter longer than head height, not a half, as in the other two species.

Description.—Scoli: Head Scolus always little curved, less so than in most specimens of *melpomene* and *numata*, slightly shorter than 2 TH Dorsal, about one-quarter longer than head height; Lateralis about as in *numata*, about equal to head height, instead of longer, as in *melpomene*. As noted in the description of *numata*, however, the small differences in relative scoli length and the large range of variation in the three species make the scoli of slight practical taxonomic value, without extensive analyses of long series.

Head: Upper lateral profiles of head from front resembling *H. numata* and *Philaethria dido* rather than the more convex *melpomene*; anterior epicranial profile from the side, however, is notably convex; length of head in respect to its height intermediate between the short-headed *numata* and long-headed *melpomene*; head length about 6.5% or less of maximum total length.

Prothoracic Plate: Narrow, with 2 long scoli on each half, as in *Dryas iulia*, *Philaethria dido*, *H. melpomene* and *H. numata*.

Color: Head pale buff, usually with a pair of black patches on epicranium, adjacent to adfrontals and immediately above level of upper margin of ocelli groups. Body white with black spots, their arrangement as in *melpomene* (p. 140), although the individual spots are larger;

bases of most scoli orange, their color being most extensive on Dorsals and Supralaterals. The white of dorsal and lateral surfaces extends to below level of Sublaterals and posteriorly below anus; below the white area is a band of dull, translucent orange, including legs and prolegs; ventral surface pale. Two small black patches, one below the other, on external side of each proleg; two dark blotches, often indistinct, above proleg bases. Prothoracic and anal plates, spiracles and scoli jet black.

Maximum Total Length: 36 mm.

c. SECOND, THIRD AND FOURTH INSTARS.

Scoli: Obviously shorter than in corresponding *melpomene* and *numata*, their bases more tumid.

Color: Second Instar: Head pale buff, about as in fifth instar, but anteriorly without markings, bordered posteriorly with black. Prothoracic plate black; scoli dark dusky, the sublateral series least dark; prothoracic and anal segments like head. General color dorsally and laterally light gray with dark dusky spots already visible in positions found in later instars; dorsoventrally on each segment dull yellowish bands run through levels of bases of Dorsals and Supralaterals; the bands merge, at level of Sublaterals, with the general yellowish color of the lower sides. Legs black; a single large dusky spot on external surface of each proleg, paler on anal proleg.

The second instar of *erato* differs from the corresponding stages in *melpomene* and *numata* in the feebler development of pale grayish pigment (the precursor to the later white), and in the presence of distinct dull yellow bands through the scoli.

Third and Fourth Instars: The typical pigmentation of black, white and yellow is very well developed, although the white has a grayish cast and differs from the fourth chiefly in that it dies out at the end of 8 AB or the middle of 9 AB, instead of extending to below the anus; the orange is still extensive, being confluent around the scoli except dorsally, so that the three rows of scoli on each side are joined by a dull orange band on most segments; the orange, however, does not extend up into the bases of the scoli proper, as it does in the Dorsals and Supralaterals during the fifth instar, but is confined to the area of their insertion; the spots are relatively larger than in the fifth; the head still shows a black posterior margin, as in young larvae; the legs are still entirely black.

The third and fourth instars differ clearly from the corresponding stages of *melpomene* and *numata* in the strong presence of yellow

around the scoli bases, and its relatively weak development on the last abdominal segments, while the reverse is true in the other two species.

11. *Heliconius ricini* (Linnaeus)

a. FIRST INSTAR. (Pl. III, Figs. 22, 23; Pl. VII, Fig. 40).

Setae and Crochets: Fleming, 1960, p. 91; Text-figs. 4, 5.

Color: Head buff yellow, edged posteriorly with black; body yellowish, paler than head; bases of setae slightly dusky; setae dusky with pale tips; abdominal spiracles dusky; legs and prolegs like body, without dark pigment. No trace of dark bands or white spots.

Length: At hatching, 1.8 mm.; maximum, 2.9 mm.

b. FIFTH INSTAR. (Text-figs. 6K, 7K, 13; Pl. VI, Fig. 33; Pl. VII, Fig. 44; Pl. IX, Fig. 60; Pl. XI, Fig. 68).

Diagnosis.—Head Scolus clearly shorter than head height; 2 TH Dorsal about one-quarter longer than head height, slightly longer than Lateral or remaining Dorsals. Head brown to black; body yellow with black spots.

Description.—Scoli: All shorter than in *H. melpomene*, *numata* and *erato*, the species which it resembles closely in color pattern. In their relative lengths, the scoli resemble those of *Agraulis vanillae* most closely. The Head Scolus is even shorter, about four-fifths of head height, scarcely curved, and directed more upward than forward. All scoli more slender than in *vanillae*, but thicker in relation to body length than in *melpomene* and its relations. No striking differences in body scoli, all of which are somewhat longer than Head Scolus; 2 TH Dorsal slightly the longest, measuring about one-fourth longer than head height. Sublaterals almost as long as corresponding Supralaterals.

Head: In frontal view, much like *melpomene*, with epicranial profiles even more convex; from the side the greater resemblance is to *erato*, although the epicranial profiles are less convex. Length more than 9% of maximum total length, relatively much longer than in *melpomene*, *numata* and *erato*.

Prothoracic Plate: As in *vanillae* and similar species, divided by dorsal midline into two broadly triangular sections, each with two long, one moderate and a number of small setae; it shows no resemblance to the elongate form found in *Dryas iulia*, *H. melpomene*, etc.

Color: Head black, along with prothoracic and anal plates, scoli, legs and an outer distal spot on each proleg. Body bright greenish-yellow with black spots arranged very similarly to those

of *melpomene*. The spots are irregular or absent on the thorax and on 9 and 10 AB, but strongly developed on 1-8 AB. A thin sprinkling of black speckles is often apparent on back and sides. The spiracles are so strongly pigmented that each gives the appearance of a spot.

Maximum Length: 27 mm.

c. SECOND, THIRD AND FOURTH INSTARS. (Pl. VII, Figs. 41, 42, 43).

Color: In these instars there is considerable variation in the time of darkening of the head; heads of siblings in the third instar may range from creamy yellow to light brown and in the fourth from brown to almost black; the head also pales to an exceptional and variable extent before the molt. The body color is more clearly yellow, less greenish, in these younger stages. All of the dark spots, along with the dark pigment of thoracic and anal plates and of the legs, become apparent in the second instar. Scoli black, or practically so, throughout development.

12. *Heliconius sara* (Fabricius)

a. FIRST INSTAR. (Text-figs. 8A, 9A; Pl. III, Fig. 21).

Setae and Crochets: Fleming, 1960, p. 91; Text-figs. 4, 5.

Color: Head translucent buffy yellow, posterior margin black. General body color pale buffy; no trace of dark bands or white spots. Setae dark and their tumid bases dark, developing strongly first around dorsal setae groups. Prothoracic plate, suranal plate and legs black. Prolegs with dark patches externally.

Length: Maximum, 4.5 mm.

b. FIFTH INSTAR. (Text-figs. 6L, 7L, 8E, 9E, 11E, 11F; Pl. V, Fig. 34; Pl. IX, Fig. 61; Pl. XI, Fig. 69).

Diagnosis.—A brownish-black or reddish-black larva with Head Scolus less than half head height; 2 TH Dorsal more than one and one-half times length of any other scolus; 2 TH Lateral shorter than 4 AB Dorsal.

Description.—Scoli: Head Scolus less than one-half head height, directed almost vertically, its tip pointing backward; from the front the two members of the pair converge. 2 TH Dorsal more than one and one-half times longer than any other scolus, but still shorter than head height. 2 TH Lateral clearly shorter than 4 AB Dorsal. Supralaterals and Sublaterals short, half or less than half corresponding Dorsals, the Sublaterals only slightly shorter than Supralaterals. Spinules very short.

Head: Higher than wide in frontal view, considerably narrower at base of scoli than between eyes, the upper lateral epicranial margins little

convex. Anterior epicranial profile moderately convex in lower portion. Head length more than 10% of maximum total length.

Prothoracic Plate: Each half broadly triangular with 2 long, 1 moderate and a number of short setae.

Color: Head, prothoracic and suranal plates, scoli, legs and outer sides of prolegs glossy black. Body color otherwise very dark brown, usually tinged with reddish.

Maximum Total Length: 29 mm.

c. SECOND, THIRD AND FOURTH INSTARS. (Text-figs. 8B, 8C, 8D, 9B, 9C, 9D).

Color: Head, prothoracic plate, suranal plate and legs black throughout these instars; scoli usually black, sometimes brown posteriorly, as late as third. Body color buffy yellow in second, variably yellowish-brown in third, variably dark brown, but without reddish tinge of fifth, in fourth. Prolegs pale through third, black in fourth except anal proleg, which may be dusky in third. Spiracles black in third.

13. *Heliconius wallacei* Reakirt

a. FIRST INSTAR.

Setae and Crochets: Fleming, 1960, p. 91; Text-figs. 4, 5.

Color: Differs from *H. sara* as follows: Head darker, yellowish-brown instead of buffy yellow; dusky patches on anal proleg only, instead of on ventral prolegs also.

Length: At hatching, 2.1 mm.; maximum, 3.7 mm.

b. FIFTH INSTAR. (Text-figs. 5C, 6M, 7M).

Diagnosis.—A black or reddish-black larva with long yellow scoli; Head Scolus about as long as head height; 2 TH Lateral at least as long as 4 AB Dorsal; prothoracic plate broadly triangular with more than 2 pairs of setae; no spinules nearly as long as vertical diameter of ocelli group.

Description.—**Scoli:** Head Scolus about equal to head height, almost straight, but directed obliquely forward, as usual, rather than backward as in *H. sara*. 2 TH Dorsal conspicuously elongated; although less than one and one-half times head height. 2 TH Lateral at least as long as 4 AB Dorsal. Supralaterals and Sublaterals well developed, more than half length of corresponding Dorsals, the scoli in the three series on each segment progressively smaller ventrally.

Head: Head from front differs conspicuously from that of *sara* not only in its greater width, in which it resembles most other species under discussion, but in the strongly convex lateral profile of the epicranial lobes; it is notably more

setose in this view than any other species except *Agraulis vanillae* and *Dryadula phaetusa*, which are comparable. Head length more than 7% of maximum total length.

Prothoracic Plate: As in *H. sara*.

Color: Head, prothoracic and suranal plates, legs and prolegs, black. Body, velvety brownish-black faintly tinged with reddish-purple. Scoli all bright yellow except those of head, which are yellowish suffused with dusky. Spinules dark brown.

Maximum Length: 38 mm.

c. SECOND, THIRD AND FOURTH INSTARS.

