

Evolution in Modern Amazonian Non-Forest Islands: *Heliconius hermathena*¹

Keith S. Brown, Jr.

and

Woodruff W. Benson

Centro de Pesquisas de Produtos Naturais, ICB, CCM, Universidade Federal do Rio de Janeiro, Ilha do Fundão, Rio de Janeiro ZC-32, Brazil and Departamento de Zoologia, Instituto de Biologia, Universidade Estadual de Campinas, C.P. 1170 Campinas, São Paulo 13.100, Brazil.²

NEXT

ABSTRACT

Heliconius hermathena is a little-known butterfly which is restricted to certain non-forest habitats in the Brazilian Amazon. Unlike forest species of the genus, *H. hermathena* has not undergone subspeciation in areas of presumed Quaternary forest refugia, but rather shows a unique racial distribution apparently related to present occurrence of isolated non-forest habitats. Three subspecies (two previously undescribed) are non-mimetic and little differentiated, whereas a fourth, *H. b. vereatta*, is strongly mimetic of sympatric *H. m. melpomene* and *H. erato bydara*. The non-mimetic subspecies are apparently widespread, although of patchy occurrence and often at very low population densities. In contrast, the mimetic subspecies is very restricted geographically, being known only near Faro, Pará (though its models are widespread and even microsympatric with non-mimetic *hermathena* in many other areas). It occupies essentially continuous habitats within its limited range, and attains population densities and sizes much greater than do non-mimetic races. Adult morphology places *H. hermathena* near *H. erato* and *H. charitonia*, but the pupal characters suggest that the species is relatively primitive, near to the *melpomene*-group of the genus. Both *erato* and *charitonia* are widespread and successful species, whereas the distribution of *hermathena* suggests that it is a specialized relict. The larva is uniquely colored bright red or orange, possibly for the purposes of signaling (aposematism linked to Müllerian mimicry, or ease of location by adults). Imaginal *hermathena* are very sedentary, with individuals apparently establishing restricted home ranges, generally within a radius of 100 m of their nocturnal roosting sites. Roosting behavior is unique among *Heliconius* in that the butterflies aggregate on the undersides of leaves and grass blades about one-half meter from ground level. This behavior seems to afford maximum protection from weather and predators in their specialized habitats. As larval host plants, *hermathena* uses only two woody sclerophyllous species of primitive *Passiflora*, *P. feroana* and *P. hexagonocarpa*, characteristic of natural Amazonian scrub-vegetation communities on deep sandy soils. Alluvial sands supporting these communities are widely distributed over the Amazon, especially along the outwashes of the Brazilian and Guianan shields. The genetic basis for mimicry in *H. b. vereatta* is apparently a single factor with essentially dominant effects. The mimetic subspecies intergrades with a non-mimetic race north of Faro, resulting in a narrow hybridization zone. The mimics of *vereatta* become progressively rarer northwards across this zone, and are decreasingly microsympatric with *hermathena* where the non-mimetic phenotype exists in higher frequencies. Mimetic selection appears to be even strong enough to maintain local differences in genic frequencies, with mimetic forms becoming more common in closed habitats where models fly, and non-mimetic forms (perhaps profiting by "flash-disruptive" coloration) predominating in adjacent more-open habitats.

RECENT RESEARCH has suggested that past climatic fluctuations were important in producing the parallel patterns of geographic differentiation observed in Neotropical plants and animals (Turner 1965, 1971a; Haffer 1967, 1969, 1974; Vanzolini 1970; Vuilleumier 1971; Müller 1972, 1973; Prance 1973; Brown, Sheppard, and Turner 1974; Brown 1976, 1977a, 1977b), as has been demonstrated in other tropical regions (Moreau 1963, 1966, 1969; Mayr 1969; Kingdon 1971; Vanzolini 1973). In the American tropics, the locations of races and semi-species, and the zones of contact and hybridization between them, are repeated with minor variations across a wide variety of taxonomic groups, and occur over an area in excess of 8×10^6 km², which today is practi-

cally continuous humid forest, broken only by occasional broad rivers, low mountain ranges, and isolated savannas. It has been proposed that these many local differentiates were produced during drastic reductions and fragmentations of an earlier near-continuous forest, caused by one or more major climatic cycles during the Quaternary, probably corresponding with well-known northern glaciations (Vuilleumier 1971). The resulting forest islands formed isolated refuges which acted as centers of evolution for previously widespread species, giving new subspecies, semispecies, and full species. According to the model, each differentiate spread out during wetter periods with the advancing forest, and eventually met sister forms from other refuges. Zones of secondary contact were formed where the populations met one another, in areas which can often be recognized today by their relatively heterogeneous flora and fauna, including relict non-forest elements (Haffer 1974, Brown 1976, 1977a, 1977b).

¹ This paper is Part VII in the series "The Heliconians of Brazil (Lepidoptera, Nymphalidae)." For Part VI see Brown and Benson, 1975a. Contribution number 15 of the Programa de Ecologia, Instituto de Biologia, Universidade Estadual de Campinas.

² Present address of both authors.



FIGURE 1. Map of localities of *Heliconius hermathena*.

Recent studies using the Heliconiini (passion flower butterflies) as indicators of the continental refugia (Brown, Sheppard, and Turner 1974; Brown 1976) have located 42 Neotropical forest centers of differentiation (including at least four isolated islands which may still be acting in the present time). The principal isolation and differentiation, however, probably occurred no less than three, and more likely ten to twenty thousand years B.P., and surely over many thousands of generations. As the forest is today near its peak expansion, the differentiation of forest organisms may have stalled relative to its previous importance, being presently only inferrable in highly sedentary species with very patchy distributions (such as *Heliconius demeter*; Brown and Benson 1975a). However, the expansion of the Neotropical forests has more recently enclosed and cut off islands of natural scrub and field vegetation (referred to in Brazilian scientific studies as "campo," "cerrado," "pseudocatinga," "campina," etc.³). In these habitats species adapted to the high-light, low-humidity, and often harsh conditions of more open areas might be expected to be undergoing current divergent evolution.

Such a species is *Heliconius hermathena* Hewitson (Brown 1972). While systematically quite close to typical forest species in the genus, it does not show clear-cut differentiation patterns linked to well-defined refugia as do its closest Amazonian relatives (Brown, Sheppard and Turner 1974; Brown 1976), and is today restricted to hot, bright "campina" and similar open habitats. As these areas were presumably united in the past (Müller 1973, Haffer 1974), but are now widely fragmented in the range of *hermathena* (which includes the Brazilian Amazon near the Rio Negro, Rio Amazonas, and lower Rio Madeira; fig. 1), it might be expected that local race formation, related to historical patterns of ecological conditions, could be found to exist in this species and those in close association with it. Such has been confirmed to be the case.

³ These terms refer to distinct classes of vegetational formations, and are useful for distinguishing among different communities of sub-forest vegetation. A general treatment of Brazilian vegetation types is outside the scope of this paper; the interested reader is referred to the following works: Ducke and Black (1953), Beard (1953, 1955), (1969), Janzen (1974), Eiten (1975), and their contained references.

SYSTEMATICS

Until 1972, only one form of *hermathena* (fig. 2A) was known to most entomologists. It corresponded with Hewitson's original description (1853) and could be captured only in select scrubby vegetation mixed with open "cerrado" (fig. 2B) south of the Amazon and Negro rivers (localities near Santarém, Juruti, Maués, Uypiranga across the Rio Negro from Manaus, and Tomar; see map, fig. 1). Two additional names, *vereatta* and *hydarina* (male and female, respectively), were applied by Stichel (1912) to a pair of specimens sent him by Adolph Ducke, collected in 1911 near Faro, Pará, a locality which was correctly suggested by Emsley (1965) to be "near the periphery of the species' range." The other 10 specimens of the series from which the types were designated were donated by Ducke to the Museu Goeldi in Belém and remained undiscovered by entomological taxonomists. Only the two types existed in the British Museum (Natural History) as tangible evidence for the reality of these strange and presumably mimetic forms, which were described as essentially lacking all the yellow spots and stripes on the hindwing characteristic of *hermathena*, thereby strongly resembling *H. melpomene melpomene* and *H. erato hydara* which are matt black with a broad, red post-median band on the forewing.

On 28 October 1971, a population of a new *hermathena* subspecies was discovered by Dr. and Mrs. Philip M. Sheppard in the company of the first author, in the Reserva Campina of the Instituto Nacional de Pesquisas da Amazônia, located about 60 km north of Manaus on the new highway being built to Caracaraí (fig. 1). This population was studied in February 1972, and July-August and November-December 1974. A small series of specimens was captured and bred from eggs and larvae found in the field and obtained from a female in the insectary. These specimens are uniformly different from *hermathena* from south of the river in that they possess a narrower red band on the forewing, which is less mixed with yellow pigment on the ventral surface (more easily compared in fresh specimens), and have a more truncate line over the forewing cubitus. As the restricted habitat and sedentary habits of *hermathena* make crossings of the broad Rio Negro most unlikely, it is virtually certain that populations north of the river are isolated from typical *hermathena* to the south. The factors of geographic isolation and morphological differences justify the designation of the new subspecies *H. b. sheppardi* (fig. 2C), which we dedicate to its discoverers. The only other known populations of this subspecies occur on and around a sandstone rockfield approximately 70 km

north of the type locality (fig. 1). Ducke reported seeing the species, presumably this new subspecies, on a number of campinas not far from Manaus (Stichel 1912), although apparently no specimens found their way to generally available collections. It may be expected to occur in naturally scrubby habitats (figs. 2D, 2E) near to the north bank of the Amazon and Negro rivers, from the eastern part of the state of Amazonas west perhaps into eastern Colombia and southern Venezuela. The known *hermathena* from the upper Rio Negro (Barcelos, Tomar, São Gabriel da Cachoeira) are apparently from south-bank localities and represent the nominate subspecies. The only known specimen from southern Venezuela (Yavita, 7-IX-47, "brought in by an Indian boy," in the collection of René Lichy, see figs 1, 2F) is closer to *b. sheppardi* than to *b. hermathena*, but differs from both in the wider costal end of the red forewing median band. When this population is adequately sampled, it will probably merit a further new name.

Microsympatric heliconians at the type locality of *b. sheppardi* (Reserva Campina) include *Philaethria pygmalion*, *Heliconius numata*, and *H. sara thamar* (all of which sometimes use the same foodplant as *hermathena*), *Agraulis vanillae*, and *Dryas julia*. Occasional *Heliconius erato amalfreda* and *Eueides tales tales* fly through the campina, and *H. demeter beebei* is found around its edges, but all of these are more frequent in nearby woods along with *H. aoede astydamia*, *H. wallacei wallacei*, and *H. burneyi catherinae*. No sympatric heliconian or any other butterfly found in campina habitats bears even a remote resemblance to *H. hermathena sheppardi* (fig. 2C), indicating that the new subspecies represents one of the very few known non-mimetic *Heliconius* (see Turner 1971).

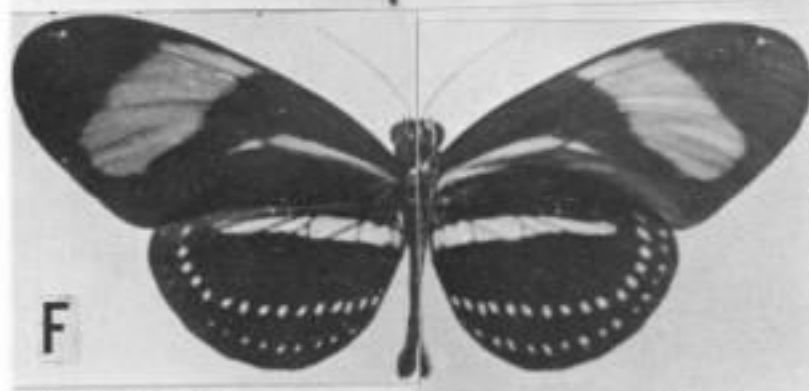
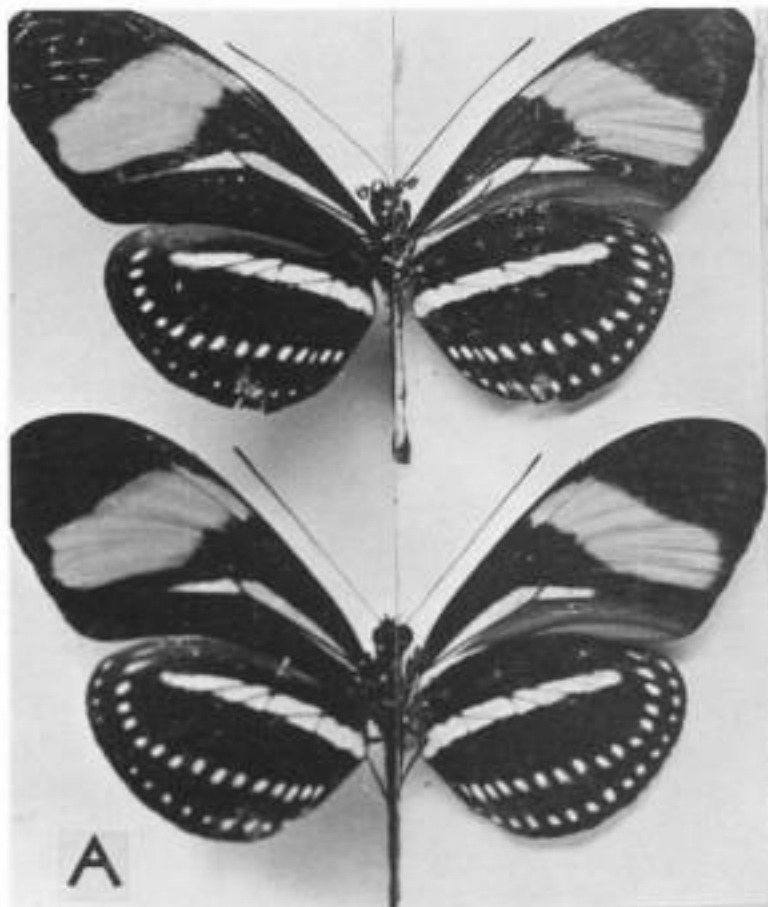
The small village of Faro, Pará, guards the lower Rio Nhamundá where it turns abruptly eastward to parallel the main course of the Amazon River through a wilderness of channels and seasonally submerged islands, before joining far to the east with the Rio Trombetas near its junction with the Rio Amazonas (fig. 1). Across and down the river from Faro is the village of Nhamundá, in the state of Amazonas (the river forms the state boundary). North-east of this settlement, along a broad inlet on the Pará side, are cleared fields bordered by heavy woods, which, after less than a kilometer, give way suddenly to a large natural field (fig. 3A) on deep sandy soil. In this locality, Campos do Tigre (about 7 km due east of Faro), Adolph Ducke collected a new *Passiflora* later described as *P. fvaroana* Harms (see Killip 1938: 545). This circumstance led us to be-

PREV

NEXT

PREV

NEXT



lieve that it was also the exact locality where he collected the type series of the most unusual mimetic subspecies, *H. hermathena vereatta*.

