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THE HELICONIANS OF BRAZIL (LEPIDOPTERA: NYMPHALIDAE). PART IV. SYSTEMATICS AND BIOLOGY OF *EUEIDES TALES* CRAMER, WITH DESCRIPTION OF A NEW SUBSPECIES FROM VENEZUELA

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INTRODUCTION AND HISTORICAL BACKGROUND

The mimetic heliconian species *Eueides tales*, locally common in the Amazon Basin, western Guianas, Venezuela, and Colombia, was first described by CRAMER in the first volume (1775–1776) of his „Papillons Exotiques." The Guianian form he figured (reproduced in Figure 1) was captured in Suriname; modern collectors in (French) Guyane have not encountered the species, but it continues common in parts of (formerly British) Guyana and probably in Suriname. Like many sympatric species of heliconians and ithomiines, it possesses a succession of red, yellow, and black colors from the base to the apex of the forewing, with the hindwing essentially black on the dorsal surface. The ventral hindwing (right half of Figure 1) bears a series of red rays overlying the veins (not between the veins as in all other similarly rayed heliconians) and fused into an antesubmarginal red line, which is bordered externally by two parallel rows of paired intervenal submarginal white spots.

As *Nereis Festiva thales*, Jacob HÜBNER illustrated in the first volume of his „Sammlung Exotischer Schmetterlinge" (1810) a different form of the same species, presumably from Pará (Figure 2), which although very similar to CRAMER's *tales* on the ventral hindwing surface, possesses larger yellow markings on the forewing, and well-developed red rays over the veins of the dorsal hindwing. Recognizing these differences, KIRBY, 1900 rebaptized this rayed form *pythagoras*, and STICHEL, 1903, unaware of KIRBY's action, renamed the same figure *heraldicus*.

These two forms (*tales* and *pythagoras*, plus intermediates where populations of the two meet near the Amazon and Negro Rivers) occupy nearly the entire Amazon Basin and the western Guianas; the only important variety is that of *tales* which lacks the rays on the ventral hindwing (Figure 3), named *surdus* by STICHEL, 1903. In the north-western part of the species' range (see Map), populations isolated in the past (probably during Pleistocene dry spells; see BROWN, SHEPPARD, and TURNER in preparation) have evolved into well-differentiated and still essentially isolated subspecies. In the presumed Napo refugium (HAFFER, 1969) in the upper Amazon Basin of Ecuador and Peru, the subspecies *calathus* STICHEL, 1909 originated and is found locally today, with the same appearance (Figure 4) as that of other rayed heliconians in this area. As with the other species, this phenotype in *tales* appears today in mixed populations over much of the Amazon Basin west of Manaus (Figure 5).

The unity of the various subspecies of *tales* was recognized early in the systematic study of the Heliconiini, and was presented in essentially complete form by STICHEL and RIFFARTH, 1905, SEITZ, 1913 (with inaccurate illustrations), and NEUSTETTER, 1929. Only the east Colombian subspecies, then known as *heliconioides* (auct. nec. FELDER), was maintained separate by these authors. It was correctly joined to *tales* in EMSLEY's more recent revision (1965). The recent discovery that the description of *heliconioides* FELDER, 1861 showed it to possess intervenal rays reaching nearly to the hindwing margin, and a single row of paired white submarginal dots (HOLZINGER and HOLZINGER, 1969), placed this form with the upper Amazonian species *Eueides eanes* HEWITSON, 1861; the east-Colombian subspecies of *tales* (Figure 6) thus acquired the name *cognatus** WEYMER, 1890. The paper which clarified this systematic aspect also discussed the synonymy of the central Colombian subspecies *xenophanes* FELDER, 1865 (Figure 7), and commented on some further names in the *tales* complex.

Other recent papers by the present authors have described a new subspecies of *Heliconius xanthocles* from Venezuela (HOLZINGER and HOLZINGER, 1971), and discussed the taxonomic status of *Heliconius clysonymus* and *hygiana* (idem., 1970), some new transitional forms of *H. cydno* (idem., 1968), the ecology and biology of the dis-

* Emended from original *cognata;* note, however, that the preservation of author's original names, a practice which would encourage greater nomenclatural stability but which is not approved by the present International Code of Zoological Nomenclature, has been defended in heliconians by TURNER, 1967 and BROWN & MIELKE, 1972.

appearing primitive species *H. nattereri* (BROWN, 1970, 1972), and the species of heliconians known from Brazil, with a supplementary revision of the tribe (BROWN and MIELKE, 1972). This paper presents a complete systematic revision of the species *Eueides tales*, with comments on the subspecies and their distributions (including description of a new subspecies from the Sierra Perijá, Venezuela), and description of the juvenile biology of this species, which represents one of the few reported cases of evident Müllerian mimicry in Lepidopterous larvae.