Color: Head brownish-black to black in second instar, completely black thereafter. Body color deep buffy yellow in second instar to yellowish-brown or darker brown by fourth. Prothoracic plate, anal plate and legs black throughout; prolegs dusky in second, black in third and thereafter. Scoli faintly to moderately dusky in second, varying with the individual; in some the duskiness is chiefly anterior, in others posterior; considerable change also takes place in an individual from one molt to the next, since the darkest scoli in successive instars are not necessarily in the same region. In the third and four instars, the Head Scoli are always black. The body scoli are dark dusky, darkest anteriorly, throughout the third. There is no hint in either second or third instars of the clear yellow which colors the body scoli of older larvae; this characteristic appears abruptly in the fourth and is unique among all the species under consideration.

14. *Heliconius doris* (Linnaeus)

a. FIRST INSTAR. (Pl. II, Fig. 12).

Setae and Crochets: Fleming, 1960, p. 91; Text-figs. 4, 5.

Color: Head brownish-black. Body clear pale green-yellow. Setae and their tumid bases dark. Thoracic and anal plates black. Legs and prolegs dusky.

Length: At hatching, 2.31 mm.; maximum, 4.2 mm.

b. FIFTH INSTAR. (Text-figs. 5D, 6N, 7N).

Diagnosis.—No scolus on anal segment; all scoli notably shorter than head height except 2 TH Dorsal, which is about one and one-half times head height and one and two-thirds times length of next longest scolus. Supralaterals shorter and more slender than Sublaterals. Body greenish-yellow with dark transverse bands.

Description.—**Scoli:** Head Scolus scarcely more than a spiniferous tubercle, as in *Dione juno*, its height less than half that of ocelli group. Body scoli all short, except for 2 TH Dorsal,

which is about one and one-half times head height, and about one and two-thirds times length of other Dorsals. 2 TH Lateral relatively shorter even than in *H. sara*, half head height and only three-fifths length of AB Dorsals; Supralaterals thinner and no longer than Head Scolus. Sublateral Scoli almost twice as long and thick as corresponding Supralaterals, about one-fourth head height. Spinules short, more closely set on Laterals and Sublaterals than on Dorsals. No trace of a scolus on anal segment except for a small, round, flat, black spot in the usual position, bearing several small setae; this character is unique among all the species under consideration.

Head: Narrowed dorsally in frontal view, somewhat as in *sara*, but with upper sides more convex; front very narrow. Head from side with anterior profile sloping almost straight from top down, little convex. Head length more than 7% of maximum total length.

Prothoracic Plate: As in *sara*, but with small setae more numerous.

Color: Head, prothoracic and anal plates, scoli, spiracles, legs and lateral proleg patches all glossy jet black. General body color greenish-yellow, with 10 brownish-black bands, one through level of each Dorsal Scolus, from 2 TH through 8 AB. The band on each segment stops partway down the sides; on the thorax it ends slightly behind Laterals; on abdomen it passes through Supralaterals and continues, narrowed, to level of Sublaterals. Minute secondary setae, which do much to dull the appearance of the body color, are brown.

Maximum Total Length: 35 mm.

c. SECOND, THIRD AND FOURTH INSTARS.

Color: Head, Head Scolus, some anterior scoli, prothoracic plate, suranal plate and legs glossy black throughout growth. General body color pale green-yellow, clearer and more yellow than in fifth instar, partly because of the less pigmented secondary setae; no trace of dark vertical bands before fifth. Scoli, spiracles and proleg patches mostly dusky in second instar, completely black by third.

V. PUPAE

A. CHARACTERISTICS OF THE SUBFAMILY

The pupae of the Heliconiinae show a remarkable variety in shape and ornamentation. The color range is from dark brown to almost white, the wing veins are often marked with dark pigment, and gold-colored spots are a frequent characteristic of the dorsal parts of the thorax and abdomen. Within the group, the most useful taxonomic characters are the relative devel-

opment of projections from the head, and of flanges, tubercles, spines and gold-colored spots on the thorax and abdomen. Minor characters are furnished by the tip of the abdomen and the development of small tubercles on the wings.

Abbreviations and Terminology.—The following list defines the use of terms in the following section.

1 TH, 2 TH, 1 AB, etc. First thoracic segment (prothorax), second thoracic segment (mesothorax), first abdominal segment, etc.

Postmedian tubercles of forewing. A series of tubercles occurring slightly distal to the area of the wing midway between its base and its outer margin.

Submarginal tubercles of forewing. A series of tubercles occurring near the outer margin of the wing, distal to the postmedian tubercles, close to them and parallel with them.

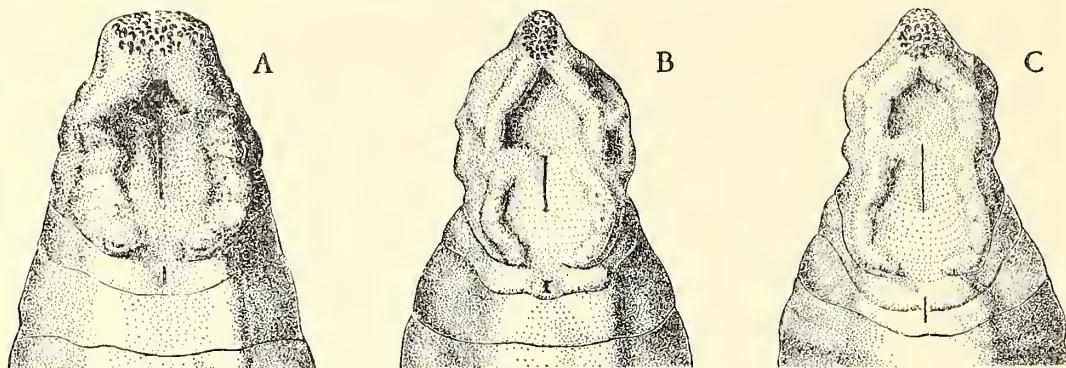
Cells M_2 , M_3 and Cu_1 ; Vein M_2 . As in the wings of adult butterflies (e.g., Klots, 1951, p. 50 ff.; figs.). The postmedian and submarginal tubercles occur only in these areas, as described below and shown in Pls. XIV and XV. For diagrams of heliconiine wing venation, see Michener, 1942, figs. 1-8.

Cremaster. The hook-bearing prolongation of the last (tenth or anal) segment of the abdomen (Text-fig. 14).

Description.—The pupae, in accordance with the general characteristics of the Nymphalidae, are naked, suspended only from the tip of the cremaster, lack the epicranial suture, have the legs of 1 TH and 2 TH extending cephalad to the eyes, and the legs of 2 TH extending slightly between the sculptured eyes and the antennae. In general appearance the chrysalids range from almost smooth with few tubercles to rugose with large flanges, tubercles and spines. The wings, along with the attached antennae, often protrude well below the abdomen.

Head with a pair of projections varying from small tubercles to long, flattened, scalloped appendages. Antennae with segments usually marked, except proximally and distally, with tubercles or short spines.

Thorax: 2 TH with a medio-dorsal crest or blunt ridge. Paired dorsal tubercles or spinous projections present or absent on 1 TH, always present on 2 and 3 TH. Shiny, gold-colored spots present or absent at bases of these tubercles or spines on 1 and 3 TH; never present on 2 TH. At base of forewing on 2 TH, dorso-laterally, two tubercles and a longitudinal ridge are always present; the lower tubercle is always the larger, the ridge follows behind it and both form characteristic features of the pupa's profile as seen in



TEXT-FIG. 14. Anal segments of pupae: Ventral views. **A**, *Agraulis vanillae*, male; **B**, *Heliconius melpomene*, male; **C**, *H. melpomene*, female.

the dorsal and ventral view. Forewing with a group of three postmedian tubercles or three submarginal tubercles, or both, ranging from rudimentary to spinous; the postmedian series always occurs in Cells M_2 , M_3 , and Cu_1 . In the submarginal series the first is almost continuous with Vein M_2 and the third opposite posterior part of Cell Cu_1 . Ventral profile of wing ranging from gently rounded and projecting little beyond that of abdomen to sharply angular and strongly projecting.

Abdomen: Mediodorsal tubercles always present on anterior margins of 5, 6 and 7 AB, never on other segments. One pair of gold-colored spots present or absent on 1 and 2 AB. Paired dorsal tubercles or spinous projections always present on 1-7 or 8 AB; those on at least 3 and 4 AB are often enlarged and flange-like, sometimes partly fused and overlapping. Supralateral tubercles always present on 3 and 4 AB, sometimes on 1 and 2 AB. Sublateral (subspiracular) tubercles present in *Philaethria* only.

Cremaster usually as broad as long, distally truncate, or with the median distal portion produced into a terminal triangle. Tip always flattened and covered with numerous hooked setae.

The fourteen Trinidad species may be divided into three groups, as follows:

Group A

Dione juno, *Agraulis vanillae*, *Dryadula phaetusa*, *Dryas iulia*, *Philaethria dido*, *Heliconius doris*.

Pupa without spines; cephalic projections no longer than broad except in *D. phaetusa*; paired subdorsal tubercles on abdomen not strongly modified into large flanges; gold-colored, shiny spots on thorax and abdomen present or absent.

Group B

Heliconius aliphera; *H. isabella*.

Spines present on thorax and abdomen, but absent on antennae; no subdorsal flanges on abdomen, no gold-colored spots.

Group C

Heliconius melpomene, *H. numata*, *H. wallacei*, *H. sara*, *H. erato*, *H. ricini*.

Spines present on thorax, abdomen and antennae; subdorsal flanges present on abdomen, those at least on 3 AB strongly developed; 3 to 5 pairs of gold-colored spots on thorax and abdomen.

Of the six species in this group, *numata*, *melpomene*, *wallacei* and *sara* are more similar to one another than they are to *erato* and *ricini*, while the latter two species resemble each other more than the others. Within the first group, *numata* and *melpomene* on the one hand and *wallacei* and *sara* on the other form similar pairs.

The distinguishing characteristics among the six species consist of: (a) the degree of basal spinulation on the antennae; (b) the form of the cephalic projections; (c) the presence or absence of paired gold-colored spots on 1 TH; (d) the form of the paired subdorsal flanges on 3 and 4 AB; (e) the length and direction of the spines on these flanges; (f) the relative length of the corresponding subdorsal spines on 5, 6 and 7 AB and the relative sizes of the small, supporting flanges, if any; (g) the shape of the ventral profile of antennae and wings; and (h) the relative development of postmedian and submarginal wing tubercles.

Duration of Pupal Stage: Nine to ten days, rarely eight.

B. KEY TO PUPAE

- Pupa without spines or spine-like tubercles more than twice as long as their basal width.
- Cephalic projections more than twice as long as broad; gold spots present.