Both the plant and the insect are indeed present and common in this field, occurring principally on the edges of small hummocks of vegetation 1-4 m high. On the day of rediscovery of this population (23 July 1973), *vereatta* (fig. 3B) was the commonest butterfly in the field. Of the 54 individuals seen between 0830 and 1200, only one (fig. 3C) had any yellow markings on the hindwing (one of Ducke's 10 specimens deposited in Belém also possesses yellow marks). The population was almost equally divided between males, with a yellow streak over the forewing cubitus, and females with a much-reduced red streak in the same position. Stichel baptized the female form *hydarina*, which is here declared a synonym of *vereatta*. Also present in the same habitat with *vereatta* were the very similar and widespread forms *H. m. melpomene* and *H. erato bydara* (fig. 3D), confirming the mimetic nature of the *vereatta* color-pattern. In fact, on the day of rediscovery, a *vereatta* was captured in an isolated woods near the center of the open area on a flower which was visited immediately afterwards by a nearly identical female of *H. erato bydara*; the two were indistinguishable to the collector.

About 15 kilometers north-northeast of the Campos do Tigre, near Km 27 of the track from Faro

to Terra Santa, there exists another large and ecologically similar field (fig. 1). Here another colony of *hermathena* was discovered on 7 February 1973, and studied more extensively in July. The population was very dense on both visits. Flying in patches of scrub (fig. 4A) and swamp ("campo brejo," fig. 4B), the population was unequally divided between *vereatta* (fig. 3B) and a commoner, previously unknown form (fig. 4C). This latter, like *vereatta*, was larger and more richly red-colored than typical *hermathena*, and possessed a series of red postmedian spots on the ventral hindwing. However, the hindwing was otherwise very similar to that of *H. hermathena sheppardi*, with a variable but normally complete array of yellow markings. This dimorphic *hermathena* population was microsympatric with *H. m. melpomene* on the edge of the field and inside the brushy swamp; a hybrid population of *H. erato amalfreda* x *hydara*, including about 40 percent of red-banded individuals and occasional typical *bydara* (fig. 3D), was present in the nearby woods in July (in February *H. erato* was very infrequent near the field and those few observed were of the *amalfreda* phenotype, with a yellow forewing band).

Fifteen km farther northwest, by an inlet on the north side of the east to south bend of the Rio Nhamundá about 20 km due north of Faro (fig. 1), a further *hermathena* population was encountered, this time in typical dry "pseudocaatinga" (= ex-

FIGURE 2. *Heliconius hermathena hermathena*, *H. b. sheppardi* nov. subsp. and their habitats. The butterflies are life size; color is black, yellow, and red; and in each illustration the left side of the butterfly is dorsal, the right side ventral. 2A. *H. b. hermathena*, male (upper) and female (lower), Santarém, Pará (coll. K. Brown). 2B. Habitat of *H. b. hermathena*, near Santarém. 2C. *Heliconius hermathena sheppardi* new subspecies. 2D. Reserva Campina, north of Manaus; where the first specimen of *H. b. sheppardi* was captured (note *Passiflora faroana* vine in left foreground). 2E. Reserva Campina where additional specimens of *sheppardi* were captured. 2F. *H. hermathena* subsp., male, Yavita, Territorio Federal Amazonas, Venezuela, 7-IX-47 (R. Lichy). Adult male *H. b. sheppardi* (fig. 2C) dorsally (left side of upper illustration) similar to nominate subspecies (fig. 2A) but has a distinctly narrower forewing postmedian red band (less than 10 mm wide along vein M_2 in normal 40 mm forewing individuals, vs. 10-12 mm in *b. hermathena*). On ventral surface (right side upper illustration) the forewing band is reddened in color, whereas in the nominate subspecies it is lighter, orange or salmon-rose, which is best seen in fresh specimens as the red fades with passage of time. The yellow streak over the forewing cubitus is not strongly elongated into space Cu_1 - Cu_2 , usually for less than 5mm whereas in *b. hermathena* it is usually 6-15 mm long. Adult female (fig. 2C lower illustration) is similar to male, but has the extension of the cubital streak tending to red distally. Both sexes have a narrow yellow median band (more distal than that of *b. hermathena*) and two series of doubled intervenal submarginal yellow spots on the hindwing, which bears on the ventral surface four red basal dots and a yellow cubital stripe.

MATERIAL STUDIED: Brazil, Amazonas, Reserva Campina of the Instituto Nacional de Pesquisas da Amazônia, on the Manaus-Caracará highway 45 km north of the Polícia Rodoviária which is at the bifurcation of the Manaus-Itacoatiara and Manaus-Caracará highways, pseudocaatinga on the east side of the highway (figs. 2D, 2E), south of a dip with a stream flowing west into the upper Rio Tarumã: 11 February 1972, holotype male and one paratype female donated by the authors to the Museu Nacional, Rio de Janeiro; 28 October 1971, three female paratypes, two captured by Philip and Pat Sheppard (one donated to the British Museum (Natural History), the other two in the collection of K. Brown); 11 February 1972, four male paratypes (one donated to the Instituto Nacional de Pesquisas da Amazônia, one in the collection of K. Brown, two in the collection of W. Benson); 28 December 1975, one male in the Instituto Nacional de Pesquisas da Amazônia, collected by Lindalva P. de Albuquerque; 11 April 1976, two male paratypes, collected by P. F. Bührnheim in the collection of the Departamento de Zoologia, Universidade Estadual de Campinas; 8 July 1974, one male paratype; 7 August 1974, two male and two female paratypes; and 6 December 1974, two male paratypes (in the collection of W. Benson). Km. 130 on the Manaus-Caracará highway in a rockfield with some campina vegetation in the headwaters of the Rio Urubu: 1 December 1974, two males and one female paratypes (in the collection of W. Benson). "Manaus, Tarumã": one male paratype in the Museu Nacional, Rio de Janeiro, No. 16/049. "Tabocas, Rio Caquetá, Colombia", one male paratype in the Museu Nacional (May collection, No. 4/337; this locality is probably erroneous, as most of the other *Heliconius* in the same lot are *H. melpomene meriana*, a subspecies known only from north and east of Manaus into the southwestern Guianas).

tensive campina, as fig. 2D). The population was of low density, and in our two visits we only succeeded in taking four specimens and in seeing two more. All the individuals were smaller and less richly colored than *vereatta*, and were very similar

to *H. b. sheppardi* except for the retention of the full series of red dots in the postmedian area of the ventral hindwing, as in *vereatta*, and the consistently smaller size of the hindwing median yellow stripe. As no butterflies comparable to *vereatta* in size and

PREV

NEXT

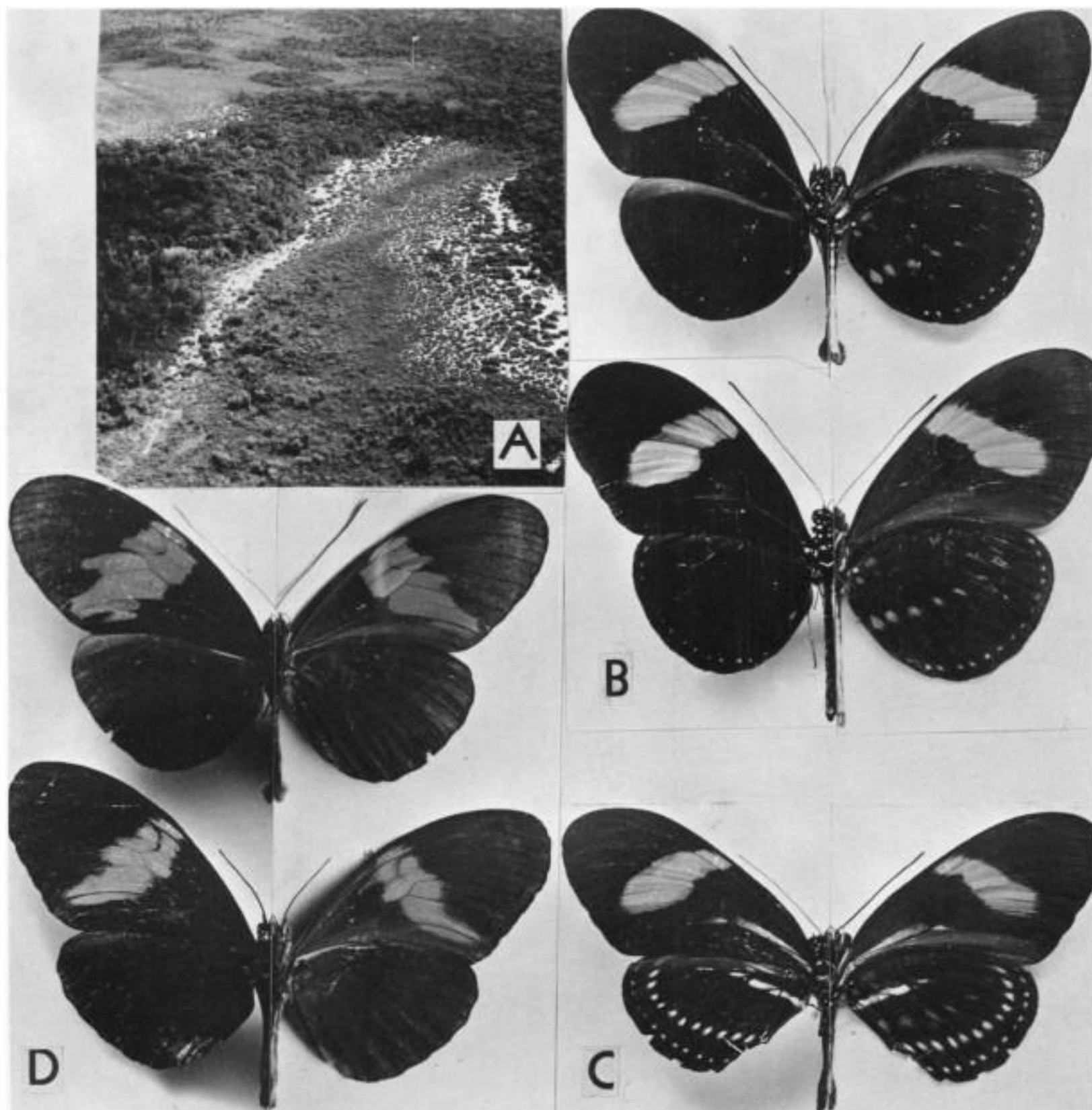


FIGURE 3. *Heliconius bermathena vereatta* Stichel (probably topotypic), its habitat and its mimics. Butterflies are life size; color is black and red with a yellow forewing streak in male *vereatta* (the left side of each butterfly illustration is dorsal, the right side is ventral). 3A. Campos do Tigre seen from a light airplane at about 500 m, looking north from lower part of field. 3B. *H. b. vereatta*, male (upper) and female (= *hydarina*) (lower), dorsal (left) and ventral (right) wing surfaces, Campos do Tigre, east of Faro, Pará, 23 July 1973, K. Brown collection. 3C. *H. b. vereatta*, variety with yellow marks on the hindwing, Campos do Tigre, 23 July 1973. 3D. *Heliconius erato hydara*, female, Campos do Tigre, 23 July 1973, K. Brown collection (upper). *Heliconius melpomene*, male, Km. 27 Faro-Terra Santa track, 20 July 1973, K. Brown collection (lower).