SYSTEMATICS

We have briefly presented support for the maintainance of the genus *Eueides* separate from *Heliconius* (BROWN and MIELKE, 1972); the character differences which suggest the biological validity of this separation, in contradiction to the fusion proposed by MICHENER, 1941 and adopted by EMSLEY, 1965 and other recent authors, are summarized in Table I.

The morphology of *Eueides tales* was amply discussed by EMSLEY, 1965; we have also illustrated a comparison of the male genitalia with those of the externally similar but not closely related species *Eueides eanes* (HOLZINGER and HOLZINGER, 1969), the only other rayed species in the genus. The species *tales* may be immediately separated from all other known heliconian species, and indeed from all other butterflies in the local mimetic complexes in which *tales* subspecies participate, by the ventral surface of the hindwing, which carries a unique combination of a double row of paired intervenal submarginal white spots, and red scaling, usually including well-developed rays, overlying the veins (actually concentrated immediately alongside the veins on both sides). Occasional individuals in the more western part of the Amazon Basin show a partial obliteration of the inner row of submarginal white dots, but still possess rays overlying the veins rather than between them; one such individual, from São Gabriel on the upper Rio Negro, was named „*Eueides eanes* f. *lucretius*“ by ZIKÁN, 1937 (Figure 8).

The division of *Eueides tales* into subspecies and acceptable named forms is delineated in the accompanying Key. Many individuals, especially found near large rivers or where two subspecies intermingle, will not correspond exactly in color pattern with the named forms pictured in Plate I; these, as well as two of the forms pictured (Figure 5), are not judged to be worthy of new names. The distributions and interactions of the subspecies are pictured in the Map, and further discussed below under Behavior and Genetics. The only subspecies of *tales* which intergrade in well-marked hybrid zones are those found in the Amazon Basin (*tales*, *pythagoras*, *cognatus*, and *calathus*); the patterns of their separation, and the locations of the secondary hybrid zones today, strongly suggest the action of forest refugia during dryer periods of the Pleistocene (see HAFFER, 1969; TURNER, 1971; and BROWN, SHEPPARD, and TURNER, in preparation). The sizes of the secondary contact zones between subspecies indicate appreciable mobility for the species (see below, under Behavior).

TABLE I

SIGNIFICANT CHARACTER DIFFERENCES BETWEEN *EUEIDES* AND *HELICONIUS*

Criteria	*Eueides*	*Heliconius*
1) MORPHOLOGICAL		
Female foretarsi	Four-segmented	Five-segmented*
Signa on female bursa copulatrix	Often unsymmetrical and/or curved more than 90°	Symmetrical, curved less than 90°, or completely absent*
Spermatheca	Narrow duct	Broad duct*
Male androconia	Usually confined to veins on hindwing	Spread out over hindwing membrane*
Antenna length	Shorter than one-half FW radius*	Longer than one-half FW radius
2) KARYOLOGICAL (Suomalainen, Cook, and Turner, 1972; Brown, Emmel, and Suomalainen, in prep.)	N=30–32, as in most other primitive heliconian genera*	N=21 except in *doris* (N=20–30) and three highly evolved species in the *sapho*-group (N=32–33 or 56–59)
3) CHEMICAL (Brown, 1967; Brown and Domingues, 1971)	No storage of 3-hydroxykynurenine as yellow pigment in wings or body	All species except the very evolved *sapho* store 3-hydroxykynurenine as a wing/body pigment*
4) BIOLOGICAL (JUVENILE)		
Egg	Usually small, white*	Usually large, yellow
Head-pattern of mature larva	Normally all black, or with a harlequin striped pattern*	Usually yellow, sometimes black, rarely with any stripes
Chrysalis position (Turner, 1968)	Bowed to lie horizontally under leaf*	Hangs vertically
5) BEHAVIORAL (ADULT)		
Pollen collection (Gilbert, 1972)	No species collect*	All species collect
Home-range near foodplant	Many species rarely leave near vicinity	Many species range far away from foodplant*
Egg-laying by female	Usually on the ventral surface of older leaves	Usually on a growing meristem, or on younger leaves*

* The *aoede*-group of the genus *Heliconius* (*aoede, metharme, godmani* and possibly *hierax*) shows a mixture of important characters of the two genera, and some major characters of its own, and seems to merit the erection of a new genus (Turner, 1968); the description of this genus is awaiting breeding studies on its members.

The new subspecies from northwestern Venezuela partakes of characteres of the neighboring extra-Hylaean subspecies of *tales* [*pseudeanes* BOULLET & LE CERF, 1910 (Figure 9), *xenophanes* FELDER (Figure 7), and *cognatus* WEYMER (Figure 6)], but populations intermediate between it and any of these neighboring forms are as yet unknown. To date, the new subspecies has not been collected outside of a very limited area, at moderate elevations on the eastern slope of the Sierra Perijá, which divides Venezuela from Colombia near the Caribbean Sea; it was probably derived in the Catatumbo refugium of HAFFNER, 1969 during the Pleistocene. A description follows:

Eueides tales franciscus, n. ssp.