Dryadula phaetusa, p. 148

- BB.** Cephalic projections no longer than broad; gold spots present or absent.
- C.** Cephalic projections absent except for a tubercle at each angle of front.
- D.** Abdomen with small subdorsal flanges; gold spots present.....*Dryas iulia*, p. 148
- DD.** Abdomen with subdorsal tubercles but no flanges; gold spots absent.
Heliconius doris, p. 150
- CC.** Cephalic projections palmate, distally minutely tuberculate or with short digitiform processes.
- E.** Subspiracular tubercles present; hooks of cremaster each with a single prong; gold spots present.....*Philaethria dido*, p. 148
- EE.** Subspiracular tubercles absent; hooks of cremaster two-pronged; gold spots absent.
- F.** Supralateral tubercle on 1 and 2 AB absent; dorsal flanges on 3 AB bidentate, projecting well above level of other flanges.....*Agraulis vanillae*, p. 147
- FF.** Supralateral tubercle on 2 AB always present. Paired dorsal flanges on 3 AB distally multi-tuberculate, scarcely projecting above level of other abdominal structures.....*Dione juno*, p. 147
- AA.** Pupa with true spines, some of which are more than four times as long as their basal width.
- G.** Antennal segments tuberculated but not spinous; 3 and 4 AB each with 2 pairs of long spines, directed obliquely forward and backward, respectively; no subdorsal abdominal flanges; gold spots absent.
- H.** Spines on 3 and 4 AB each with a small, basal posterior tubercle; supralateral tubercle present on 2 AB; small paired subdorsal tubercles present on 8 AB.
Heliconius isabella, p. 149
- HH.** No tubercles at bases of spines on 3 and 4 AB; no supralateral tubercle on 2 AB; no subdorsal tubercles on 8 AB.
Heliconius aliphera, p. 148
- GG.** Antennal segments distinctly spinous; 3 and 4 AB with enlarged dorsal flanges each surmounted by a spine; gold spots present.
- I.** Cephalic projections palmate, little longer than broad.
- J.** Dorsal spine on 4 AB at least as long as spine on 3 AB, directed straight outward; flanges on 3 and 4 AB not overlapping; no gold spot on 1 TH.
Heliconius wallacei, p. 149
- JJ.** Spine on 4 AB small, much shorter than that on 3 AB; flanges of 3 and 4 AB overlapping; gold spot present on 1 TH.
- K.** Spines on 3 AB at least as long as height of supporting flanges; height of wing at level of 3 AB greater than height of segment 5 AB.
Heliconius melpomene, p. 149

KK. Spines on 3 AB much shorter than height of supporting flanges; height of wing at level of 3 AB less than height of segment 5 AB.

Heliconius numata, p. 149

II. Cephalic projections more than twice as long as wide.

L. Spines on 3 and 4 AB much longer than height of supporting flanges; no supraspiracular gold spot on 3 TH.

Heliconius sara, p. 149

LL. Spines on 3 and 4 AB much shorter than height of supporting flanges; supraspiracular gold spot present on 3 TH.

M. Flanges on 3 and 4 AB closely apposed, but not overlapping.

Heliconius erato, p. 149

MM. Flanges on 3 and 4 AB overlapping.
Heliconius ricini, p. 150

C. DESCRIPTIONS OF THE SPECIES

1. *Agraulis vanillae* (Linnaeus)

(Text-fig. 14 A; Pl. XII, Figs. 71, 72)

Cephalic appendages about as broad as long, each with two large, rounded antero-inner projections and about seven to nine much smaller, unequal, external projections. Antennal segments marked only by low tubercles.

Paired dorsal tubercles on 1 TH present; 2 TH strongly carinate; post-median and submarginal tubercles of forewing represented by very low, rounded mounds. Ventral profile of wing almost rectangular, projecting far beyond that of abdomen at level of 3 and 4 AB.

Paired dorsal tubercles on 1-7 AB, that on 3 AB enlarged into a moderate, bidentate flange; tubercle on 4 AB very small; 5-7 AB also with flanges, progressively smaller than on 3 AB and all scarcely more than compound tubercles, although larger than tubercle on 4 AB. No supralateral tubercles on 1 and 2 AB; sublateral tubercles altogether lacking. Cremaster as broad as long, truncate distally, broadly quadrilateral and with a pair of tubercles dorsally; hooks 2-pronged, completely covering the distal surface.

General color brown.

Length about 26 mm.

2. *Dione juno* (Cramer)

(Pl. XIV, Figs. 82, 83)

Pupa similar to that of *Agraulis vanillae*, from which it differs as follows:

1. Cephalic appendage even shorter, although distinct; flattened dorso-ventrally; distally minutely tuberculate.

2. Postmedian and submarginal tubercles of forewings much stronger.

3. Paired dorsal tubercles of 3 AB enlarged into flanges which are larger, distally tuberculate and with the entire surface rugose and finely tuberculous, as is that of the entire dorsal area of the abdomen. 4 AB with a similar flange only slightly smaller, and 2 AB with an even smaller structure, carina-like. These three flanges run practically the full lengths of their segments, and appear fused basally to form an elongate single flange on each side of dorsal midline. Segments 5, 6 and 7 AB each with a progressively smaller flange, rugose and distally tuberculate.

4. A small, supralateral tubercle on 2 AB and, sometimes, on 1 AB; the usual tubercle, exceptionally large, on 3 and 4 AB.

5. Tip of cremaster more flattened; however, as in *A. vanillae*, the hooks are two-pronged.

3. *Dryadula phaetusa* (Linnaeus)

Pupa similar to that of *A. vanillae*, from which it differs as follows:

1. Cephalic appendages present, moderately long, not compressed, triangular in cross section; length about one-seventh or one-eighth total length of chrysalid.

2. Four pairs of dorsal gold-colored spots present, on 1 and 3 TH and on 1 and 2 AB, respectively.

3. Paired dorsal tuberculate flanges present on 3, 4 and 5 AB, but vestigial on 5 AB, and all are less well developed than in *A. vanillae*.

4. *Dryas iulia* (Fabricius)

(Pl. XII, Fig. 70; Pl. XIV, Figs. 84, 85)

Pupa similar to that of *A. vanillae*, from which it differs as follows:

1. Cephalic projections absent except for a compressed, blunt tubercle at each distal angle of the broadly truncate front.

2. Paired gold-colored spots present on 3 TH, 1 AB and 2 AB; first two pairs large; third pair small and longitudinally elongate.

3. Venation of wings obscure.

4. Postmedian tubercles on wing vestigial or absent; submarginal tubercles distinct.

5. Paired dorsal tubercles absent on 1 TH, but present and larger than in *A. vanillae* on 2 TH, 3 TH, 1 AB and 2 AB. Tubercle on 3 AB enlarged into a moderate flange, larger than in *A. vanillae*, but much smaller than is usual in *Heliconius* spp. (p. 149 ff.). Segments 4-7 AB all with smaller, subequal flanges, each larger, however, than in *A. vanillae*.

6. Cremaster as broad as long, the distal middle third produced into a triangle, about as in *Heliconius* spp.

7. Profile of wing projecting little beyond abdomen, gently rounded.

5. *Philaethria dido* (Clerck)

Very similar to *Dryas iulia* from which it differs as follows:

1. Cephalic projections distinct, palmate, though very small, very much as in *Agraulis vanillae*.

2. An extra tubercle, set in a gold-colored base, present on 2 AB, as in *H. melpomene*, *H. numata* and *H. ricini*.

3. Carina on 2 TH at wing base tuberculated.

4. Postmedian tubercles of wings well developed, sharp, almost as spine-like as in some *Heliconius*; 4, not 3, submarginal tubercles, of which the second is elongated into a small flange.

5. A sublateral compound tubercle present on 5, 6 and 7 AB, slightly below and behind spiracle. This has not been found in any other member of the group.

6. This pupa is the largest in the group, measuring at least 28 mm. in total length.

6. *Heliconius aliphera* (Godart)

(Pl. XIII, Figs. 78, 79; Pl. XIV, Figs. 88, 89).

This species and *H. isabella* are too distinct to compare directly, either with members of Group A (p. 146) or with the other species of *Heliconius* (Group C). In addition, they are much closer to each other than either is to another species. Of the two, *aliphera* appears the less specialized, principally because of the less exaggerated subdorsal spines.

Cephalic projection short, about equal to diameter of eye, smooth, without scallops or projections, moderately compressed laterally, divergent from the longitudinal axis and curved dorsally and posteriorly, distally tapering and pointed. Antennae without spines.

Gold-colored spots absent. 2 TH with a slight median crest in posterior half of segment only. Paired dorsal projections of three thoracic segments short blunt spines. Postmedian tubercles of forewing absent; the three submarginal tubercles well developed, each connected with margin by a stripe of black pigment. Veins marked more or less distinctly with brown or black. Ventral profile of antennae and wings projecting little ventrally.

Abdomen with paired dorsal projections as follows: 1 AB, a minute tubercle; 2 AB, a moderate tubercle; 3 AB, a long, thick, black-tipped spine, directed forward and anteriorly hooked at tip; 4 AB, a similar spine, also anteriorly hooked, but directed backward; 5, 6 and 7 AB each with a large, trifid tubercle, the anterior cusp in each case being longer and sharper. Supralateral tubercles on 3 and 4 AB very small. Cremaster from above almost perfectly triangu-

lar in cross section; tip compressed laterally and with a ventral extension.

Color: greenish to greenish-white. Veins marked by dark pigment.

Length: About 18 mm., the smallest pupa in this study.

7. *Heliconius isabella* (Cramer)

(Pl. XIII, Figs. 80, 81)

Differs from *H. aliphera* as follows:

1. Spines and tubercles are in the same positions as in *aliphera*, but all are relatively longer. This tendency shows well in the paired dorsal projections on 7 AB, in which the bifid tubercle of *aliphera* is represented by a bifid spine, of which the anterior portion is three times longer than the blunt posterior part, slender, and bent forward in a sigmoid curve. Each of the giant spines on 3 and 4 AB has a small posterior projection at the base. They are unpigmented except, occasionally, at the tips. Spine lengths variable.

2. There are two additional tubercles, as follows: First, there is a supralateral tubercle on 2 AB, as well as supralateral spinous tubercles in the usual position on 3 and 4 AB. Second, an additional paired dorsal tubercle, small and simple, not found in *aliphera*, occurs on 8 AB.

3. Length greater, about 21, not 18, mm.

8. *Heliconius melpomene* (Linnaeus)

(Text-figs. 14B, C; Pl. XIII, Figs. 76, 77)

With the characteristics of Group C (p. 146). Antennae with spines commencing at base; cephalic projections about as broad as long, palmate, with five short digital processes and a single larger, thick, ventral tubercle. Five pairs of gold spots present, one each on 1 and 3 TH and on 1 and 2 AB, plus a small spot on 3 TH above and behind spiracle. Subdorsal flanges on 3 and 4 AB moderately large, partially fused and overlapping; spine of flange on 3 AB more than half height of flange, directed obliquely forward; corresponding spine on 4 AB very short, directed almost straight outward; spine on 5 AB longer than that of 4 AB, sometimes longer even than that of 3 AB; spines of 6 and 7 AB longer than spine of 4 AB, subequal.

Ventral profile of antennae and wings moderately projecting ventrally. Postmedial and submarginal wing tubercles moderately developed.

General color brown.

Length about 27 mm.

9. *Heliconius numata* (Cramer)

(Pl. XV, Figs. 90, 91)

Very similar to *H. melpomene*, from which

it differs as follows: 1. Subdorsal spines on 3 AB shorter and directed more laterally. 2. Spines on 6 and 7 AB slightly shorter, directed more anteriorly. 3. Postmedian tubercles on wings less well developed. 4. Ventral profile of antennae and wings projecting less ventrally.