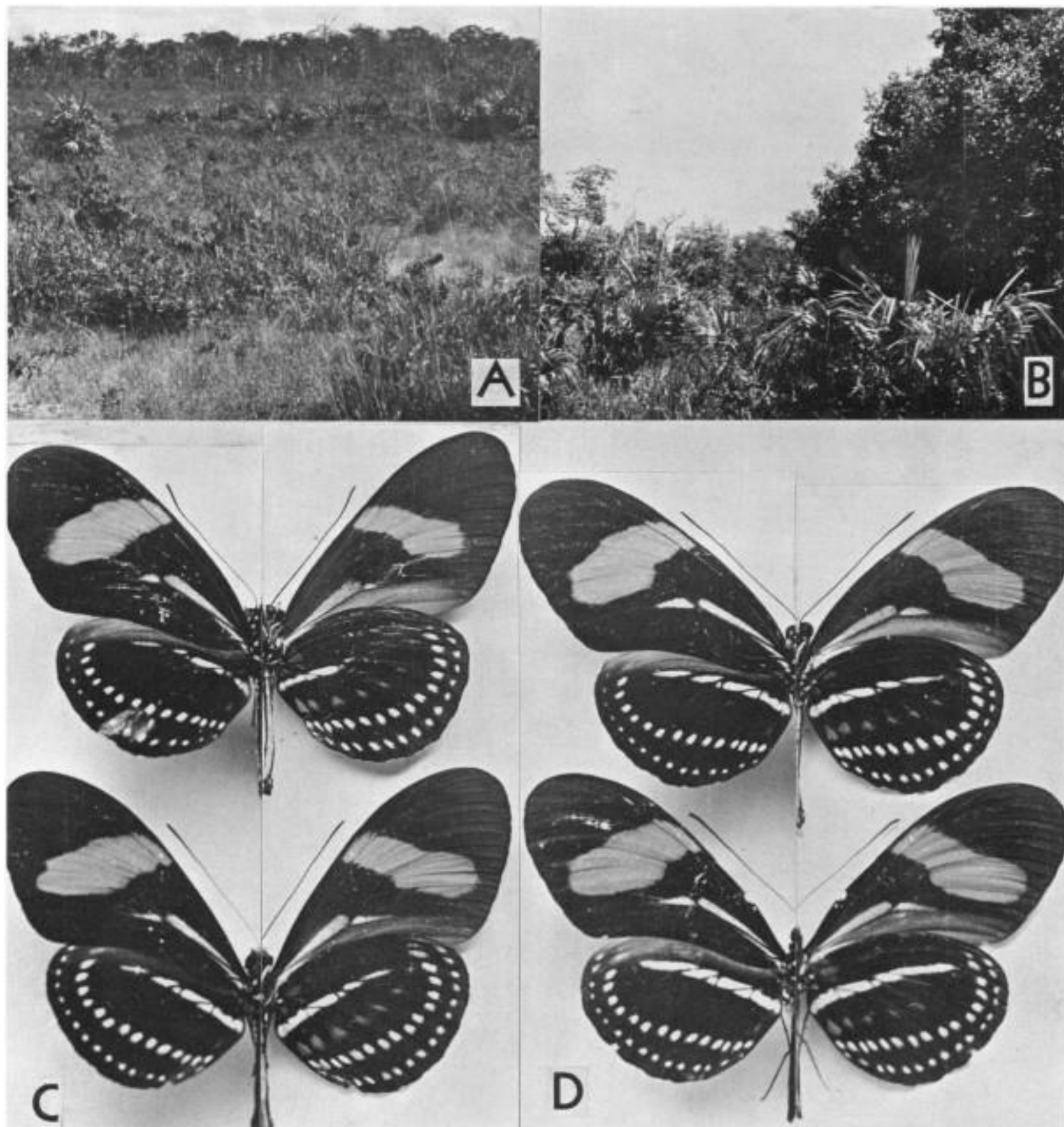


FIGURE 4. *Heliconius hermathena duckei* nov. subsp., varieties and habitat. Butterflies are life size; color is black, yellow, and red (the left side of each butterfly illustration is dorsal, the right side ventral). 4A. "Field" colony habitat, looking west from road across archipelago of scrub patches, Km. 27 Faro-Terra Santa track. 4B. "Swamp" colony habitat, edge of vegetation on east side Km. 27. 4C. Morphs similar to *hermathena* found mixed with *vereatta* in the field at Km. 27 of the Faro-Terra Santa track; male (upper) and female (lower), K. Brown collection. 4D. *Heliconius hermathena duckei* new subspecies. Adult male (upper) and female (lower) dorsally (left) very similar to *H. b. sheppardi*, differing principally in the reduction of the yellow median bar on the hindwing. Ventrally (right) different in the consistent presence of a series of five to seven intervenal red dots in the postmedian area of the hindwing, forming a very slightly marginally convex series from the anal border to near the apex (these dots are occasionally, though weakly, represented in eastern populations of *b. hermathena* south of the Amazon River).

MATERIAL STUDIED: Brazil, Para: scrub along northeastern inlet at bend of Rio Nhamundá, 20 km due north of Faro, 22 July 1973, HOLOTYPE MALE donated by the authors to the Museu Nacional, Rio de Janeiro, K. Brown leg. One paratype female, same locality and date, donated by the authors to the British Museum (Natural History), K. Brown

color were seen in this area, it may be presumed that this colony is homogeneous. The form is thus described (fig. 4D) on the assumption that it represents a northeastern subspecies of *hermathena*, carrier of the red dots which persist in *vereatta*. No additional populations of this form have been discovered to date in this poorly explored region, but it should be looked for in campina vegetation in upland north-central Pará. The name is proposed in homage of the well-known Amazonian botanist Adolph Ducke, collector of *H. hermathena* and its foodplants in many parts of the Amazon Basin. The red dots on the ventral hindwing characteristic of *vereatta* and *duckei* appear very occasionally in populations south of the river (see Emsley, 1965); one individual in 75 taken in late 1975 near Juruti, Pará, across from Terra Santa (fig. 10), showed them, indicating that individuals may be able to cross the relatively narrow Amazon River in western Pará, perhaps aided by predominantly northeasterly winds.

ECOLOGY

In our studies of *Heliconius hermathena* we have had the opportunity to make numerous observations of ecology and behavior. For the most part, observations made in different subspecies correspond fairly closely, except for *H. b. vereatta*. Therefore, we present here our general observations on *H. b. hermathena* and *H. b. sheppardi* in some detail, and save the specific comments on *vereatta* for the discussion of the ecological genetics of this race. *H. b. duckei* has not been observed sufficiently to draw any conclusions concerning its ecology, although from first impressions it seems very much like *sheppardi*.

GREGARIOUS ROOSTING

H. hermathena roosts gregariously, as do most *Heliconius* and many species in related genera (Benson 1971, Turner 1975). On the night of 12 August 1974, after a rain and wind storm in the afternoon which terminated just before dark, a roost area was observed in the Reserva Campina. Of the five *hermathena* present, one was under a large leaf, one was on a dead twig tip, and three were grouped on the tip of a grass blade. All of these were within a radius of 2 m and located 50 to 60 cm above ground level. Two days prior, this and other roosting sites had been located by tracking loose groups of flying

butterflies in the late afternoon. By 1700 hrs three insects had already begun roosting on small plants in scattered localities, all on the undersides of larger leaves about 50 cm from the ground. In February 1973 observations were made on four individuals of *vereatta* x *duckei* captured near Faro and kept in a large insectary in Rio de Janeiro. Two or three of these butterflies were observed to roost repeatedly in a group on the underside of a single leaf about 50 cm from the floor of the cage (see fig. 5A). These data are sufficiently uniform to suggest that *hermathena* typically roost gregariously, near to the ground, under the living leaves of grasses and broad-leaved plants. This behavior differs markedly from that observed in other *Heliconius* (including *hermathena*'s closest living relatives *H. erato* and *H. charitonia*) which roost almost exclusively on the tips of dead twigs from 1 to 8 or more meters above the ground. Heliconians of the genus *Eueides*, however, typically rest under leaves, and in at least one case, *E. lybia lybioides*, they may aggregate on the same or immediately adjacent leaves. *Dryadula phaetusa*, a species of open areas, and in this way similar to *H. hermathena*, also roosts gregariously and persistently under narrow leaves close to the ground (Turner 1975), often only 20 to 30 cm high (pers. obs.).

Roosting sites in the Reserva Campina were in open, litter-strewn "glens" under low, spreading trees (fig. 2E), distributed through the vegetation patches. These provided the most protected places within the campina, and the isolated small plants used for sleeping probably received little disturbance from potential predators. On the other hand, the trees themselves were thick with epiphytes (fig. 2E), with ant nests occurring commonly in the root mats. Moreover, thin elongated twigs, of the type preferred by most *Heliconius*, are uncommon on campina plants, their stems more often being thick and stubby. Thus, the roosting preferences of *hermathena* seem adaptive and are related to the structural and biological features of their unusual habitat.

INDIVIDUAL MOVEMENT AND HABITAT SELECTION

Marking experiments, and observations on density patterns within continuous habitats, show that *H. hermathena*, like other species of *Heliconius* (Benson 1971; Turner 1971b; Brown 1972; Ehrlich and Gilbert 1973), have restricted home ranges. A limited mark-recapture study was performed on *H. b. shep-*

leg.; one male paratype, same locality and date (in the collection of K. Brown); one paratype male, 8 February 1973 (in the collection of W. Benson). Larger or more richly colored specimens (fig. 4C) from populations mixed with *vereatta* are not regarded as typical for this subspecies, though they are very similar; many apparently possess modifying genes from *vereatta* which alter the wingspread and the extent and form of the hindwing yellow markings.

pardi in a large continuous section of the Reserva Campina on 10-11 July 1974, to determine the degree of individual movement in these butterflies. With equal capture effort, 18 individuals (12 males and 6 females) were caught and marked on the first day, and four additional ones (two of each sex) on the second. Highly visible white and yellow spots were painted in coded positions on the wings so that movement could be observed without physically having to recapture individuals and possibly interfere with normal behavior as a result of handling (Benson 1972). Judging from the rate of encounter of unmarked butterflies on the second and subsequent days after marking was begun, the total population in the area (about 0.5 ha) was on the order of 30 butterflies. The marking area formed a *cul de sac* about 70 m on a side, surrounded by "campinarana,"⁴ or closed forest on sandy soil with an open undergrowth, into which the marked *hermathena* did not usually penetrate. The majority of the butterflies roosted near the blind end of the *cul de sac*, and most were observed repeatedly in the study area. Only one, a male, was observed to fly the length of the area and enter the larger section of campina at the open end, which occupied about 2 ha. No other marked butterfly was observed among the sparsely distributed *hermathena* outside of the marking area, and most observations were made within 40 m of blind end of the study site. The general pattern seemed to hold over at least a month, since a brief visit into the marking area on 8 August turned up two marked individuals among the four observed, whereas none of the four *hermathena* observed in the adjacent area carried marks. Several revisits to the area during November and December of 1974 turned up only a single *hermathena* in the original study area, whereas the butterflies had become frequent in an isolated 1 ha patch of campina, surrounded by forest, in which previously butterflies had not been observed.

Limited observations on another *H. b. sheppardi* locality, a ca. 1 km² rockfield at Km 130 on the Manaus-Caracará highway, indicated that even within apparently continuous and uniform habitats the *hermathena* existed in isolated pockets. Extensive search turned up two areas about a kilometer apart in which the butterflies were flying, but none of these insects were encountered elsewhere. One spot was obviously close to a roosting site, for the insects were only flying in the area in the early part of the morning, afterwards disappearing into the thickets. The second area was on a sandy slope with abundant

⁴ Ecotonal wooded areas separating humid forest from natural campina or field vegetation, from *campina*, Braz. Amaz. Port. (=savanna, scrub, field) + *-rana*, Tupi (=like, similar to).

larval foodplant. Butterflies started appearing in the open after 1000 hrs and became increasingly more frequent as the morning progressed. A total of approximately 10 butterflies was seen in about three hours of observation. We suppose that *hermathena* is generally distributed in the habitat but only attains densities sufficient for notice at scattered points. Since only a very small portion of the area was examined, no generalizations can be made about the over-all distribution and movement in the Km 130 populations.

In the Reserva Campina, the restricted patterns of individual movement seem to be sufficiently strong to inhibit gene flow even over short distances, and the local concentrations give additional support to this idea. It would seem that the butterflies disperse little from their sites of birth, and that colonization, even of contiguous areas, may delay until occasional "wide-ranging" females lay eggs in other areas, and these grow up to produce a resident population. We know of no case of isolated *hermathena* being seen or captured far from (or even wandering in inappropriate habitats close to) their usual haunts. Thus, gene flow and colonization ability may be even lower in this species than in other *Heliconius* (Turner 1971b, Ehrlich and Gilbert 1973).

FLOWER VISITING

H. hermathena avidly visit flowers for nectar and pollen, and are thus nearly identical with other *Heliconius*. However, the number and kind of flowers available to them appears to be very restricted in comparison with forest species, and interactions are probably somewhat more specialized. Plants visited by adult *hermathena* near Manaus include several species of Rubiaceae, some Apocynaceae and Leguminosae, and Humiriaceae. Especially favored are two species of *Palicourea* (Rubiaceae), one with pink flowers and the other with white flowers and violet-red bracts (fig. 5B, 5C). The other species like *Pogamea duckei* Standl. (Rubiaceae) have white flowers (as figs. 5D, 5E), often with only a few small inflorescences available on any given plant. *Humiria balsamifera* (fig. 5E), one of the most abundant plants on the campina, does not seem to be much preferred; it possesses large inflorescences of small, cup-shaped, white flowers, and is more typically visited by small bees.

After a short period of sunning in the morning, one of the first activities of the butterflies is flower visiting. At the Reserva Campina this began before 0700 hrs and continued at a high but decreasing rate until around 1100 hrs. During July 1974 several butterflies would often visit, and continually return to, a given preferred flower throughout the morning

presumably after most nectar and pollen had been removed. The probing behavior of the butterflies indicated that collecting pollen was their goal, and suggests that pollen-derived nitrogen may be an important limiting factor to adult reproduction (see Gilbert 1972, 1975).