(Figure 10)

Wing size (FW radius 32–34 mm.) and shape, and body markings (white dots), exactly as in nominate subspecies. Forewing dorsally black; red markings reduced to two narrow lines in basal half of wing, one along the inner margin and one between the anal and cubital veins; a yellow median area, divided into a square or subtriangular spot at the distal end of the cell, and a wide compact curved band, uniform in width, lying outside the cell between the radius and vein Cu2; a short yellow streak anterior to this patch, near the costal margin. Forewing ventrally similar, either without red markings or with a narrow red streak in the basal third of the cell; 1–3 pairs of submarginal white dots above the anal angle; and a short yellow costal streak.

Hindwing dorsally black, with very limited red scaling over the basal parts of the cubital and anal veins, in some specimens also over veins Cu1 and Cu2. Hindwing ventrally as in nominate subspecies, with moderate development of red rays overlying the veins, these usually fused into a submarginal red line, and two rows of paired intervenal submarginal white dots. Costal stripe yellow, reddish at the distal tip, extending to above the end of the cell.

Sexes similar, except that the female has fuller and rounder wings and bears somewhat more red scaling at the base of the dorsal surface of the hindwing.

HOLOTYPE MALE, 28–VIII–1970, Tucuco, Zulia (1200 ft. = 360 m.), eastern slope of the Sierra Perijá, Venezuela; donated to the collection of the Facultad de Agronomia, Universidad Central de Venezuela, Maracay, by H. and R. Holzinger; Buderacky leg.

ALLOTYPE FEMALE, no date, same locality, in the collection of Harold Skinner, La Victoria, Aragua, Venezuela.

PARATYPES: One male, 30–X–1960, Tucuco, in the collection of the Facultad de Agronomia; one male, 21–VI–1969, Tucuco, in the collection of Harold Skinner; one male and two females, 26–XI–1969, and one male and one female, 27–XI–1969, Tucuco, in the collection of Koroku Negishi, Kanazawa, Japan; one male, 24–XI–1969, Tucuco, in the collection of K. Brown, Rio de Janairo, K. Negishi leg.; two males, 18–VII–1970, one male, 6–XI–1970, and one male, 30–X–1970, Tucuco, in the collection of H. and R. Holzinger, Vienna, Buderacky leg.

The subspecies name is a noun in apposition, in the masculine nominative singular, and is proposed in honor of *Dr. Francisco Fernández Yépez* of the Facultad de Agronomia in Maracay.

MIMICRY

All of the Amazonian subspecies of *tales* participate in mimetic complexes, consisting principally of other dennis or dennis-rayed heliconians (which vary in close parallel over the entire Amazon area), with some additional heliconians and ithomiines, dysschematid (= pericopid) moths, and a variety of Batesian mimics among nymphalids, riodinids, pierids, and papilionids. Table II presents a synopsis of some of the Müllerian mimics in these complexes (most of the Batesian mimics are rare and little-known, as the theory predicts that they should be). The lists are based upon field experience and reliable data from recent collections within *tales* colonies. The extra-Amazonian subspecies have very reduced mimetic associations. It is interesting to note that many other Amazonian heliconians have differentiated to a greater degree than has *tales* during the Pleistocene isolations (or *tales* has since managed to eliminate more effectively the results of differentiation).

No subspecies of *tales* has yet been found in the extreme southwestern Amazon (northern Bolivia), where the predominant pattern in the dennis-rayed heliconians is a compact square yellow forewing area centered over the end of the cell (as in *cognatus*, Figure 6), and reduced dark red dennis and rays. This area is locally inhabited by the similar *Eueides eanes heliconioides* (= *eanides* STICHEL; see HOLZINGER and HOLZINGER, 1969), and may harbor an as yet undiscovered and similar subspecies of *Eueides tales*, similar to *cognatus* but with better ray development; specimens of typical *cognatus* in the Museu Nacional, Rio, labelled „San Felippe, Alto Juruá" (= Eirunepé, Amazonas) and in the Naturhistorisches Museum in Vienna, labelled „Bolivia", are almost surely mislabellings, however. Some evidence for the existence of this suspected but undiscovered subspecies near *cognatus* may be found in the occurence of the form barcellinus ZIKÁN, 1937 (Figure 11) in southern Rondônia, where many other sympatric heliconians show at least a part of their populations with constricted forewing bands. This form was described from far north on the Rio Negro, and probably results from an infusion of *cognatus* genes into the *pythagoras* population present at Barcelos (see Map).