10. *Heliconius wallacei* Reakirt

(Pl. XV, Figs. 92, 93)

Differs from both *H. melpomene* and *numata* as follows: 1. No gold spot on 1 TH; *wallacei* is the only species in the subgroup lacking a gold spot in this position. 2. Flanges on 3 and 4 AB narrower, not partially fused, their spines very long, much longer than height of larger flange. 3. Spine of 4 AB directed strongly outward. 4. Spines of 5, 6 and 7 AB about as long as in *melpomene* but arising from small flanges. 5. Ventral profile more strongly arched; postmedian and submarginal tubercles very distinct. 6. Veins strongly pigmented.

11. *Heliconius sara* (Fabricius)

(Pl. XII, Figs. 74, 75)

Intermediate between *H. melpomene*, *numata* and *wallacei*, above, and *erato* and *ricini*, which follow. It shares with the first three the long subdorsal spines on the abdomen, which are very similar to those of *wallacei*. Unlike *wallacei*, a gold spot is present on 1 TH, although the supra-spiracular gold spot on 3 TH is absent and the spines of 5, 6 and 7 AB arise almost directly from the abdominal surface instead of being elevated on small flanges. Flanges of 3 and 4 AB about as in *wallacei*, unfused and even somewhat separated. The ventral profile of antennae and wings projects little and is only slightly arched.

H. sara differs from all the three preceding species in the subgroup, and resembles *erato* and *ricini* in having the first few segments of the antennae non-spinous, almost smooth, although small spinules are present beginning at about the 5th segment, and in having the cephalic projections prolonged to more than twice their breadth and lacking a ventral tubercle. The projections are about as long as the longest abdominal spines; internally they have three broad scallops, externally about 4 to 7 or more small tubercles or spinules, not symmetrically placed or totalling the same on the two projections.

General color light brown with well marked dark pigment over veins.

Length about 25 mm.

12. *Heliconius erato* (Linnaeus)

(Pl. XV, Figs. 94, 95)

Along with *H. ricini*, below, *erato* differs from

the four preceding members of the subgroup in having all the abdominal spines short.

In *erato*, the cephalic projections are produced as in *sara*, but are relatively longer, extending up to five times their maximum breadth. Two or three broad, widely separated scallops on inner margins; external tuberculation coarser than in *sara*. Gold spot present on 1 TH, and supraspiracular gold spot on 3 TH. Flanges on 3 and 4 AB closely apposed but not fused. A minute flange present under spine base on 5 AB; flange on 6 AB well developed, almost as large as that on 4 AB; a smaller but distinct flange also on 7 AB. Ventral profile of antennae and wings moderately arched and projecting; post-medial tubercles well developed, submarginal tubercles moderately.

Length about 27 mm.

13. *Heliconius ricini* (Linnaeus)

(Pl. XV, Figs. 96, 97)

Pupa very similar to that of *sara*, from which it differs chiefly as follows: 1. Antennae with fewer spines; this character is of course dependent on the presence of the fewer antennal segments characteristic of this species. Antennal spines all shorter than in other species with spinous antennae. 2. Postmedian wing tubercles feebly developed; submarginal tubercles strongly. 3. Flanges on 3 AB larger, their posterior edges strongly overlapping flange on 4 AB. 4. Flange on 6 AB, though still larger than those on 5 and 7 AB, is smaller than in *erato*.

Color: Medium brown; veins not strongly pigmented.

Length: About 26 mm.

14. *Heliconius doris* (Linneaus)

(Pl. XIV, Figs. 86, 87; Text-figs. 5D, 6N, 7N)

The pupa of *H. doris* is the most aberrant of the Trinidad heliconiines, and has more in common with the species in Group A (p. 146) than with other members of the genus *Heliconius*.

Pupa almost smooth, without spines or abdominal flanges; all tubercles feebly developed except on the antennae, where they are pointed but too low and thick to be designated as spines. Cephalic appendages represented only by a projection of the external angle at each side of the head. Gold-colored spots absent. Paired, low, subdorsal tubercles present on 1-3 TH and 1-7 AB. Supralateral tubercles on 3 and 4 AB feebly developed. Two low, postmedian tubercles distinct on wing; submarginal tubercles indistinct, confluent; ventral profile of antenna and wings little projecting. Cremaster triangular and flattened, its hooks with a single barb, much as in other *Heliconius*.

Although spines are absent from 10 sibling pupae from Trinidad, they are present on the abdomen in 5 of 18 specimens from Surinam. The spines take the form of thick projections, scarcely tapering, on 3, 4, 5 and 6 AB; when unbroken, they are apparently of similar length, but vary from one individual to the next. Whether these Surinam pupae were siblings is unknown. In all other respects the five, representing both sexes, were unremarkable, and not to be distinguished either from the remaining Surinam examples or from the Trinidad specimens.

VI. DISCUSSION

This study of immature stages makes it apparent that a number of previous ideas on relationships within the Heliconiinae are erroneous. It would, however, be premature to present a systematic revision at this time, or to draw conclusions on the phylogeny of the subfamily. Instead, a few observations will be made concerning similarities among groups of species.

Never has the necessary use of a linear order of species seemed more unrealistic, since it is clear that the heliconiines have evolved explosively in a number of directions. It is equally apparent that the developmental stages in various species have evolved at different rates and not necessarily in parallel directions. Since mimicry between imagos is certainly a factor in some cases, it is to be expected that the larvae of two mimics do not necessarily also appear similar to each other. Aside from the complications of mimicry, however, further complexities arise, in which the larvae resemble larvae of one group of similar species, while the pupae show affinities to another; it does not seem in these latter cases that mimicry is evolved.

One clearly apparent result of this study is that the old division of the genus *Heliconius*, in the original narrow sense, into two parts, is artificial. The division was proposed by Stichel and Riffarth (1905) and accepted by a number of subsequent authors. According to this concept, groups of similarly colored species, on each side of a dividing line, mimic each other. The division was based on details of the genitalia and on the extent of the area covered by specialized scales on the wings. For example, *H. melpomene* and *H. erato*, two well-known red and black butterflies, supposedly are widely separated in the genus and resemble each other only through mimicry. The present study of their growth stages seems to us clearly to indicate a close relationship. The falsity of the Stichel & Riffarth division forms one more bit of evidence for the ever more obvious necessity of basing systems

of classification on numerous aspects in the life of any group of animals.

Based only on similarities in external characters of the immature stages, the following groups of species may be made:

Eggs. *Dione juno* and *Heliconius doris* alone lay eggs in large groups in a single layer. In *H. ricini*, *H. sara* and *H. wallacei*, the eggs are laid in clusters. In all other species the eggs are laid singly.

First Instar. (For a discussion of the chaetotaxy, see Fleming, 1960, p. 91).

Color: In *Agraulis vanillae*, *Dryadula phaetusa*, *Dryas iulia* and *Philaethria dido*, white spots and dark bands occur on the same segments and are a prominent feature of the coloration throughout the instar; in *H. isabella*, *H. melpomene* and *H. erato*, the dark bands appear for only a few hours shortly after the middle of the instar; no dark bands are present in any of the other species during the first instar. In the first group of species, the bands and spots are traceable at least through the second instar and sometimes longer; in *D. iulia*, they are traceable throughout all of the larval instars.

In *D. juno* and *H. ricini* the larvae have black heads on hatching; in no other species does black develop on head before the second instar.

Older larvae. Scoli: In *D. juno*, all scoli are very short; in *H. doris* all except those on the second thoracic segment are short. The longest scoli are found in *H. aliphera* and *P. dido*, which are, respectively, the smallest and the largest species in the group; thus, development of scoli is not dependent merely on the principle of heterogonic growth. Species with notably elongate scoli on the second, or second and third, thoracic segments are *H. sara*, *H. wallacei* and *H. doris*. In company with *D. juno* and *H. doris*, *H. sara* has the head scoli remarkably short. *D. juno* alone has a scolus on the first thoracic segment, as do some non-heliconiines. *H. doris* is the only species in the group lacking a scolus on the anal segment.

Color: In coloration, the bodies of *D. juno*, *D. phaetusa*, *H. sara* and *H. wallacei* are practically without patterns and very dark. *A. vanillae* is characterized by narrow longitudinal stripes on the dorsal half of the body. In *H. isabella* and *H. aliphera* the markings are also chiefly longitudinal, but are in the form of very broad, boldly contrasting stripes. In *D. iulia* alone is an obviously disruptive pattern, coupled with cryptic coloration, well developed; it is effected by a complex combination of bands, stripes and spots. It is certain, however, that

under field conditions some of the other species also appear inconspicuous. Finally, *H. melpomene*, *H. numata* and *H. erato* have very similar patterns of black spots on a white background; in *H. ricini* it is similar, but the ground is yellow. It appears from the literature that *H. phyllis* and *H. charithonius* also belong to this spot-patterned group (Edwards, 1868-1897; Bourquin, 1955).

During development, it is often possible to trace similar pigment patterns in a number of species, through the tendency of the dark pigment to develop in three to five vertical bands on each segment, at least partly in accordance with the positions of the annules. Even the spots of *H. melpomene* and those similarly pigmented can be homologized with parts of the bands visible in, for example, *D. iulia* and *P. dido*. Again, the development of the longitudinal bands in *A. vanillae* may be clearly traced during the middle instars to similar origins.

In any phylogenetic survey of this group, the occurrence and development of color patterns will assuredly prove a useful tool; it will compare, perhaps, in value with the well-established use of larval pigment patterns in helping to trace affinities in many families of fishes.

Pupae. The pupae of the various species fall more readily into homogeneous groups than do the larvae. The pupae of *D. juno* and *A. vanillae* resemble each other more closely than they do those of other species, while *D. phaetusa*, *D. iulia* and *P. dido* also resemble *A. vanillae* to varying extents. *D. phaetusa* is equipped with well-developed cephalic appendages which, in that character, make it resemble *H. sara*, *H. erato* and *H. ricini*.

All of the species referred, in the present classification, to *Heliconius* are spinous and equipped with enlarged flanges, except *H. doris*. The latter, although sometimes furnished with atypical spines, is in other respects altogether aberrant.

H. isabella and *H. aliphera* resemble each other very closely, and show little similarity to any of the others in the group.

H. melpomene, *H. numata* and *H. wallacei* form an exceedingly similar group, as do *H. erato*, *H. ricini* and *H. sara*.

Imagos (Pl. XVI). For comparison there is listed below the general coloration of species in the study which form similar pairs or groups. These species include several of the most famous examples given in support of the concept of Müllerian mimicry.

1. *D. iulia*, *D. juno*, *H. aliphera*. Orange with a few narrow black markings. *A. vanillae* is less similar, being orange with black spots.

2. *A. vanillae*, *D. juno*. Under surfaces of wings spotted with silver as in the Argynninae.

3. *H. numata* and *H. isabella*. Primarily brownish-orange, marked with yellow and black.

4. *H. melpomene* and *H. erato*. Black with red forewing bands.