Most campina plants, like tropical trees in general (Janzen 1967), are highly seasonal in their flower production. It is not known what effect this has, if any, on *bermathena* populations, or if *bermathena* itself has promoted coevolutionary modifications in morphology or phenology of campina endemics. Studies of campina vegetation are underway at the Instituto Nacional de Pesquisas da Amazônia, and these will possibly cast light on this question.

OVIPOSITION AND HOST PLANT CHOICE

Heliconius bermathena is very restricted in its use of larval foodplants. Only two closely related *Passiflora* of the primitive subgenus *Astrophea* (Benson, Brown, and Gilbert 1976) are known to be used by the species. These are allopatric, *P. hexagonocarpa* being used by *h. bermathena* in Santarém and presumably other southern localities, and *P. faroana* being the choice of *h. sheppardi* (Reserva Campina and Km 130 Manaus-Caracarái, near Manaus) and *h. vereatta* and *vereatta x duckei* (Campos do Tigre and Km 27 Faro-Terra Santa, near Faro) and presumably other populations to the north of the Rios Amazonas and Negro.

Observations made at the Reserva Campina and



FIGURE 5. Behavior and community relationships of *Heliconius bermathena*. 5A. Female from Reserva Campina roosting under palm blade 50 cm above insectary floor, Rio de Janeiro, February 1972. 5B. *Palicourea nitidella* (M. Arg. Standl.) (Rubiaceae) from Reserva Campina pollinated by *H. bermathena*. 5C. *Palicourea* cf. *lupulina* Benth. from Reserva Campina, especially sought by *bermathena* adults. 5D. A leguminous flower being visited by *H. b. duckei* in its campina habitat type locality north of Faro, July 1973. 5E. *Humiria balsamifera* (Humiriaceae) in flower, Reserva Campina.

confirmed at other localities show that oviposition occurs mainly throughout the mid-part of the day. Females apparently locate the foodplants by random search in suitable habitats, and perhaps by concentrating in areas where plants have been found previously. The butterflies chemically test the leaves of the plants by tapping with their forelegs before ovi-

position, as is the habit in the genus. An isolated egg is placed usually on the upper surface of a young growing leaf immediately below an actively growing meristem (fig. 6A). Two or three eggs are sometimes found on the same stem; it is unknown whether this situation represents multiple oviposition by a single female or the contribution of different

PREV

NEXT

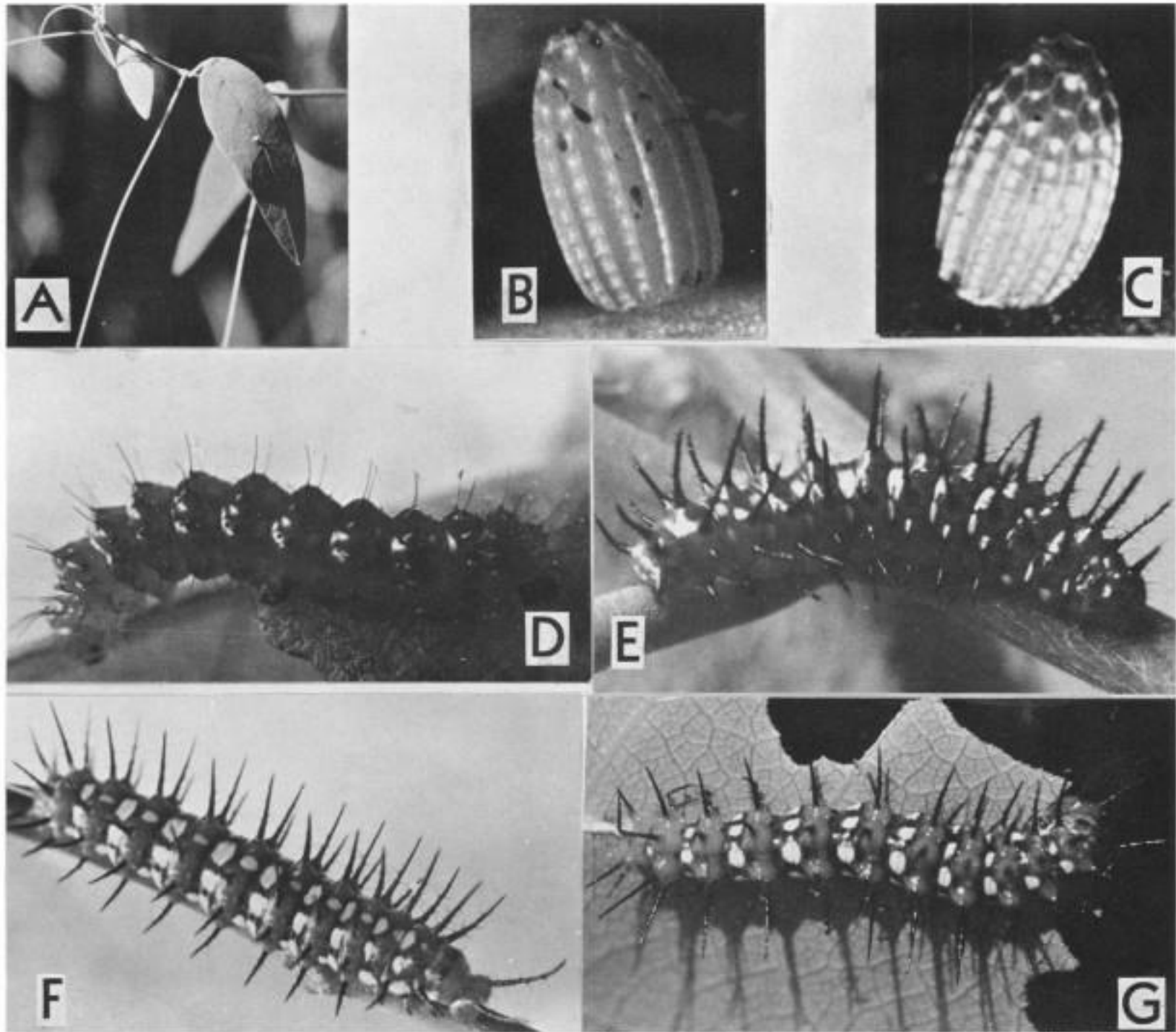


FIGURE 6. Early stages of *Heliconius bermathena*. 6A. An egg placed singly on the upper surface of a young leaf of *P. hexagonocarpa* from Santarém. 6BC. The egg is an elongate ribbed ovoid, truncated at the bottom, strong yellow in color, approximately 1.3 mm in height and 0.7 mm in diameter, with 16 vertical and 11 horizontal compressions, plus 2 in an irregular series at top; of 3-5 days duration. 6D. The first instar larva is uniform light yellow and about 2 mm long when hatched, rapidly turning greenish, then brownish yellow, reaching a total length of about 6 mm. The head is dark brown, the pseudoocelli black, the setae long and translucent; of 2-4 days duration. 6E. The second instar larva is similar to the first, but somewhat darker, with short scoli on head, thorax, and abdomen (on the head 0.6x, on the body up to 1.3x head height). The maximum length is about 10 mm; and the duration is 2-4 days. 6F, 6G. The fourth instar larva, with an increasing amount of deep red (Manaus) or dark orange (Faro, Santarém), white, and black pigment, has a strongly calico appearance, essentially banded red (or orange)-black/white-black by the end of the instar. The scoli are black; head 1.7x, others up to 2x head height. The maximum length is 24 mm; the duration is 3-5 days.

individuals. Ovipositing females frequently choose very small plants, and larvae are most often found on such plants in the Reserva Campina.

H. hermathena shares its foodplants with a limited number of other heliconians, such as *H. sara* (Manaus and Faro), *H. numata* (Manaus, Reserva Campina), and *Philaethria pygmalion* (Faro, and probably Reserva Campina). *P. pygmalion*, the only one of the three species which also prefers non-forest habitats, has been found attacking *P. hexagonocarpa* near Santarém. Apparently *H. numata* does not get into *hermathena* habitats at Faro, and *H. sara*, although present on the Reserva Campina, has not been found using *P. faroana* there. Although it is quite possible that these and other *Heliconius* do occasionally attack *hermathena* foodplants, they are strictly alternative hosts which are for the most part unavailable to these forest-loving species. *P. pygmalion* feeds upon old leaves and should not directly compete with *Heliconius*. No other *Passiflora* have been observed by us to occur in *hermathena* habitats, although many species are often abundant in adjacent habitats.

JUVENILE BIOLOGY (see figs 6-7)

The mature larva of *H. hermathena* (figs. 7A, 7B) diverges strongly in color from its closest relatives, *H. erato* and *H. charitonia* (figs. 8A, 8B). The red (or orange) ring-banded pattern of the *hermathena* larva is superficially similar to that of the primitive heliconian *Philaethria pygmalion*⁵ (fig. 8C), with which it is microsympatric. Such extreme departures from the normal color patterns, which are usually characteristic of entire groups of heliconians, have been reported in several cases, apparently always associated with mimetic convergence to larvae of common species in other groups. Thus, the larva of *Eueides tales* has converged to mimic those of common microsympatric silvaniform *Heliconius* (Brown and Holzinger 1973), and *H. demeter eratosignis* larvae do not resemble those of other subspecies of *demeter* and closely related *Heliconius*, but accurately imitate those of sympatric *Laparus doris* and *H. xanthocles* (Brown and Benson 1975a). *P. pygmalion*

⁵*P. pygmalion* should be considered as a separate species from *P. wernickei* from southern Brazil. The larval color patterns of the two species differ in a number of respects. The larva of *P. wernickei* (fig. 8D) has a yellow head like that of *P. dido*, but is more strongly banded than the latter species (Beebe, Crane, and Fleming 1960; Young 1974; pers. obs.), and has only two full black rings per body segment, whereas there are three in *pygmalion* (fig. 8C). Moreover, the *pygmalion* larva is unique in having a brick-red head. The "wernickei" larva, from a Mato Grosso population, mentioned by Brown and Mielke (1972), was in fact *pygmalion*; the area is well northwest of the limits of *wernickei*'s range in central Brazil.

or its characteristic leaf damage (fig. 8E; Alexander 1961; Young 1974) have been observed on *hermathena* host plants in all the areas we have studied, and it seems possible that the similarity of the coloration of *hermathena* larvae, although admittedly quite imperfect, to that of *pygmalion* may have been brought about by selection for mimetic convergence.

A further possibility has suggested itself from observations of adult male behavior in *hermathena*. Unlike any other species of *Heliconius* we have watched, male *hermathena* seem to search out and fly around larval foodplants much as do the females. Although males do not tap *P. faroana* or *hexagonocarpa* with their forelegs, as do the females before ovipositing, it is obvious from our observations that they recognize foodplants and find them interesting, making careful visual inspections up and down the vines over several minutes. Since it is known that males of many advanced species of *Heliconius*, especially *H. sara*, *hewitsoni*, *eleuchia* (pers. obs.), and especially *charitonia* (Jones 1930) (and *erato* under insectary conditions; L. Gilbert, pers. comm.) rest on maturing female pupae, sometimes for extended periods, and mate with the female as she emerges, it is not unreasonable to hypothesize that *hermathena* may be taking this activity a stage further, perhaps hunting out large larvae so as to know where female pupae are likely to appear. Other aspects of the behavior of *Heliconius* butterflies are sufficiently well developed to admit such a mechanism (Gilbert 1975; Benson, Brown, and Gilbert 1976), which has obvious implications for the fitness of the searching male. Indeed, mating efficiency is probably critical in low-density *hermathena* populations, and females derived from conspicuous red (or orange) larvae might enjoy a considerable mating advantage. We have no observations, however, on the behavior of *hermathena* with respect to female pupae.

Our two suggestions to account for larval color divergence in *hermathena* are neither mutually exclusive nor exhaustive, and detailed studies of larval ecology and mating behavior are needed.

The variation in pupal coloration in *hermathena* (figs. 7C, 7D) may be simply a reflection of that observed in most *Heliconius* (see, for example, Turner 1968, Brown 1972) or may correspond to environmental conditions: in the darker campina undergrowth, most pupae are dark (fig. 7D), even when raised from campina larvae transplanted to the laboratory, while eggs from the Faro field population gave uniformly white pupae (fig. 7C). The short subequal spines of the pupa are of uncertain evolutionary significance, but the abbreviated head appendages suggest a primitive phyletic position for

the species, close to the *melpomene* group, all of whose members show these structures strongly shortened (fig. 8F; Brown 1972). The species possibly derived from an early stock transitional between the precursors of *melpomene* and those of *erato*; all members of the *erato* group have pupae with very long, strongly branched head appendages (figs. 8G; Turner 1968; Brown and Benson 1975a, 1975b). It is tempting to suggest that *hermathena* is the most primitive member of the *erato-sara* line of the genus *Heliconius* ("signa absent on bursa copulatrix," Brown 1972: 56), little removed from the line which gave rise to *H. nattereri* and the *numata-melpomene* series. It would thus be antecedent to both *erato* (with which *hermathena* shares forewing markings, and probably a red-released courtship sequence, since *h. vereatta* has no other significant color) and *charitonia* (the most primitive member of the *sara* line, with which *hermathena* shares hindwing markings). Adult morphology (Emsley 1963, 1965) would also place *hermathena* as intermediate between primitive heliconian genera (such as *Dryas*) and *erato* or *charitonia*.

POPULATION FLUCTUATIONS

Besides being very localized, *hermathena* populations often exist at very low densities, with very small total sizes. In our first three visits to the Reserva Campina, the total numbers seen by several observers in a full day were 3 (28/X/71), 6 (11/II/72), and none (30/VII/73). When the butterflies were common there in July 1974, perhaps 30 to 50 *hermathena* occupied a very restricted part of the campina, while in the remaining area (greater than 80% of the total habitat) the butterflies were rarely encountered. A liberal estimate would give a total population size of 100 adult butterflies for the entire campina. By November the population had fallen to such a level that a two-hour search in the 2.5 ha section of campina turned up but a single *hermathena*. Over the same period, the population in a nearby 1 ha section had increased from near absence to approximately 30 butterflies, and the total campina possibly had no more than 75 adults. Thus, temporal and spatial changes in density can be quite pronounced.

Considering the great local variation in density of *hermathena* even in the relatively large Reserva Campina, it seems surprising that this species has been able to persist in such an isolated site. We have examined a very small campina (ca. 0.25 ha) about 3 km from the Reserva, and another medium-sized campina directly across a stream from the principal *hermathena* area; in the first neither *hermathena* nor its foodplant were found, in the second the foodplant was abundant and although no *hermathena*

were seen on several visits between 1970 and 1975, the butterfly was abundant in this area in July 1976. Disturbed campinas closer to Manaus, although larger, have for the most part been burned over, and the endemic plants and insects are much reduced. Neither *H. hermathena* nor *P. faroana* has been encountered on four such sites we have examined. To the west of Manaus is an extensive sandy beach on the Rio Negro (Ponta Negra) where *P. faroana* can be found growing. The area is at present very disturbed, although it obviously used to be very different from the *hermathena* localities we have studied, especially in terms of the greater development of the forest and the abundance of general forest *Passiflora* species and their heliconian herbivores. Since *hermathena* has never been reported from Ponta Negra, we suppose that it has been unable to colonize this habitat because of distance or unsuitable ecological conditions.

The most likely mechanism for the production of the great fluctuations in density which we have observed in *H. h. sheppardi* at the Reserva Campina is parasitism. Smith (1974) among others has pointed out the conventional wisdom that parasitism and predation often tend to produce large population fluctuations, while this is not true of competitive interactions. In the case of *hermathena*, variations in climatic conditions and resources do not seem to be of adequate intensity to account for the fluctuations we have observed, and they do not explain how adjacent populations act in completely opposite manners. Larval foodplants suitable for oviposition seem to be always common. We have found no evidence of parasitism in the several dozen *hermathena* eggs we have collected at the Reserva Campina; however, both larvae (one third, one fifth instar) collected during a single day in the 1 ha section of the campina (11 February 1972) possessed tachinid parasites. The same occurred with two fourth instar larvae collected on 28 October and 6 December 1974. We have not succeeded in rearing adults from field-collected late instar larvae from this locality. We should note here that larval parasitism, while widespread, is not common in the heliconians, and most tropical *Heliconius* populations appear very stable through time (Ehrlich and Gilbert 1973). Egg parasites develop rapidly in comparison to the reproductive period of a *Heliconius* butterfly, and would therefore be much less likely to exhibit the time lags that might produce instabilities in the adult population. Vandermeer (1975) analyzed an analogous situation involving seed predators and has come to essentially the same conclusion. On the other hand, long-lived tachinid parasitoids, especially if specialized, could produce time lags in their density-dependent responses

and might produce density fluctuations such as we have observed in *H. hermathena*. It is interesting in this respect that *H. ethilla* in Trinidad, although seemingly subject to a high level of egg parasitism, does not fluctuate greatly in density or recruitment rates (Ehrlich and Gilbert 1973).

PREDATION AND MIMICRY

The nominate subspecies, *h. sheppardi*, and *h. duckei* are shady-undergrowth flyers, with a coloration and flight habits which can best be described as flash-disruptive. *Hermathena* is found in scrubby but rather dense woods (fig. 2B) and *sheppardi* in dry "pseu-

PREV

NEXT

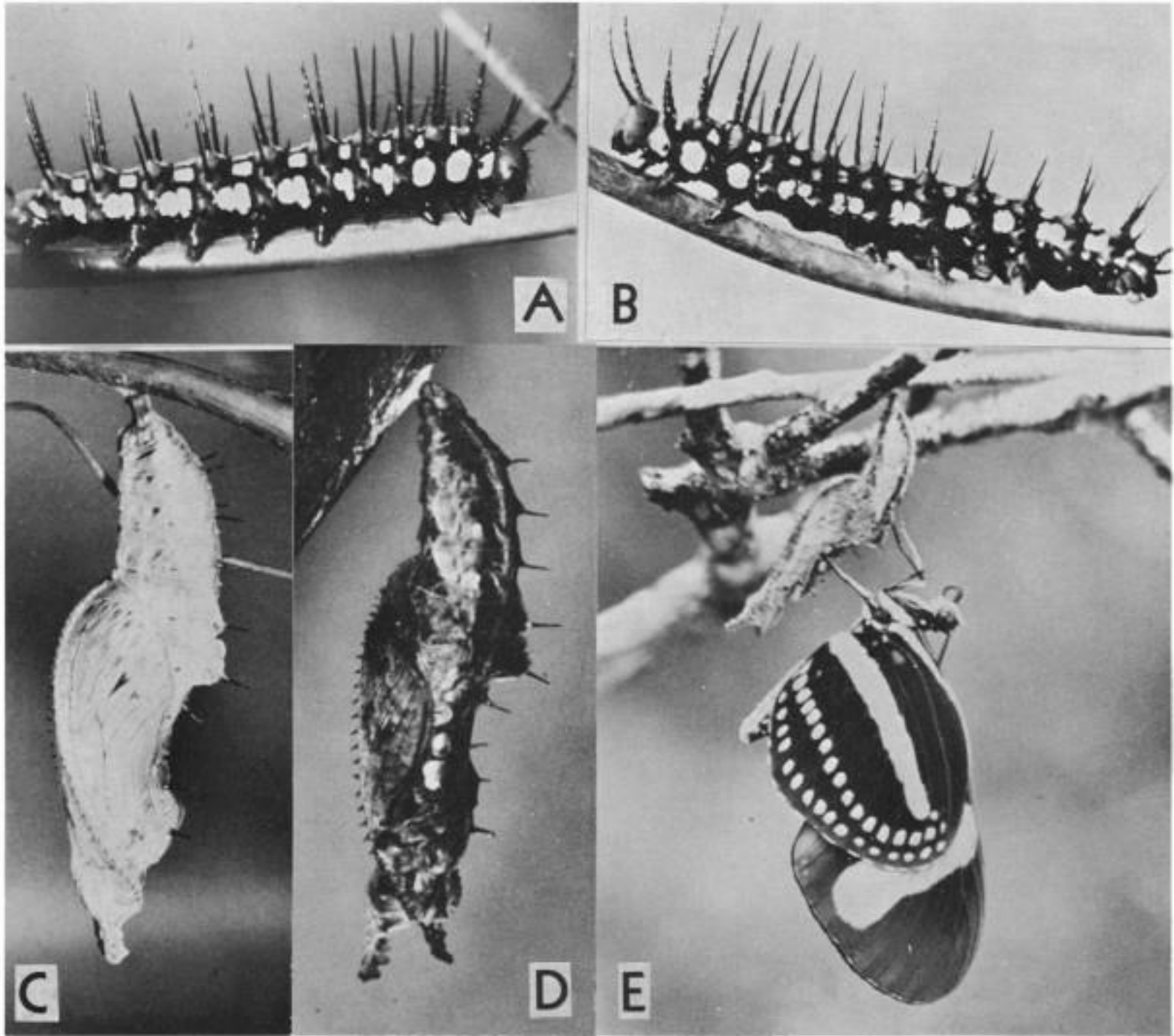


FIGURE 7. Early stages of *Heliconius hermathena* (continued). 7A, 7B. The fifth instar larva is strongly banded, each segment containing two rings of black and white and two of black and red (Reserva Campina) or orange (Faro), with the black areas essentially corresponding to those of other larvae in the *numata*, *melpomene*, and *erato* groups of *Heliconius*. The head is brick red (or orange) with frontal black dots as in *erato* and *charitonia* larvae. The head and abdominal scoli are black, about 2x head height; the anal segment is red (or orange); the underparts are dark brown. The maximum length is 36 mm; and the duration is 5-9 days. The prepupa is colored like the fifth instar, but "washed-out," and hangs by the anal segment from a pad of silk for 24 hours before splitting the larval skin. 7C, 7D. The pupa, when first formed, is soft and whitish, rapidly hardening and taking the final form which is medium to deep gray (as in D from Manaus) or shining white (as in C from Faro, Santarém, and occasionally in Manaus), hanging vertically by the cremaster, about 28 mm in over-all length. There are small, paired, dorsolateral flanges, fused, on the third and fourth abdominal segments, and short, subequal, paired dorsolateral spines on these flanges, on the thoracic segments and on other abdominal segments up through the seventh; four pairs of reflective spots on the prothorax, metathorax, and first two abdominal segments; and short, shallowly branched, head appendages. The duration is 10-15 days. 7E. The imago emerges in the early morning (Reserva Campina), hanging from the pupal case until the wings dry and harden, usually flying well before midday.

PREV

NEXT

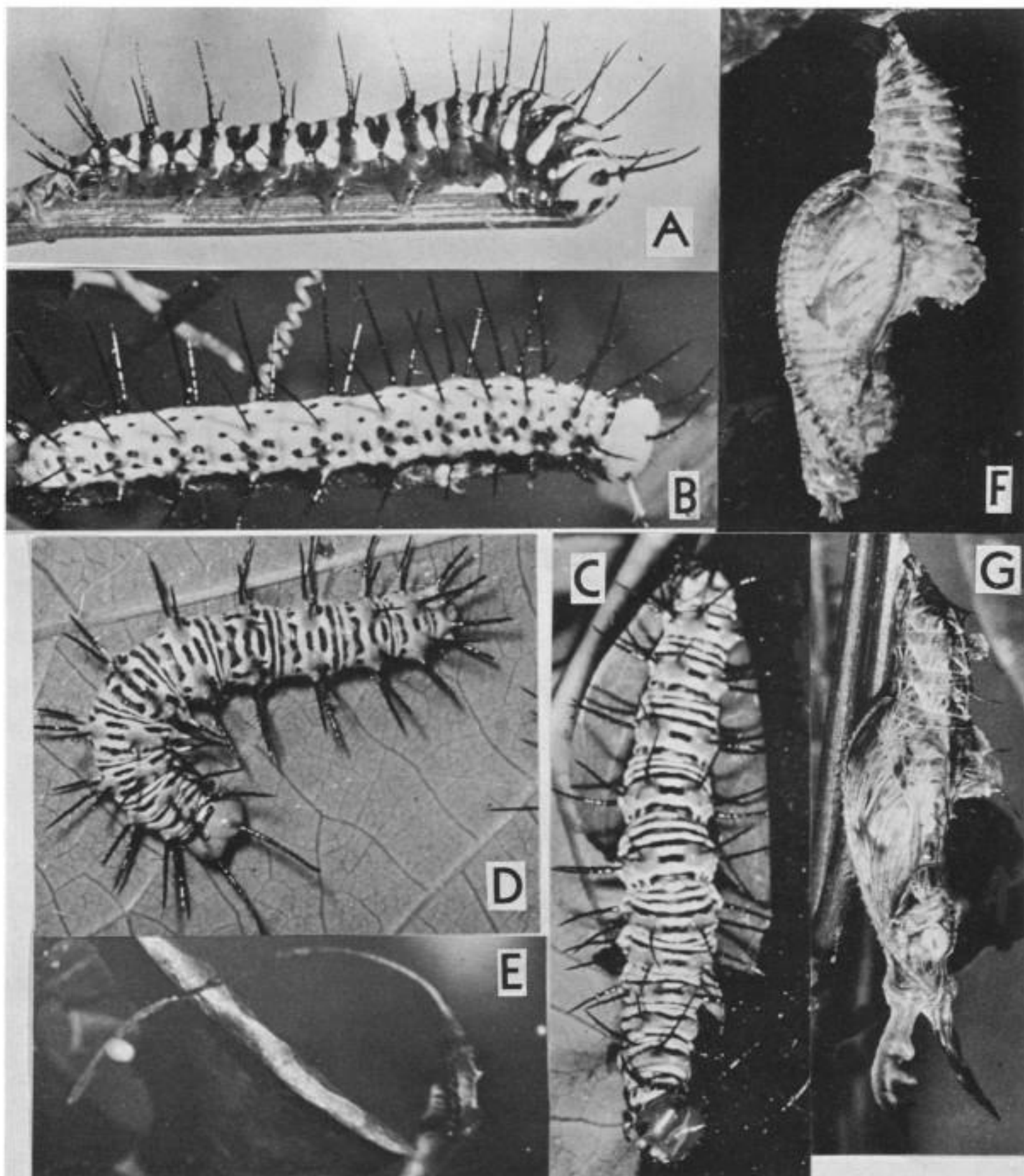


FIGURE 8. Early stages of species related to *hermathena*. 8A. Larva of *Heliconius charitonia simulator*, Kingston, Jamaica, fifth instar 3x. (Note that the larva is banded in this subspecies, though in others it is spotted like *erato* and *melpomene* larvae.) 8B. Larva of *Heliconius erato phyllis*, Rio de Janeiro, Brazil, fifth instar, 3x. 8C. Larva of *Philaethria pygmalion*, Santarém, Pará, Brazil, fifth instar, 2x. 8D. Larva of *Philaethria wernickei*, Petrópolis, Rio de Janeiro, fifth instar, 2x. 8E. Larva of *Philaethria dido*, La Macarena, Colombia, second instar on pseudotendril cut by its channeling, with an egg of the same species laid later on this, *Passiflora skiantha*. 8F. Pupa of *Heliconius melpomene melpomene*, Itacoatiara, Amazonas, Brazil, 3x. 8G Pupa of *Heliconius erato phyllis*, Rio de Janeiro, Brazil, 3x.

docaatinga" (campina, figs. 2D, 2E), corresponding with the habitats of their respective foodplants. Both fly principally inside low bushes (a habit also typical of *duckeii* at its type locality), in mottled shade and sun flecks, with erratic, jerky movements which defy visual following for any distance. Under these circumstances, the red band on the forewing becomes inconspicuous, and the butterfly appears as a broken series of light and dark stripes, easily lost from sight in the similarly light-dark illumination of the undergrowth. In this behavior *hermathena* closely resembles most subspecies of its close relative *charitonia*. We have seen *hermathena* and *sheppardi* in the open most often early or late in the day or in dark pre-storm weather, visiting flowers or warming, but never far from bushy retreats.