5. *H. sara*, *H. wallacei* and *H. doris*. Black, with yellow spots on forewings and, on hind-wings, blue ray-like markings or blue iridescence.

To conclude, when eggs, larvae and pupae are all considered, the following groupings are apparent:

1. *A. vanillae*, *D. phaetusa*, *D. iulia* and *P. dido* appear to form a very loosely knit group having more in common with other nymphalid groups, notably the Argynninae, than do members of the genus *Heliconius*, excluding *H. doris*. Within the group, *P. dido* seems most similar to *D. iulia* and *D. phaetusa* to *A. vanillae*.

2. *D. juno* and *H. doris* both seem to be aberrant from the rest of the group. Their few similarities to each other are probably not significant.

3. *H. isabella* and *H. aliphera* are closely similar to each other and do not greatly resemble any of the other species under consideration, although they are clearly members of the subfamily. In coloration, their imagos are very different from each other.

4. *H. melpomene* and *H. numata* are more closely similar to each other than to any other species, but also have much in common with the larvae of *H. erato* and *H. ricini*, and with the pupa of *H. wallacei*. The imagos show no similarities in color.

5. *H. sara* and *H. wallacei* have similar eggs and larvae, but their pupae do not greatly resemble each other, that of *sara* being close to those of *H. ricini* and *H. erato*, while that of *wallacei* is very similar to those of *H. melpomene* and *H. numata*. In color, the imagos of *H. sara* and *H. wallacei* are very similar.

It is hoped and expected that future studies, particularly on the ethology of all stages, will shed the next types of illumination needed for clarifying the evolution of this outstanding group of butterflies.

VII. SUMMARY

External characteristics of the growth stages are described and compared in 14 species of Heliconiinae from Trinidad, West Indies. In the egg stage, size, color and numbers of ridges have diagnostic value. The colors and patterns of living larvae form the most useful taxonomic

characters in this phase, and also seem to be of importance in indicating relationships. In preserved larvae, the relative lengths of the scoli and the shape of the head are of practical use. Diagnostic characters of the highly varied pupae include length and form of cephalic projections, the development of tubercles and spines and the occurrence of gold-colored spots. The life cycle, from egg to eclosion, usually requires about four weeks.

It seems apparent that the heliconiines developed radially and that the developmental stages within species often evolved at different rates. While the needed systematic revision of the subfamily cannot be based solely on present knowledge, it is expected that this contribution will prove useful in future studies of other aspects of the group's biology, including questions of phylogeny.

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EXPLANATION OF THE PLATES

PLATE I

Eggs of heliconiine butterflies.

FIG. 1. *Dione juno*, cluster.

FIG. 2. *Heliconius ricini*, cluster.

FIG. 3. *H. sara*, cluster (laid atypically on tendril, rather than as usual on tip of terminal leaf bud).

FIG. 4. *Agraulis vanillae*.

FIG. 5. *H. ricini*.

FIG. 6. *H. melpomene*, lateral view.

FIG. 7. Same, dorsal view.

FIG. 8. *Dryas iulia*, lateral view.

FIG. 9. Same, dorsal view.

FIG. 10. *H. isabella*, lateral view.

FIG. 11. Same, dorsal view.

PLATE II

First instars of heliconiine larvae.

FIG. 12. *Dione juno*, lateral view.

FIG. 13. Same, dorsal view.

FIG. 14. *Dryas iulia*, lateral view.

FIG. 15. Same, dorsal view.

FIG. 16. *Agraulis vanillae*, lateral view.

FIG. 17. Same, dorsal view.

Diameter of wire support in all figures: 2 mm.

PLATE III

First instars of heliconiine larvae (contd.).

FIG. 18. *H. isabella*, lateral view.

FIG. 19. Same, dorsal view.

FIG. 20. *H. aliphera*, lateral view.

FIG. 21. *H. sara*, lateral view.

FIG. 22. *H. ricini*, lateral view.

FIG. 23. Same, dorsal view.

FIG. 24. *H. melpomene*, lateral view.

FIG. 25. *H. erato*, lateral view.

Diameter of wire support: 2 mm.

PLATE IV

Fifth instars of heliconiine larvae, lateral views.

FIG. 26. *Agraulis vanillae* (a pale individual; cf. Text-fig. 11A, B).

FIG. 27. *Dryas iulia*.

FIG. 28. *Philaethria dido*.

FIG. 29. *Heliconius isabella*. (Photographed on Stick).

FIG. 30. *H. aliphera*.

Diameter of wire support: 2 mm.

PLATE V

Fifth instars of heliconiine larvae, lateral views (contd.).

FIG. 31. *Heliconius melpomene*.

FIG. 32. *H. erato*.

FIG. 33. *H. ricini*.

FIG. 34. *H. sara*.

Diameter of wire support: 2 mm.

PLATE VI

Growth stages of *Dryas iulia*, lateral views.

FIG. 35. First instar (same as Pl. II, Fig. 14).

FIG. 36. Second instar.

FIG. 37. Third instar.

FIG. 38. Fourth instar.

FIG. 39. Fifth instar (same as Pl. IV, Fig. 27).

Diameter of wire support: 2 mm.

PLATE VII

Growth stages of *Heliconius ricini*, lateral views.

FIG. 40. First instar (same as Pl. III, Fig. 22).

FIG. 41. Second instar.

FIG. 42. Third instar.

FIG. 43. Fourth instar.

FIG. 44. Fifth instar (same as Pl. V, Fig. 33).

Diameter of wire support: 2 mm.

PLATE VIII

Growth stages and color variation in heliconiine larvae.

FIG. 45. *H. aliphera*, lateral view, second instar.

FIG. 46. Same, third instar.

FIG. 47. Same, fourth instar, dark individual.

FIG. 48. Same, light individual.

FIG. 49. *H. isabella*, lateral view, second instar.

FIG. 50. Same, fourth instar.

FIG. 51. *H. aliphera*, dorsal view, fourth instar, dark individual (as in Fig. 47).

FIG. 52. Same, pale individual (as in Fig. 48).

Diameter of wire support: 2 mm.

PLATE IX

Fifth instars of heliconiine larvae, dorsal views.

FIG. 53. *Agraulis vanillae*.

FIG. 54. *Dryas iulia*.

FIG. 55. *Philaethria dido*.

FIG. 56. *Heliconius aliphera*.

FIG. 57. *H. isabella*.

FIG. 58. *H. melpomene*.

FIG. 59. *H. erato*.

FIG. 60. *H. ricini*.

FIG. 61. *H. sara*.

Diameter of wire support: 2 mm.

PLATE X

Fifth instars of heliconiine larvae, frontal views of heads.

FIG. 62. *Agraulis vanillae*.

FIG. 63. *Dryas iulia*.

FIG. 64. *Heliconius isabella*.

FIG. 65. *H. aliphera*.

PLATE XI

Fifth instars of heliconiine larvae, frontal views of heads (contd.).

FIG. 66. *Heliconius melpomene*.

FIG. 67. *H. erato*.

FIG. 68. *H. ricini*.

FIG. 69. *H. sara*.

PLATE XII

Heliconiine pupae.

FIG. 70. *Dryas iulia*, lateral view.

FIG. 71. *Agraulis vanillae*, dorsal view.

FIG. 72. Same, lateral view.

FIG. 73. Same, ventral view.

FIG. 74. *Heliconius sara*, lateral view.

FIG. 75. Same, dorsal view.

PLATE XIII

Heliconiine pupae (contd.).

FIG. 76. *Heliconius melpomene*, lateral view.

FIG. 77. Same, dorsal view.

FIG. 78. *H. aliphera*, lateral view.

FIG. 79. Same, dorsal view.

FIG. 80. *H. isabella*, lateral view.

FIG. 81. Same, dorsal view.

PLATE XIV

Heliconiine pupae (contd.).

FIG. 82. *Dione juno*, lateral view.

FIG. 83. Same, dorsal view.

FIG. 84. *Dryas iulia*, lateral view.

FIG. 85. Same, dorsal view.

FIG. 86. *Heliconius doris*, lateral view.

FIG. 87. Same, dorsal view.

FIG. 88. *H. aliphera*, lateral view.

FIG. 89. Same dorsal view.

PLATE XV

Heliconiine pupae (contd.).

FIG. 90. *Heliconius numata*, lateral view.

FIG. 91. Same, dorsal view.

FIG. 92. *H. wallacei*, lateral view.

FIG. 93. Same, dorsal view.

FIG. 94. *H. erato*, lateral view.

FIG. 95. Same, dorsal view.

FIG. 96. *H. ricini*, lateral view.

FIG. 97. Same, dorsal view.

PLATE XVI

Imagos of Heliconiinae from Trinidad. All the species are illustrated in color in Seitz: Macrolepidoptera of the World; the American Rhopalocera, Vol. V, Plates (1924). For general remarks on imaginal color, see p. 151 of the present paper.

FIG. 98. *Dione juno*.

FIG. 99. *Agraulis vanillae*.

FIG. 100. *Dryadula phaetusa*.

FIG. 101. *Dryas iulia*.

FIG. 102. *Philaethria dido*.

FIG. 103. *Heliconius isabella*.

FIG. 104. *Heliconius aliphera*.

FIG. 105. *Heliconius melpomene*.

FIG. 106. *Heliconius numata*.

FIG. 107. *Heliconius erato*.

FIG. 108. *Heliconius ricini*.

FIG. 109. *Heliconius sara*.

FIG. 110. *Heliconius wallacei*.

FIG. 111. *Heliconius doris*.

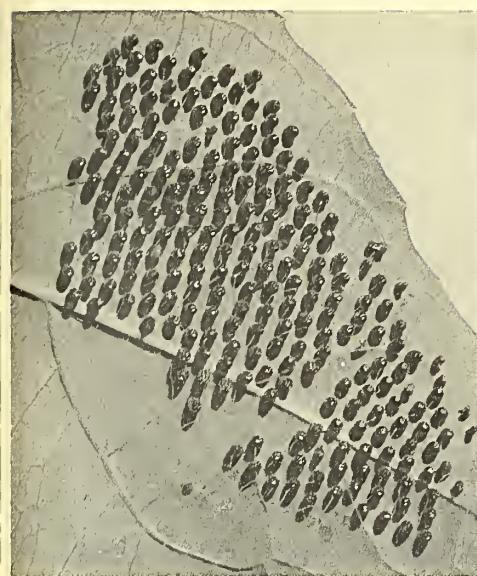


FIG. 1



FIG. 2



FIG. 3



FIG. 4



FIG. 5



FIG. 6

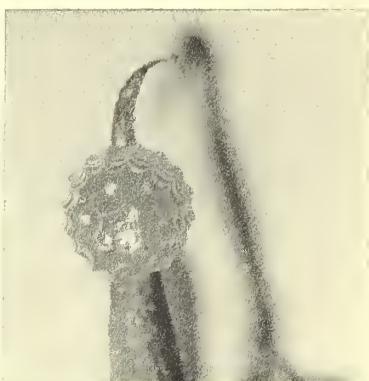


FIG. 7

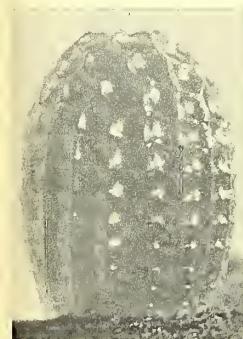


FIG. 8



FIG. 9



FIG. 10



FIG. 11

A COMPARISON OF EGGS, LARVAE AND PUPAE IN FOURTEEN SPECIES
OF HELICONIINE BUTTERFLIES FROM TRINIDAD, W.I.