Heliconius charitonia has been called a non-mimetic *Heliconius* (Turner 1971a), though in a few areas it flies with very similarly patterned aposematic heliconians and ithomiines. *H. b. hermathena*, *sheppardi*, and *duckeii* are even more non-mimetic. Their color pattern is related to those of *erato* and *charitonia*, and is identical to that of the presumably most primitive pattern shown in a number of peripherally distributed subspecies of *erato* and *melpomene*. In addition, there are two series of paired, intervenal, submarginal yellow streaks on the hindwing, reminiscent of those present in *charitonia*. However, neither the various similar subspecies of *erato* and *melpomene*, with yellow hindwing bars, nor any subspecies of *charitonia* (which reaches southeast only to the eastern slopes of the Andes from Colombia to northern Peru), nor indeed any similarly patterned butterfly are known to occur within seven hundred kilometers of any known population of *hermathena*. In spite of this situation, no apparent evolution of mimetic color-pattern has occurred in these populations of *hermathena*, showing that they have not suffered irresistible selection for mimicry in their specialized habitats.

The degree of predator activity in campina and brush habitats occupied by *hermathena* is unknown, although some insectivorous birds have high preference for these areas (E. O. Willis, pers. comm.). These birds surely occasionally attack *hermathena* despite its distinctive color pattern and presumably bad taste. It seems reasonable, in the near absence of forest *Heliconius* in the open *hermathena* habitats, that resident birds and other predators would not have opportunity to encounter and form generalized avoidance responses to *hermathena* and other *Heliconius* that might lead to mimetic selection. Although *hermathena* are often rare, other congeners are almost nonexistent in the *sheppardi* and *duckeii* habitats.

Thus, the mixed strategy of aposematic and flash-disruptive behaviors would probably be a near optimal means of avoiding predation in these races, and mimicry would bring few added benefits.

Heliconius hermathena might be considered just a specialized relict with little evolutionary potential were it not for *H. b. vereatta*. This strongly mimetic form (fig. 3) is apparently restricted to upland sandy fields and swamps near Faro where it is common all year round. Here, neither parasitism nor nectar and pollen resources appear to be important limiting factors, and densities must approach those determined by the availability of host plant meristems. This race is most exceptional because of its excellent mimicry of *H. erato bydara* and *H. melpomene melpomene* (fig. 3D), which are especially common on the margins of fields where *vereatta* fly. The rapid replacement of *vereatta* by *duckeii* at localities away from the Amazon River to the north shows clearly the adaptive nature of the mimetic pattern, for there, *bydara* is replaced in deeper forest habitats by the very different *H. e. amalfreda* (it has an open, yellow, median forewing yellow band and a triangular red patch at the base of the wing; Brown and Mielke 1972) and *H. m. melpomene*, while still present, is much rarer.

The fact that the Santarém and Juruti populations of *b. hermathena* have not also evolved mimicry is somewhat a mystery, for they are microsympatric with abundant *H. m. melpomene* and frequent red-banded *erato* forms (indeed, Santarém populations are in much more intimate and permanent contact with these than is *vereatta* along field borders). Perhaps the dense scrub thickets composing the Santarém habitat (fig. 2B) or the wooded swamps of Juruti provide a more effective cover for the disruptive pattern than do the fields around Faro. However, as avian predators are common in these woods, and *hermathena* densities are not very high, the absence of mimetic forms in Santarém and Juruti (and in Maués, where the same situation seems to apply) may simply be because the appropriate genes have not yet had a sufficient opportunity to appear south of the river. The red-banded forms of *erato* and *melpomene* are coastal in origin, and their invasion of the banks of the Amazon embayment possibly corresponded with the relatively recent warming period which occurred after the last major interglacial period. The subsequent interval (less than 10,000 years) has perhaps been insufficient to permit an adaptive mutation of this type to appear in all populations.

POLYMORPHISM AND ECOLOGICAL GENETICS

The removal of the yellow median bar and paired intervenal streaks from the hindwing of *duckeii*, to

give the pattern of *vereatta*, has close parallels in other species of *Heliconius*. The genes determining the yellow hindwing bar in several races of *H. erato* and *H. melpomene* (perhaps homologous to the *bermathena* trait) are recessive in action (Emsley 1964; Turner 1972; Sheppard, Turner, Brown, and Benson, in preparation). In northern and Andean subspecies of *erato* and *melpomene*, the hindwing yellow-bar gene, when in the heterozygous condition, is easily detected phenotypically as a light "silky" differentiation across the dark scaling on the ventral surface. This circumstance has been called the "shadow-effect" by Emsley (1964). The holotype of *vereatta* shows a similar silky differentiation in the places in which yellow markings would be expected to occur in typical *duckei* (Emsley 1965), suggesting that this individual may be genotypically heterozygous for the yellow-barred condition.

The unbarred specimens (*vereatta*) in our series from Faro were, except for a few worn specimens, easily segregated into two phenotype classes. These were distinguished by the possession of an undifferentiated, matt black, ventral hindwing (presumed homozygotes, fig 9A) or the presence of the "shadow-effect" (presumed heterozygotes, fig 9B), most easily seen near the anal margin of the hindwing. Although conditions have not presented themselves to examine formally the inheritance of this character, it seems fairly safe to assume that the black hindwing condition is almost completely dominant over yellow-bar and dots.

Using this assumption of genotypic composition,

we have examined the morph frequencies of our three collections of polymorphic *bermathena* (*vereatta* x *duckei*) from populations near Faro. Two of our samples were made approximately six months apart at the same locality (Km 27 Faro-Terra Santa track), and the third from a different locality (Campos do Tigre) about 15 km to the south and during the same period as the second of the above samples. A strong agreement between the observed phenotypic frequencies and those expected from Hardy-Weinberg could be interpreted as substantiating the original genetic assumption and the idea that the populations we have studied are local randomly breeding units. The observed and expected (in parentheses, calculated from the observed genic frequencies) phenotypic frequencies of our samples are as follows:

Collection locality	Date	<i>Vereatta</i> types (2B)		<i>duckei</i> types (2C, 3C)
		Matt black hindwing (8A)	Shadow-effect hindwing (8B)	
Km 27	II-73	0 (1.65)	15 (11.69)	19 (20.65)
	VII-73	2 (2.96)	26 (24.08)	48 (48.96)
Campos do Tigre	VII-73	13 (13.14)	8 (7.73)	1 (1.14)

The expected frequencies are very close to the observed values in every case and do not indicate any significant departure from Hardy-Weinberg conditions. We have calculated Chi-square values for goodness of fit for each sample (although they are not strictly valid, because of the presence of an excessively low expected frequency in each sample), and in no case are these significant ($P > 0.05$, 0.30, and

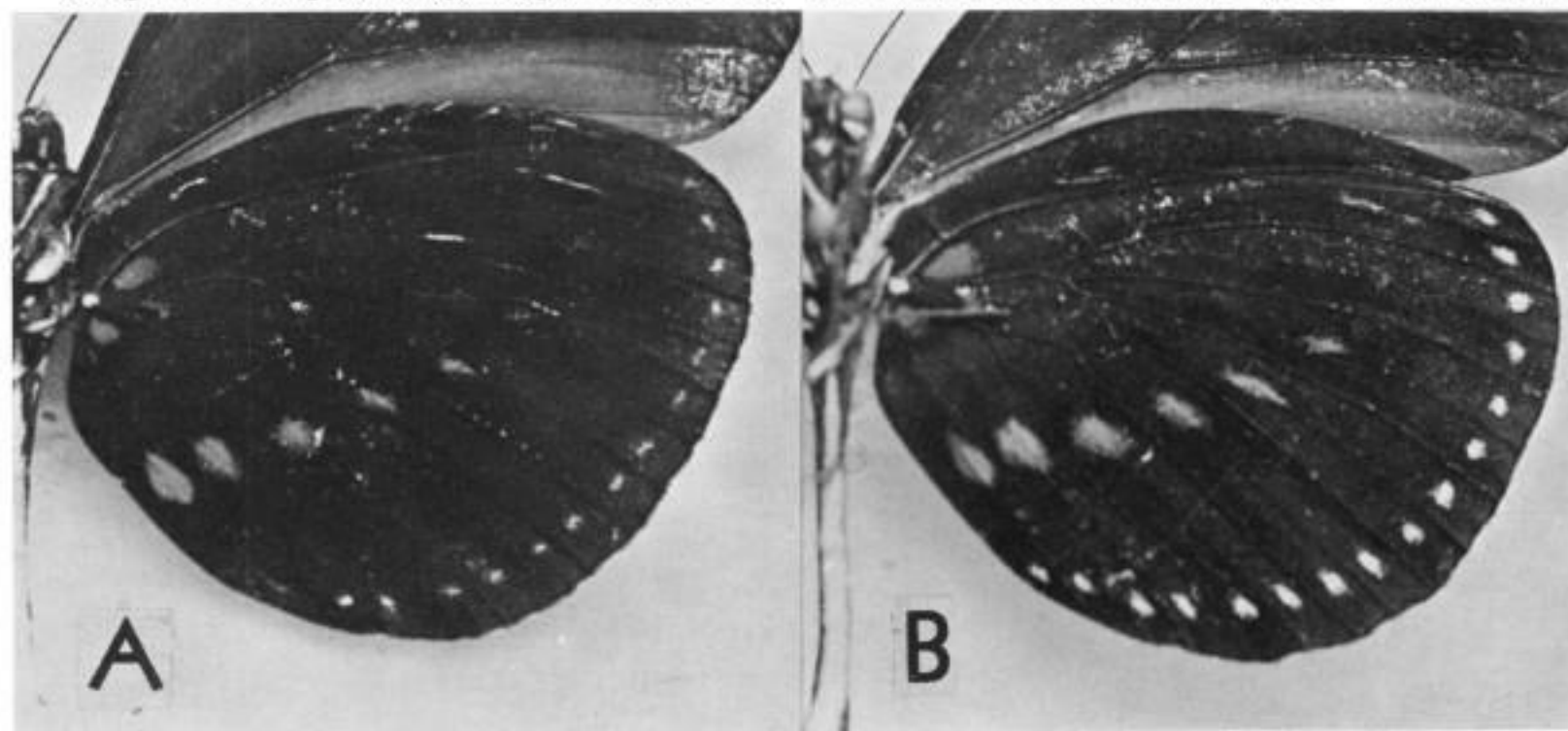


FIGURE 9. Genetics of *Heliconius bermathena vereatta*. Ventral hindwing surface, black and red, twice life size. 9A. Presumed homozygote; note lack of scale differentiation. 9B. Presumed heterozygote; note differentiation in the black scaling, especially near the anal margin, as a "shadow-effect."

TABLE 1. Comparisons of genic frequencies among populations of *Heliconius hermathena* near Faro, Pará, Brazil. Frequencies of the genes which determine the *vereatta* (V-) and *duckei* (vv) morphs of *H. hermathena* were calculated using scored phenotypes from net capture samples made in three localities, one of which was sampled on two different dates five months apart. The test was performed using the method of Sokal and Roblj (1969), G-test. (See the text for interpretation of the test results.)

Sample	Area	(date)	Gene Frequencies		Proportion V
			V	v	
A	Rio Nhamundá	(II,VII-73)	0	8 (+4) ^a	0.00
B	Km 27	(II-73)	15	53	0.22
C	Km 27	(VII-73)	30	122	0.20
D	Campos do Tigre	(VII-73)	34	10	0.77

Partitioned Tests of Heterogeneity		
Comparison	Degrees of Freedom	G
Overall (A x B x C x D)	3	60.57***
Rio Nhamundá x Polymorphic Populations (A x B + C + D)	1	8.31**
Campos do Tigre x Km 27 (D x B + C)	1	52.11***
Km 27 (II-73) x Km 27 (VII-73) (B x C)	1	0.15 ^{ns}

*** = $P < 0.001$

** = $P < 0.005$

^{ns} = not significant

^a The two visual observations of typical *duckei* are included in the analysis.

0.90, respectively). The results are completely consistent with the hypothesis that black hindwing is almost completely dominant over the yellow-striped condition, and that these populations show random breeding and are not subject to large immigration rates.