FIG. 12



FIG. 13



FIG. 14

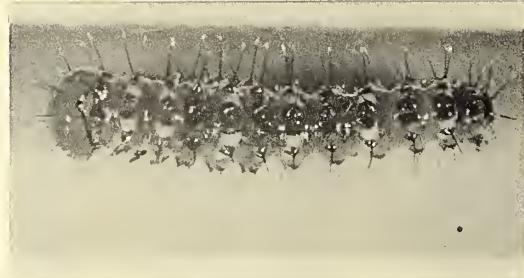


FIG. 15

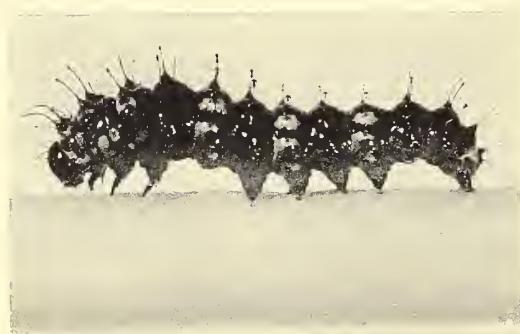


FIG. 16



FIG. 17

A COMPARISON OF EGGS, LARVAE AND PUPAE IN FOURTEEN SPECIES
OF HELICONIINE BUTTERFLIES FROM TRINIDAD, W.I.

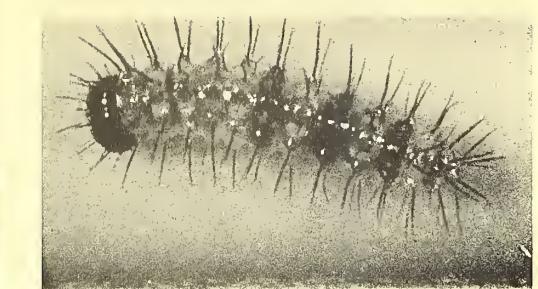


FIG. 19

FIG. 18

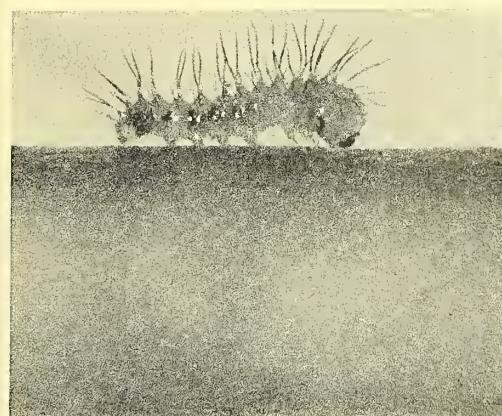


FIG. 21

FIG. 20

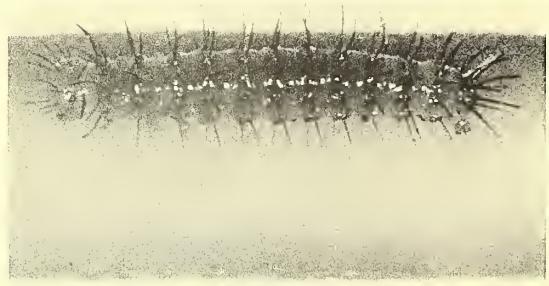
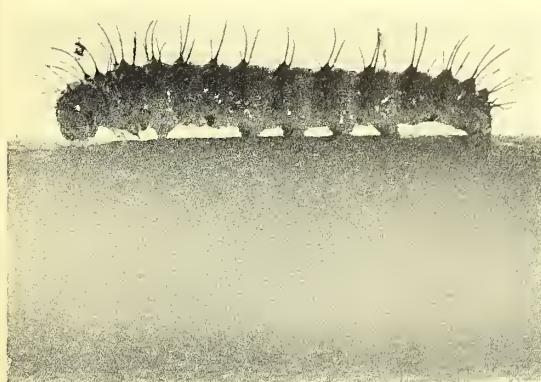


FIG. 23

FIG. 22

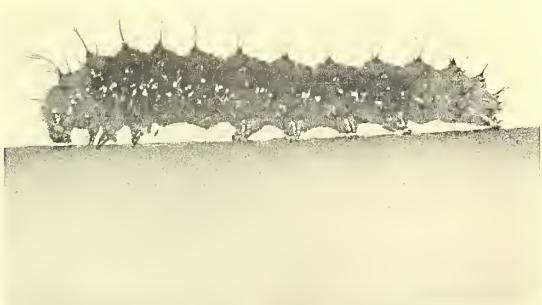


FIG. 25

FIG. 24

A COMPARISON OF EGGS, LARVAE AND PUPAE IN FOURTEEN SPECIES
OF HELICONIINE BUTTERFLIES FROM TRINIDAD, W.I.

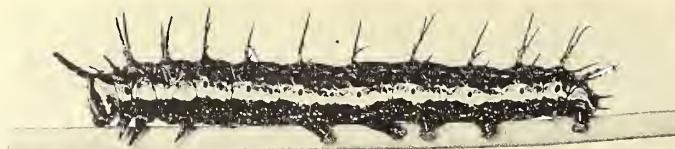


FIG. 26



FIG. 27

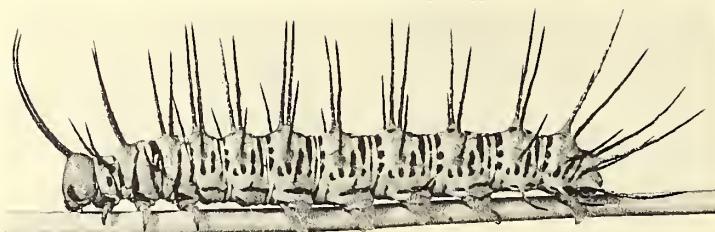


FIG. 28



FIG. 29



FIG. 30

A COMPARISON OF EGGS, LARVAE AND PUPAE IN FOURTEEN SPECIES
OF HELICONIINE BUTTERFLIES FROM TRINIDAD, W.I.

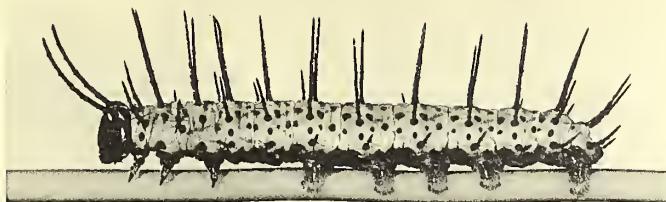


FIG. 31

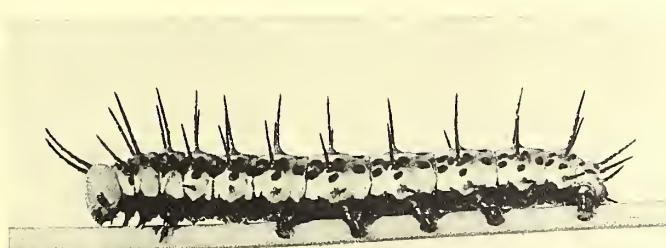


FIG. 32

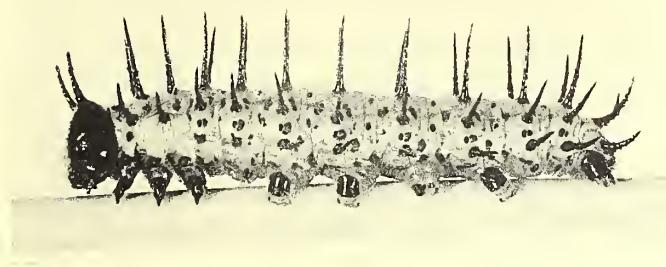


FIG. 33

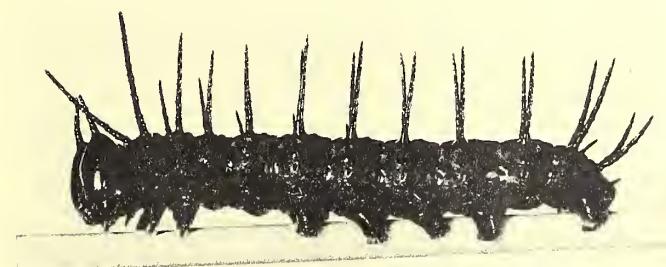


FIG. 34

A COMPARISON OF EGGS, LARVAE AND PUPAE IN FOURTEEN SPECIES
OF HELICONIINE BUTTERFLIES FROM TRINIDAD, W.I.



FIG. 35

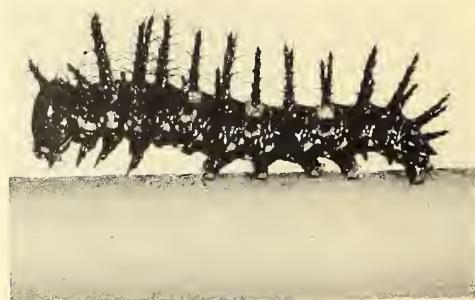


FIG. 36

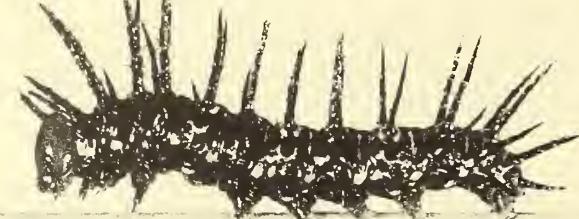


FIG. 37



FIG. 38

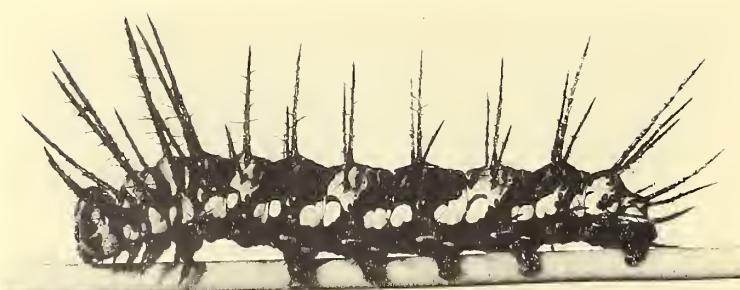


FIG. 39

A COMPARISON OF EGGS, LARVAE AND PUPAE IN FOURTEEN SPECIES
OF HELICONIINE BUTTERFLIES FROM TRINIDAD, W.I.