From our observations it seems reasonable to conclude that the *vereatta* race exhibits a clinal polymorphism with *duckei*, with near monomorphic *vereatta* populations present on the Campos do Tigre and perhaps eastward near the river, and with *duckei* prevailing in the campos along the east bank of the Rio Nhamundá northwards into the interior. The relatively undisturbed state of the fields and the pronounced mimicry between *vereatta* and *H. m. melpomene* and *H. e. hydara* would suggest that the polymorphism has been long standing, and that the cline is in a dynamic equilibrium. If these statements are true, we should expect that our three widely separated sampling localities would show significant differences in genic frequencies, whereas the two samples taken at different times of the year at the same

locality should be nearly identical. Statistical analysis (table 1) shows that indeed the genic frequencies differ greatly between the Campos do Tigre and Km 27 sites, and that the two gene-frequency estimates for the latter do not differ significantly. In the homozygous *duckei* sample (four captures and two visual observations) from the Rio Nhamundá north of the Km 27 field, the butterflies are sufficiently distinct from the *duckei*-like hybrids in a number of traits to consider them essentially pure. This sample was included in the formal analysis and compared with all the polymorphic samples as a group, from which it differs significantly. Moreover, it is also different enough from the combined Km 27 samples to be accepted as significantly distinct in spite of its small size ($P \sim 0.06$, exact binomial probability).

The *hermathena* sample collected by A. Ducke near Faro in the early part of this century included a single *duckei*-like form along with the 11 *vereatta*. If these really all came from the Campos do Tigre, as we initially hypothesized, it would indicate that the *vereatta* type in this locality has remained very constant during this century, supporting our idea of the relative stability of these populations.

We have mentioned previously our interpretation of the adaptive significance of color patterns in *hermathena*. If the color morphs presented by this butterfly near Faro really represent adaptations to avoid predation, local patterns of differentiation might be expected in areas where selective pressures for divergent ecological strategies change greatly over short distances. On the first visit to the Km 27 site early in 1973, it was noted that the *vereatta*-like (mimetic) morphs were flying during the mid-morning in a low swampy area, whereas yellow-barred individuals tended to occur outward into the drier campo. However, these observations were subjective, and it was deemed of interest to repeat and quantify them.

On the return visit in July, an initial survey proved that the insects were fully occupying a much more extensive area than was previously observed, and that many insects were flying in dry scrub well away from the swampy area where the original observations were made. This second colony was situated in the middle of a hot sandy field about 200 m west of the (unused) Faro-Terra Santa road (here simply a 3 m wide track across the campo), and it centered around an archipelago of 2 m high scrub patches (total extension about 50 x 200 m, fig. 4A). *P. faroana* was much more abundant in this area than in the surrounding grassy fields, which had apparently recently burned. The *hermathena* were common here

and moved freely among the scrub patches and out over the field, especially during cloudy spells and in the earlier part of the day. Later, in the heat of mid-day, the butterflies sat in the shade under the bushes, or flew around inside the small patches, usually only a few cm above ground level. The dark *vereatta* morph appeared to retreat to these areas earlier, such that after 1100 the butterflies encountered in the open were almost exclusively of the yellow-barred morph.

The colony in the swamp area (fig. 4B) was centered about 500 m to the east of the road, directly across it from the field population. The area had a few 8-10 m high trees but was dominated by a mosaic of 4 m high palm woods with thick thorny undergrowths, and separated by marsh, pools of open water, and scrub patches. *P. favaoana* was not so common as in the field, although it was generally distributed within the swamp and especially found in the hedge-row like tangles of low vegetation around marsh margins.

Unlike the field, the swamp harbored a population of *H. m. melpomene*, the model for *H. b. vereatta*. Although *melpomene* did not seem very abundant, it is difficult to distinguish from *vereatta* when it is flying at a distance, and was no doubt less subject to net capture than *hermathena*.

Each of the two colonies was observed on a separate day, and counts were made of the number of visual observations on each of the two morphs. In the field area, 109 observations, including no doubt some repeats, gave a ratio between yellow-barred (*duckei*-like) and unbarred mimetic (*vereatta*-like) forms of 1.7:7. As proportionally more *duckei*-like morphs were captured during the census, the ratio may well have exceeded 2:1. In contrast, the 92 observations from the swamp colony showed the *duckei*-like form to be in the minority, with a relative proportion of 0.92:1. Net captures from the swamp contained an even greater excess of dark morphs, suggesting that the true ratio may have approached 0.75:1. When we scored all dark morphs as heterozygotes (Vv), the approximate genic frequencies for the *vereatta* (V) gene in the field and swamp colonies were 0.17 and 0.32, respectively. A comparison of the actual counts from the two areas gives:

Field colony	with yellow, <i>duckei</i> -form (vv)	69
	without yellow, <i>vereatta</i> -form (V-)	40
Swamp colony	with yellow, <i>duckei</i> -form (vv)	44
	without yellow, <i>vereatta</i> -form (V-)	48

These data showed a significant difference ($G = 4.25$; $P < 0.05$, with Yates' correction, Sokal and Rohlf 1969). Because of the possibility that some butterflies were counted more than once, we cannot

assert that in the absence of multiple observations these data would continue to be significant; however, they are strongly indicative of real differences in the local occurrence of morphs. Moreover, the discrepancy fits in well with what we suppose to be the major selective force for color-pattern differentiation. Thus, in the more closed vegetation of the swamp, where *vereatta* predominates, we have *H. m. melpomene* present, and predators which have had the opportunity to learn to avoid this insect. On the other hand, the field lacks *melpomene*, but presents a more strongly lighted habitat in which the yellow-barred *hermathena* pattern blends in and would be more difficult to distinguish by predators. We suggest that the distribution patterns are real and that they are indicative of predator selection operating at different relative intensities on the two morphs in the different habitat types. Behavioral differences between the morphs may also be contributing to these observations, possibly due to genes which regulate habitat selection being linked to elements which determine color pattern. However, the maintenance of such linkage also implies selection.

It is not necessary to postulate, and indeed we do not, that selective pressures are necessarily operating in opposite directions with respect to the two morphs in different habitats, but merely that they exhibit different intensities depending on local conditions. Such variations in selection should result in "kinks" in what might otherwise be continuous morph-frequency clines. Although a single example is not sufficient to be convincing, we might suggest that correlations between morph frequencies and pertinent ecological measurements along clines would provide a sensitive method for the identification of causal factors in the differentiation of populations. With adequate sampling, random and historical noise could be controlled, or adjacent and partially crossbreeding populations could be chosen so as to reduce such effects produced by isolation.

In the two Km 27 populations of *H. hermathena*, the centers of the colonies were separated by approximately 700 m of brushy field, and potential genetic exchange between the colonies was great. A number of butterflies were observed in the intervening area, both over the open field and in a crescent-shaped scrubby "bridge" between the ends of the colonies.

The reduced range of *H. hermathena vereatta*, its persistence in the face of intimate and extensive contact with the non-mimetic *H. b. duckei*, and its close mimicry with sympatric forms of *H. melpomene* and *H. erato*, which seem to be recent invaders of the area, present the possibility that *vereatta* has differ-

entiated relatively recently in evolutionary time, and has become established because of strong local selective pressures and despite the absence of major geographic barriers.

EDAPHIC ASSOCIATIONS AND DISTRIBUTION

Thus, associated with its unusual habitats, *hermathena* has evolved a number of adaptations which seem to facilitate its survival at low densities and under rather anomalous conditions. Campina and campo formations suitable for the species are widely distributed throughout the central and northern Amazon Basin. Their geological origins are probably diverse, although many, such as the campinas near Manaus, were apparently derived from sandy stream deposits which were left as high, isolated benches when the streams took new courses and eroded deep channels. All of the deep, sandy-soiled areas which we have observed inland from Manaus are associated with larger streams. The extensive "pseudocaatingas" of the upper Rio Negro, and the large upland campos near Faro, appear to be consequences of similar processes occurring with larger rivers, although more data are needed on this point. The sand itself originated by erosion of sandstone deposits and igneous rocks of the Guianan shield (and, south of the river and less extensively, the Brazilian shield). The rockfield at Km 130 of the Manaus-Caracará highway is of a degraded sandstone nature and possesses many plants and animals, including *H. hermathena sheppardi*, characteristic of the sandy campinas (G. Prance, pers. comm.). True Amazonian grasslands, in which *H. hermathena* is in our experience always absent, have in general finer-grained soils and high water tables, and may be subject to seasonal flooding (such as those at Caracará, and elsewhere in the várzea of the Rio Branco). It is not known if *hermathena* populations occur north as far as the southern rim of the Guiana shield along the northern border of Brazil, although this possibility cannot be excluded. Unfortunately, the places it might be expected to occur are difficult to reach and are at present uncollected.

Campina-like habitats extend well up the Rio Negro into eastern Colombia (Río Vaupés) and southern Venezuela, and the parent geological formation extends along all of the northern border of Brazil and perhaps across east-central Colombia to the Serranía de la Macarena at the base of the eastern Andean Cordillera (Haffer 1974). For this reason, there is no great difficulty in postulating an essentially continuous past distribution for *hermathena* over much of the northern Amazon Basin, despite its obvious habitat restriction today, and it may even

have been in contact with *Heliconius charitonia* in the not too distant past. Moreover, it is not necessary to assume that *hermathena* ever occurred away from scrubby vegetation on sandy soils; these habitats were probably common in the past and are well represented today throughout the Amazon Basin. Reduction in rainfall and/or ground water in the past could have easily resulted in large areas of open non-forest habitats interconnected by networks of sandy stream beds. These would have permitted an essentially continuous distribution for campina endemics such as *H. hermathena*.

Many Amazonian non-forest habitats are apparently not suitable today for *hermathena*. Such are the "cerrados" near the mouth of the Amazon (fig. 10A), also known elsewhere; swampy fields on the Ilha do Marajó at the mouth of the Amazon (fig. 10B); periodically flooded "várzea" fields (figs. 10C, 10D), common near major rivers in areas of reduced rainfall; "cerrados" and "campos" of northern Roraima (fig. 10E); and "cerrados" and "cerradão" in Rondônia in the southwest Amazon (fig. 10F). The last area, however, may be too distant from the center of *hermathena* distribution to have ever been colonized. The highest probability for encounter of the species is in scrubby climax vegetation near rivers and major streams but above high water marks. Perhaps most important, but not a sufficient condition, is the presence of the required primitive *Passiflora* host plant species, which prefer deep sandy soils.

DIFFERENTIATION IN MODERN NON-FOREST ISLANDS

The differentiation of *hermathena* in isolated non-forest habitats in the Amazon Basin offers a noteworthy parallel to that observed in forest heliconians, postulated to have occurred in isolated forest refugia in the past. Thus, highly localized colonies, with much reduced rates of gene flow, have developed characteristic morphological and behavioral patterns related to local environments. The most extreme of these patterns by far is that shown by the mimetic subspecies *vereatta*, but it is to be expected that additional studies will reveal other patterns of local differentiation of important adaptive characters perhaps unrelated to adult color pattern.

The great expansion of the Neotropical forests today has rendered impractical most studies of the contemporary evolution of organisms restricted to these habitats. However, the corresponding reduction of non-forest habitats has produced widely scattered and fragmented gene pools which should be undergoing adaptive evolution in many ways. Per-

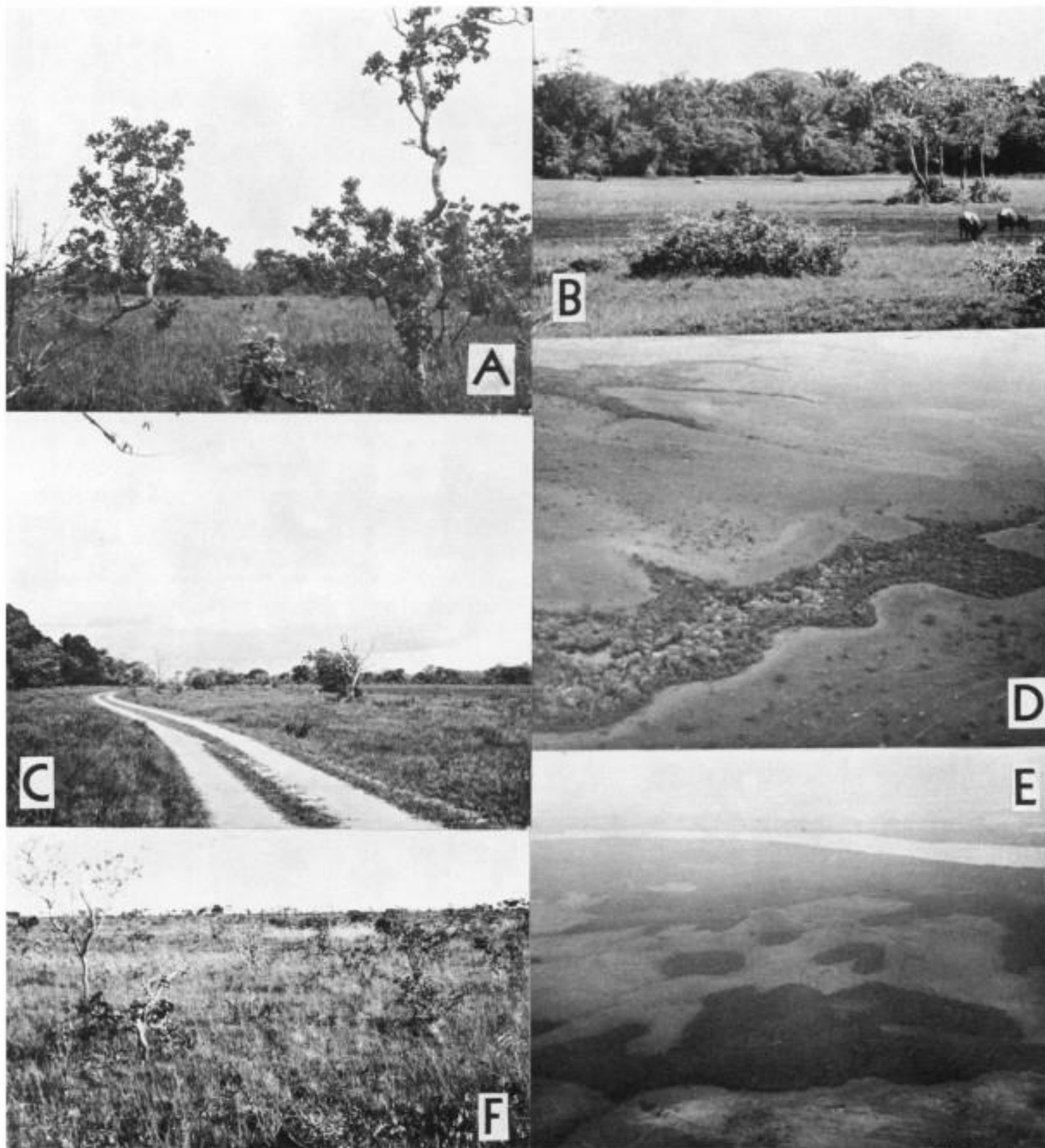


FIGURE 10. Amazonian non-forest habitats not occupied by *Heliconius hermathena* in present time. 10A. Cerrado near Vigia, Pará, northeast of Belém. 10B. Swampy fields and scrub forest in the eastern part of the Ilha do Marajó, at the mouth of the Amazon River. 10C. Terrestrial view of várzea fields near Terra Santa, Pará, just east of Faro on the lower Rio Nhamundá. 10D. Aerial view of várzea field near Terra Santa. 10E. Aerial view of fields and forest south of Boa Vista, Roraima, with the Rio Branco in the background, looking west over fields unsuccessfully explored for *H. hermathena* in 1974 and 1977. 10F. Cerrado near Vilhena, Rondônia, in the southwestern part of the Amazon Basin at high elevation (600 m).