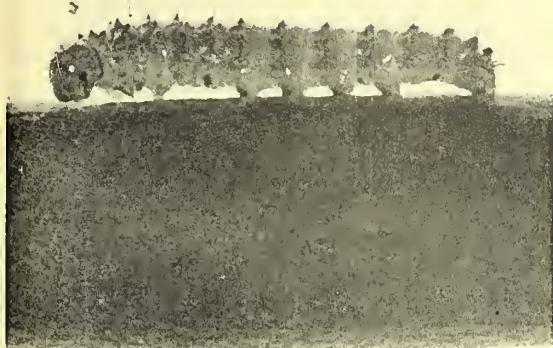


FIG. 40



FIG. 41

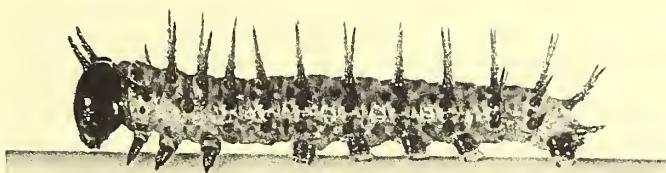


FIG. 42

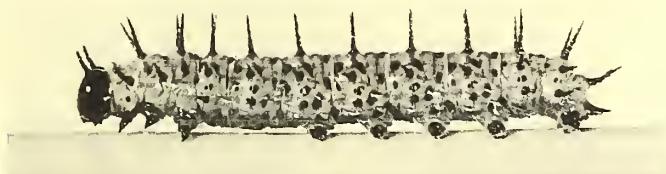


FIG. 43



FIG. 44

A COMPARISON OF EGGS, LARVAE AND PUPAE IN FOURTEEN SPECIES
OF HELICONIINE BUTTERFLIES FROM TRINIDAD, W.I.

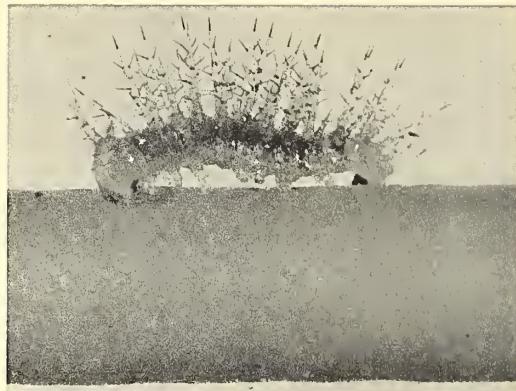


FIG. 45

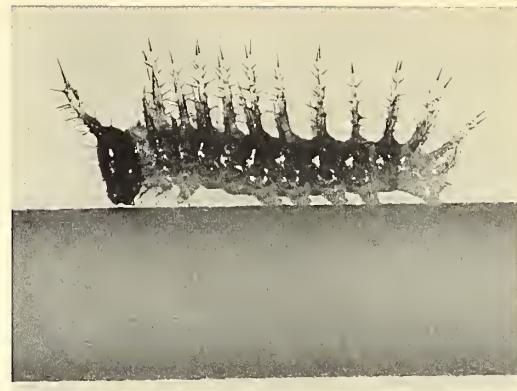


FIG. 49

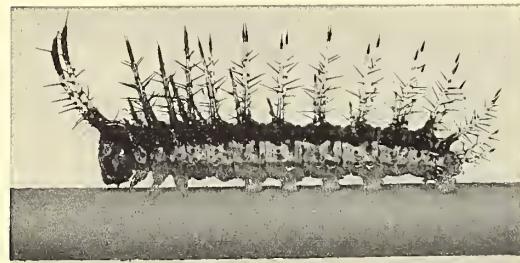


FIG. 46

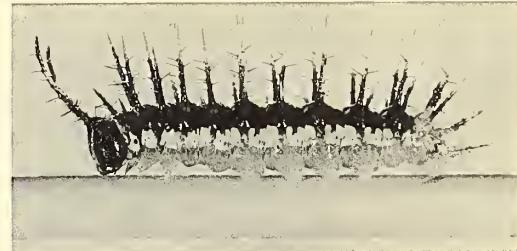


FIG. 50

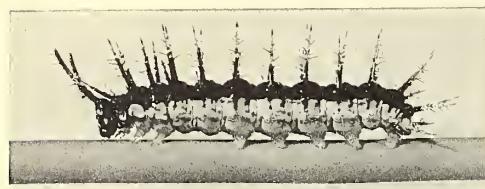


FIG. 47

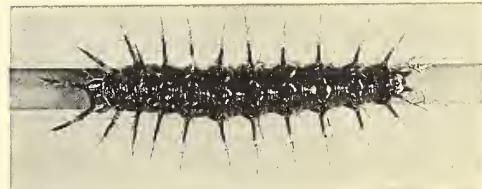


FIG. 51

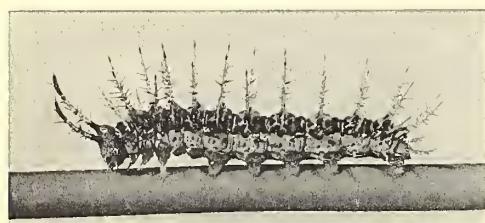


FIG. 48

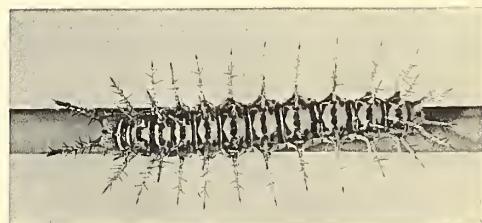


FIG. 52

A COMPARISON OF EGGS, LARVAE AND PUPAE IN FOURTEEN SPECIES
OF HELICONIINE BUTTERFLIES FROM TRINIDAD, W.I.

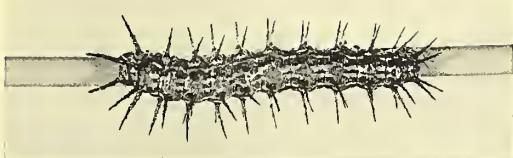


FIG. 53

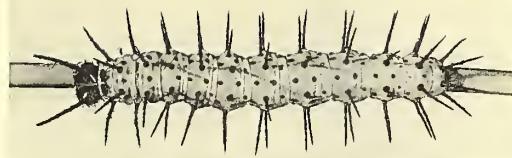


FIG. 58



FIG. 54

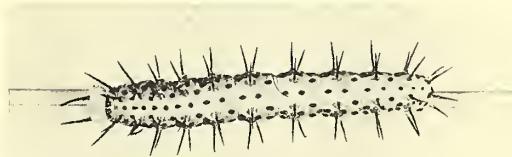


FIG. 59

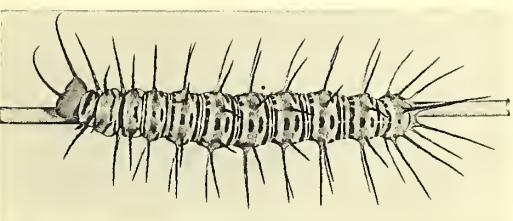


FIG. 55

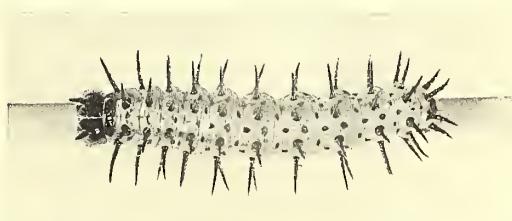


FIG. 60

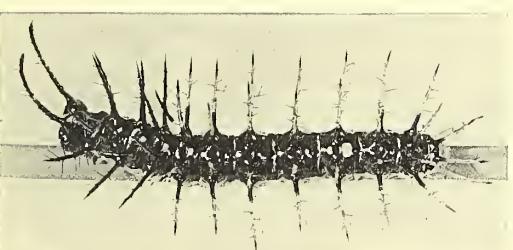


FIG. 56



FIG. 61

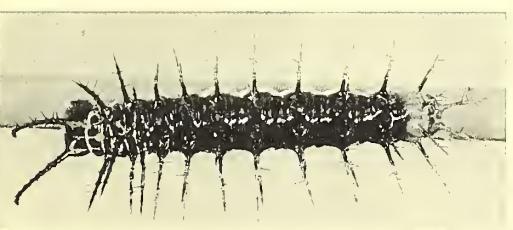


FIG. 57

A COMPARISON OF EGGS, LARVAE AND PUPAE IN FOURTEEN SPECIES
OF HELICONIINE BUTTERFLIES FROM TRINIDAD, W.I.



FIG. 62



FIG. 63



FIG. 64



FIG. 65

A COMPARISON OF EGGS, LARVAE AND PUPAE IN FOURTEEN SPECIES
OF HELICONIINE BUTTERFLIES FROM TRINIDAD, W.I.



FIG. 66



FIG. 67



FIG. 68

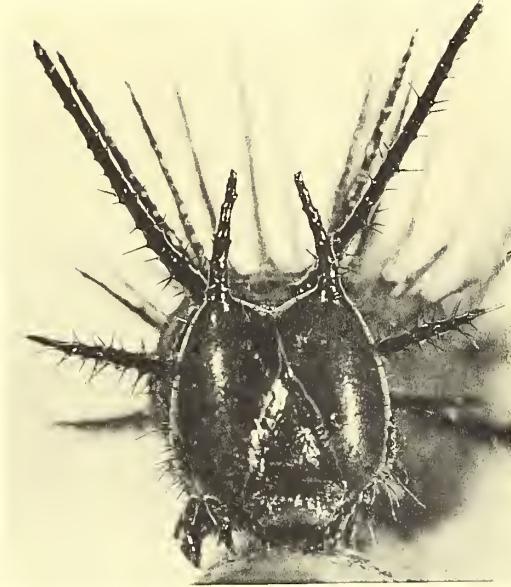


FIG. 69

A COMPARISON OF EGGS, LARVAE AND PUPAE IN FOURTEEN SPECIES
OF HELICONIINE BUTTERFLIES FROM TRINIDAD, W.I.



FIG. 70



FIG. 72



FIG. 74



FIG. 71



FIG. 73

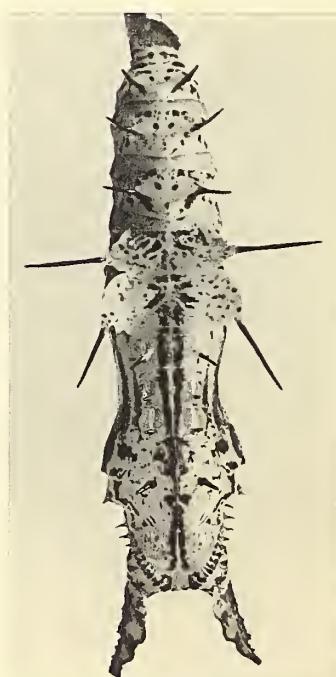


FIG. 75

A COMPARISON OF EGGS, LARVAE AND PUPAE IN FOURTEEN SPECIES
OF HELICONIINE BUTTERFLIES FROM TRINIDAD, W.I.

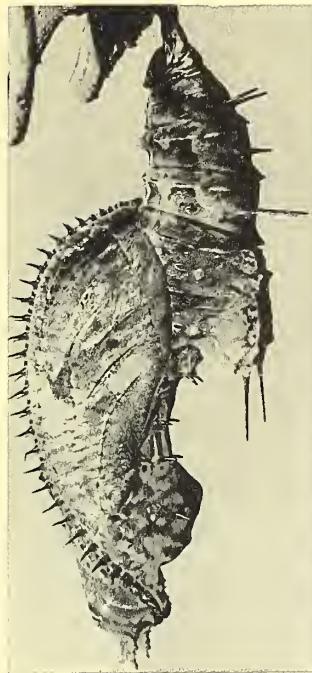


FIG. 76



FIG. 78



FIG. 80

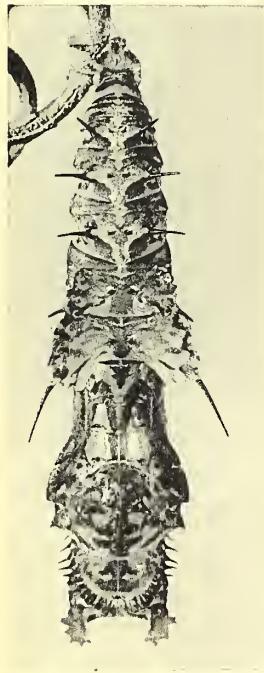


FIG. 77



FIG. 79

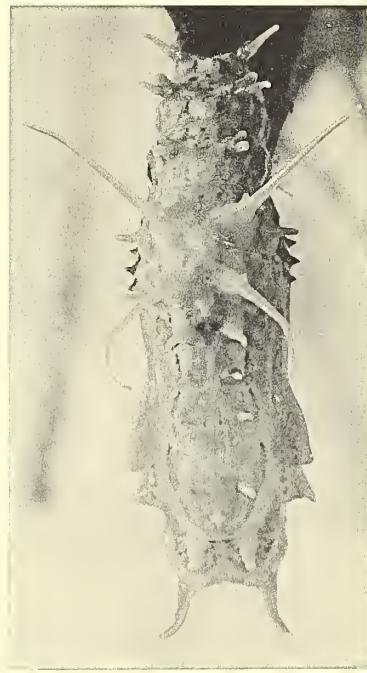


FIG. 81

A COMPARISON OF EGGS, LARVAE AND PUPAE IN FOURTEEN SPECIES
OF HELICONIINE BUTTERFLIES FROM TRINIDAD, W.I.

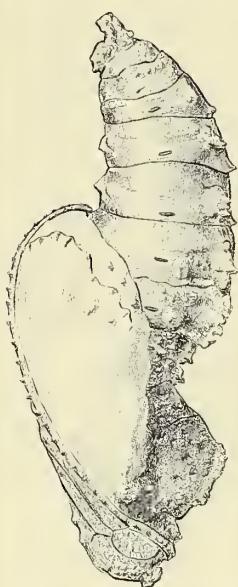


FIG. 82

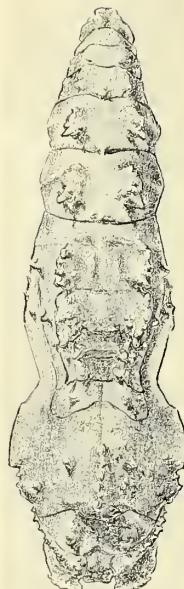


FIG. 83

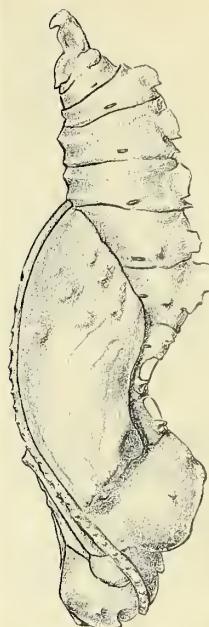


FIG. 84

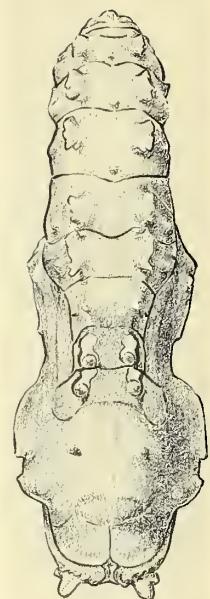


FIG. 85

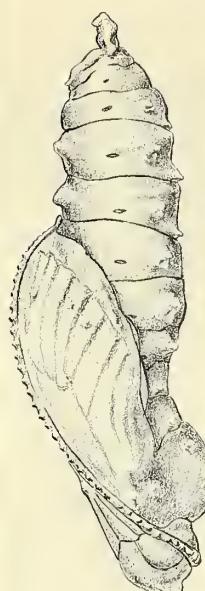


FIG. 86

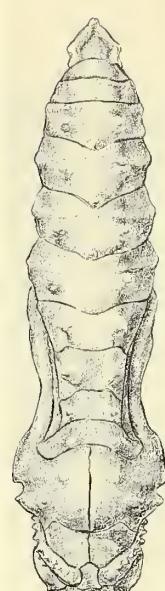


FIG. 87

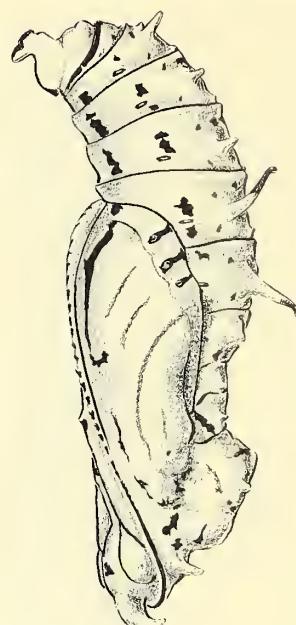


FIG. 88

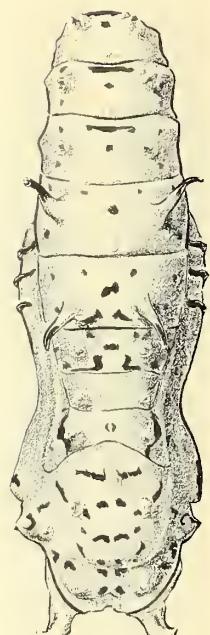


FIG. 89

A COMPARISON OF EGGS, LARVAE AND PUPAE IN FOURTEEN SPECIES
OF HELICONIINE BUTTERFLIES FROM TRINIDAD, W.I.

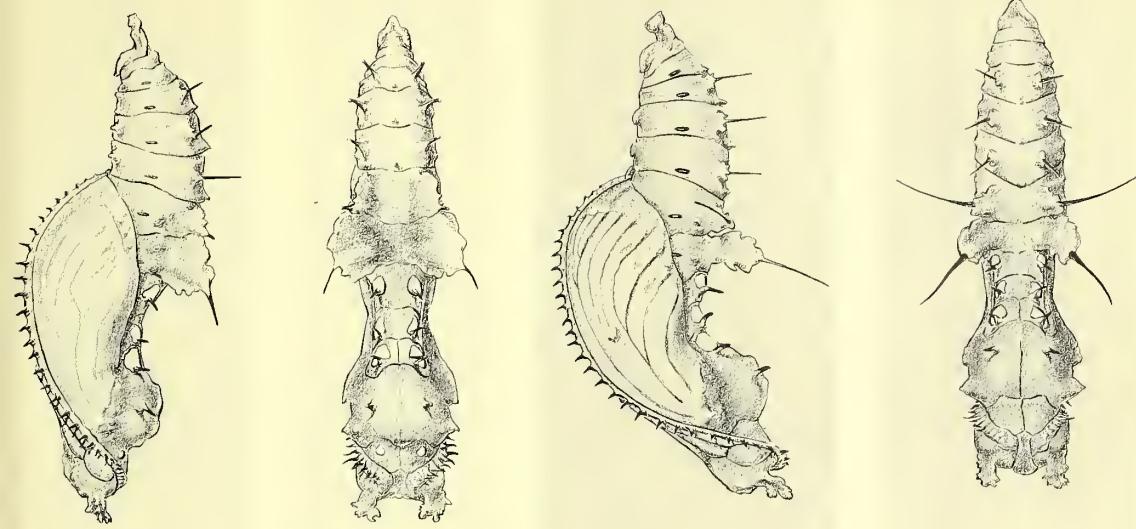


FIG. 90

FIG. 91

FIG. 92

FIG. 93

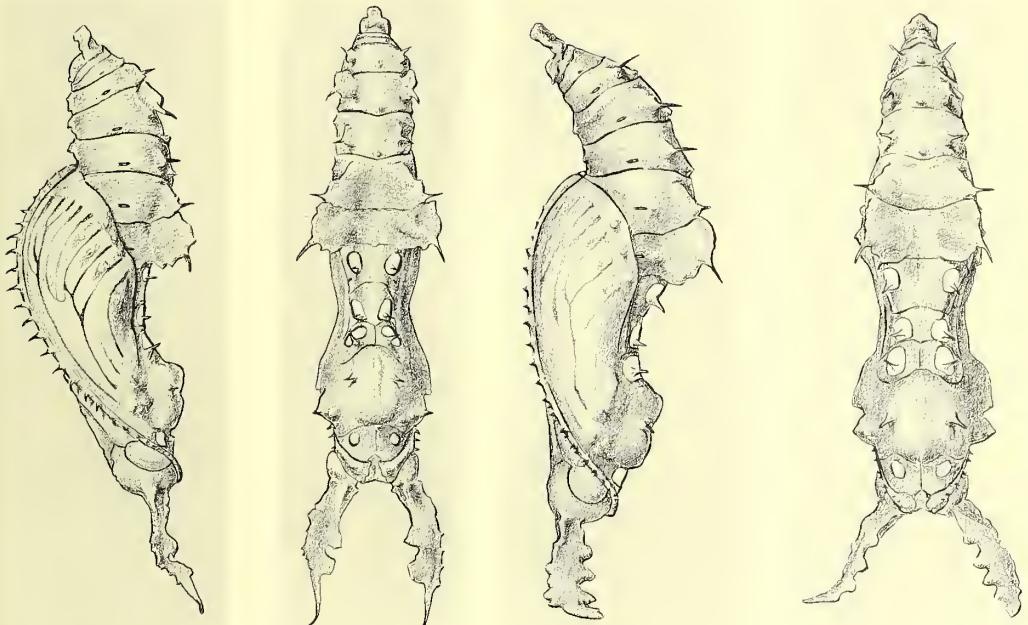


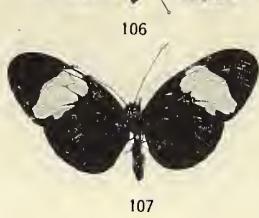
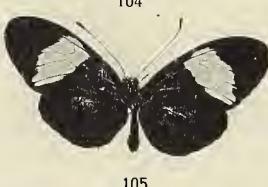
FIG. 94

FIG. 95

FIG. 96

FIG. 97

A COMPARISON OF EGGS, LARVAE AND PUPAE IN FOURTEEN SPECIES
OF HELICONIINE BUTTERFLIES FROM TRINIDAD, W.I.



A COMPARISON OF EGGS, LARVAE AND PUPAE IN FOURTEEN SPECIES
OF HELICONIINE BUTTERFLIES FROM TRINIDAD, W.I.