haps the most significant observations of the contemporary action of eco-evolutionary forces in the Neotropics can be made in these isolated non-forest islands, which merit greater attention by students of tropical ecology.

ACKNOWLEDGEMENTS

We are grateful to the Instituto Nacional de Pesquisas da Amazônia (housing in and ground transportation near Manaus), the Companhia de Mineração de Santarém (lodgings at Acampamento Céu Estrelado, north of Faro, and air transportation Santarém-Faro), the Expedição Permanente na

Amazônia of the Fundação de Amparo à Pesquisa do Estado de São Paulo (river transportation Santarém-Faro), and the Força Aérea Brasileira (extensive air transportation around Pará) for invaluable logistic support of this work. Drs. Philip M. Sheppard, F.R.S., and John R. G. Turner contributed many useful comments to the development of this paper. Photographic enlargements were prepared with the kind assistance of Jorge H. Leão. Financial aid for ecological studies of Brazilian plants and insects was received from the Conselho Nacional de Pesquisas, the Conselho de Pesquisa e Ensino para Graduados of the U.F.R.J., the Banco Nacional do Desenvolvimento Econômico (FUNTEC 47 and 101), and the Ministério de Planejamento (FINEP/FNDCT, contrato 140/CT).

PREV

NEXT

LITERATURE CITED

- ALEXANDER, A. J. 1961. A study of the biology and behavior of the caterpillars, pupae, and emerging butterflies of the subfamily Heliconiinae in Trinidad, West Indies. Part I. Some aspects of larval behavior. *Zoologica*, N.Y. 46: 1-24.
- BEARD, J. S. 1953. The savanna vegetation of northern tropical America. *Ecol. Monogr.* 23: 149-215.
- . 1955. The classification of tropical American vegetation-types. *Ecology* 36: 89-99.
- BEEBE, W., J. CRANE, AND H. FLEMING. 1960. A comparison of eggs, larvae, and pupae in fourteen species of heliconiine butterflies from Trinidad, West Indies. *Zoologica* N.Y. 45: 111-154.
- BENSON, W. W. 1971. Evidence for the evolution of unpalatability through kin selection in the Heliconiinae (Lepidoptera). *Am. Nat.* 105: 213-226.
- . 1972. Natural selection for Müllerian mimicry in *Heliconius erato* in Costa Rica. *Science* N.Y. 176: 936-939.
- , K. S. BROWN, JR., AND L. E. GILBERT. 1976. Coevolution of plants and herbivores: passion flower butterflies. *Evolution*, Lancaster, Pa. 29: 659-680.
- BROWN, K. S. JR. 1972. The heliconians of Brazil (Lepidoptera: Nymphalidae). Part III. Ecology and biology of *Heliconius nattereri*, a key primitive species near extinction, and comments on the evolutionary development of *Heliconius* and *Eueides*. *Zoologica*, N.Y. 57: 41-69.
- . 1976. Geographical patterns of evolution in Neotropical Lepidoptera. Systematics and derivation of known and new Heliconiini (Nymphalidae: Nymphalinae). *J. Ent. (B)* 44: 201-242.
- . 1977a. Geographical patterns of evolution in neotropical forest Lepidoptera (Nymphalidae: Ithomiinae and Nymphalinae-Heliconiini), pp. 118-160. *In*, H. Descimon (Ed.), *Biogéographie et Evolution en Amérique Tropicale*. Publ. Lab. Zool. Ec. Norm. Sup., Paris, 9.
- . 1977b. Centros de evolução, refúgios quaternários e conservação de patrimônios genéticos na região neotropical: padrões de diferenciação em Ithomiinae (Lepidoptera: Nymphalidae). *Acta Amazonica* 7:75-137.
- , AND W. W. BENSON. 1975a. The heliconians of Brazil (Lepidoptera: Nymphalidae). Part VI. Aspects of the biology and ecology of *Heliconius demeter*, with description of four new subspecies. *Bull. Allyn Mus.* 26: 1-19.
- . 1975b. West Colombian biogeography: notes on *Heliconius hecalesia* and *H. sapho* (Lepidoptera, Nymphalidae). *J. Lepid. Soc.* 26: 199-212.
- , AND H. HOLZINGER. 1973. The heliconians of Brazil (Lepidoptera: Nymphalidae). Part IV. Systematics and biology of *Eueides tales* Cramer, with description of a new subspecies from Venezuela. *Z. ArbGem. öst. Ent.* 24: 44-65.
- , AND O. H. H. MIELKE. 1972. The heliconians of Brazil (Lepidoptera: Nymphalidae). Part II. Introduction and general comments, with a supplementary revision of the tribe. *Zoologica*, N.Y. 57: 1-40.
- , P. M. SHEPPARD, AND J. R. G. TURNER. 1974. Quaternary refugia in tropical America: evidence from race formation in *Heliconius* butterflies. *Proc. R. Soc. (B)* 187: 369-378.
- COLE, M. M. 1960. Cerrado, caatinga and pantanal: the distribution and origin of the savanna vegetation of Brazil. *Geogr. J.* 126: 166-179.
- DUCKE, A., AND G. A. BLACK. 1953. Phytogeographical notes on the Brazilian Amazon. *Anais Acad. Bras. Ciênc.* 25: 1-46.
- EHRlich, P. R., AND L. E. GILBERT. 1973. Population structure and dynamics of the tropical butterfly *Heliconius ethilla*. *Biotropica* 5: 69-82.
- EITEN, G. 1975. The vegetation of the Serra do Roncador. *Biotropica* 7:112-135.
- EMSLEY, M. G. 1963. A morphological study of imagine Heliconiinae (Lep. Nymphalidae) with a consideration of the evolutionary relationships within the group. *Zoologica*, N.Y. 48: 85-130.
- . 1964. The geographical distribution of the color-pattern components of *Heliconius erato* and *Heliconius melpomene* with genetical evidence for the systematical relationship between the two species. *Zoologica*, N.Y. 48: 245-286.
- . 1965. Speciation in *Heliconius* (Lep. Nymphalidae): morphology and geographic distribution. *Zoologica*, N.Y. 49: 245-286.
- FERRI, M. G. (Ed.) 1963. Simpósio sobre o cerrado. Editora da Univ. São Paulo, São Paulo.
- . 1971. III simpósio sobre o cerrado. Editora Blücher, São Paulo.

- GILBERT, L. E. 1972. Pollen feeding and reproductive biology of *Heliconius* butterflies. *Proc. Nat. Acad. Sci. U.S.A.* 69: 1403-1407.
- . 1975. Ecological consequences of a coevolved mutualism between butterflies and plants, pp. 210-240. *In*, L. E. Gilbert and P. H. Raven (Eds.). *Coevolution of animals and plants*. Univ. Texas Press, Austin, Texas.
- HAFER, J. 1967. Speciation in Colombian forest birds west of the Andes. *Am. Mus. Novit.* 2294: 1-57.
- . 1969. Speciation in Amazonian forest birds. *Science, N.Y.* 165: 131-137.
- . 1974. Avian speciation in tropical South America. *Publ. Nuttall orn. Club No. 14, Mus. comp. Zool., Cambridge, Mass.* viii + 390 pp.
- HEWITSON, W. C. 1853. Exotic butterflies, vol. I, *Heliconia* II. John van Voorst, London.
- HILLS, T. L. 1969. The savanna landscapes of the Amazon Basin. *Savanna Res. Ser. No. 14, Dept. Geography, McGill Univ., Montreal.*
- HUECK, K. 1966. *Die Wälder Südamerikas*. Fisher Verlag, Stuttgart.
- JANZEN, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution, Lancaster, Pa.* 21: 620-637.
- . 1974. Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica* 6: 69-103.
- JONES, F. M. 1930. The sleeping *Heliconias* of Florida. *Nat. Hist. N.Y.* 30: 635-644.
- KILLIP, E. P. 1938. The American species of Passifloraceae. *Publ. Field Mus. nat. Hist. (Bot. Ser.)* 19: 1-613.
- KINGDON, J. 1971. East African mammals. An atlas of evolution in Africa. Vol. 1. Academic Press, London.
- MAYNARD SMITH, J. 1974. *Models in ecology*. Cambridge University Press, Cambridge. 146 pp.
- MAYR, E. 1969. Bird speciation in the tropics. *Biol. J. Linn. Soc.* 1: 1-17.
- MOREAU, R. E. 1963. Vicissitudes of the African biomes in the late Pleistocene. *Proc. zool. Soc. Lond.* 141: 395-421.
- . 1966. The bird faunas of Africa and its islands. Academic Press, New York. viii + 424 pp.
- . 1969. Climatic changes and the distribution of forest vertebrates in West Africa. *J. Zool. (London)* 158: 39-61.
- MÜLLER, P. 1972. Centres of dispersal and evolution in the neotropical region. *Stud. neotrop. Fauna* 7: 173-185.
- . 1973. The dispersal centres of terrestrial vertebrates in the Neotropical Realm. A study in the evolution of the neotropical biota and its native landscapes. *Biogeographica*, vol. 2, Junk, the Hague. vi + 224 pp.
- PRANCE, G. T. 1973. Phytogeographic support for the theory of Pleistocene forest refuges in the Amazon basin, based on evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichapetalaceae and Lecythidaceae. *Acta Amazônica* 3: 5-28.
- SOKAL, R. R., AND F. J. ROHLF. 1969. *Biometry*. Freeman, San Francisco. 776 pp.
- STICHEL, H. 1912. Zwei neue Formen von *Heliconius hermathena* Hew. *Int. ent. Z.* 6: 1-2.
- TURNER, J. R. G. 1965. Evolution of complex polymorphism and mimicry in distasteful S. American butterflies. *Proc. XII int. Congr. Ent. London 1964*: 267.
- . 1968. Some new *Heliconius* pupae: their taxonomic and evolutionary significance in relation to mimicry (Lepidoptera, Nymphalidae). *J. Zool. (London)* 155: 311-325.
- . 1971a. Studies of Müllerian mimicry and its evolution in burnet moths and heliconid butterflies, pp. 224-260. *In*, E. R. Creed (Ed.). *Ecological genetics and evolution*. Blackwell, Oxford.
- . 1971b. Experiments in the demography of tropical butterflies. II. Longevity and home-range behavior in *Heliconius erato*. *Biotropica* 3: 21-31.
- . 1972. The genetics of some polymorphic forms of the butterflies *Heliconius melpomene* (Linnaeus) and *H. erato* (Linnaeus) II. The hybridization of subspecies of *H. melpomene* from Surinam and Trinidad. *Zoologica, N.Y.* 56: 125-157.
- . 1975. Communal roosting in relation to warning colour in two heliconiine butterflies (Nymphalidae). *J. Lepid. Soc.* 26: 221-226.
- VANDERMEER, J. H. 1975. A graphical model of insect seed predation. *Am. Natur.* 109: 147-160.
- VANZOLINI, P. E. 1970. *Zoologia sistemática, geografia e a origem das espécies*. Inst. Geogr., Série Teses e Monografias, São Paulo 3: 1-56.
- . 1973. Paleoclimates, relief, and species multiplication in tropical forests, pp. 255-258. *In*, B. J. Meggers, E. S. Ayensu, and W. D. Duckworth (Eds.). *Tropical forest ecosystems in Africa and South America: a comparative review*. Smithsonian Institution, Washington. 350 pp.
- VUILLEUMIER, B. S. 1971. Pleistocene changes in the fauna and flora of South America. *Science N.Y.* 173: 771-780.
- YOUNG, A. M. 1974. Further observations on the natural history of *Philaethria dido dido* (Lepidoptera: Nymphalidae: Heliconiinae). *J. N.Y. ent. Soc.* 82: 30-41.