TABLE II. PARTIAL COMPOSITIONS OF SOME SYMPATRIC MULLERIAN MIMICRY COMPLEXES IN WHICH *EUEIDES TALES* SUBSPECIES PARTICIPATE

Subspecies & geographical area	Other dennis or dennis-rayed heliconians: Very strongly resemble (direct mimicry)	Other dennis or dennis-rayed heliconians: Weakly resemble (size differences)	Other heliconians: Poorly resemble (indirect mimicry)	ITHOMINIINAE: Poorly resemble (indirect mimicry)
tales	*H. aoede astydamia*	*H. egeria egeria*	*H. numata numata*	*Melinaea mneme mneme*
(incl. f. surdus,	*H. xanthocles xanthocles*	*H. burneyi catharinae*	*H. ethilla thielei*	*Mel. mnasias tecta*
f. aquilifer, etc.)	*H. melpomene meriana*		*H. hecale vetustus*	*Mel. satevis crameri*
Guyana, Óbidos	*H. erato amalfreda*	*H. elevatus roraima*	*Eueides lampeto copiosus*	*Mechanitis mazaeus pannifera*
	H. demeter beebei	*H. elev. tumatumari*		
pythagoras	*H. aoede faleria*	*H. astraea* subsp.	*H. numata* forms	*Tithorea h. harmonia*
including	*H. xanthocles paraplesius*	*H. burneyi burneyi*	*H. ethilla eucoma*	*Mel. mneme mauensis*
f. barcellinus)	*H. melpomene madeira*	*H. burneyi ada*	*H. hecale nigrofasciatus*	*Mel. mnasias* subsp.
Rondônia	*H. erato amazona*	*H. doris*, f. delila		*Mel. maenias pothete*
	H. erato constricta	*H. elevatus aquilina*	*Eueides isabella*	*Mechanitis polymnia*
	H. demeter eratosignis		♀ *Eueides vibilia unifasciatus* ♂	*Forbestra equicola*
Lower rivers	*H. aoede aoede*	*H. egeria hyas*	*H. numata* forms	*Tithorea harmonia*
Tapajós, Xingu,	*H. xanthocles vala*	*H. burneyi burneyi*	*H. ethilla eucoma*	*Mel. mneme mauensis*
and Madeirn	*H. melpomene thelxiope*	*H. doris*, f. delila	*H. hecale fortunatus*	*Mel. mnasias mnasias*
	H. erato amazona	*H. elevatus bari*	*Eueides isabella*	*Mechanitis lanei*
	♂ *Heliconius demeter bouqueti* ♀		*Eueides lampeto*	*Mechanitis mazaeus*
			♀ *Eueides vibilia unifasciatus* ♂	*Mechanitis polymnia*
calathus	*H. aoede bartletti*	*H. a. astraea*	*H. numata euphone*	*Mel. m. menophilus*
Eastern Ecuador	*H. xanthocles melittus*	*H. b. burneyi*	*H. hecale quitalena*	*Mel. maeonis maeonis*
	H. melpomene aglaope	*H. doris*, f. delila		*Mechanitis mazaeus*
	H. erato emma	*H. elevatus elevatus*		*Forbestra truncata*
	H. demeter demeter			*Hypothyris* ssp.
	Eueides eanes eanes			
f. michaeli	*H. aoede cupidineus*	*H. a. astraea*	*Hel. numata euphone*	*Mel. m. menophilus*
Eastern Peru	*H. xanthocles melior*	*H. burneyi huebneri*	*H. ethilla adela*	*Mel. maenas tarapotensis*
	H. melpomene flavotenuiata		*H. hecale sisyphus*, form felix	*Mel. egesta egesta*
	H. erato emma	*H. elevatus pseudocupidineus*		*Mech. isthmia eurydice*
	H. demeter demeter		*Eueides isabella*	*Mechanitis mazaeus*
	Eueides eanes eanes		♀ *Eueides vibilia unifasciatus* ♂	*Hypothryris euclea*
cognatus	*H. aoede lucretius*	*H. egeria asterope*	*H. numata messene*	*Melinaea i. isocomma*
East-central Colombia	*H. xanthocles flavosia*	*H. burneyi lindigii*	*H. hecale ithaka*	*Mel. mothone messenina*
		H. doris eratonius		*Mechanitis mazaeus messenoides*
			♀ *Eueides vibilia unifasciatus* ♂	
		H. elevatus perchlora		

BEHAVIOR

Adults of *Eueides tales*, like most members of the genus, are usually to be found within a few dozen meters, and often within less than ten meters, of their food-plant. The females, especially, spend much of the day flying around the *Passiflora* vines on which they place their eggs, individually, on the ventral surface of older leaves. The males indulge in much small-scale promenading, usually from five to ten meters above the ground, and demonstrate well-marked territoriality, vigorously chasing other males which pass through their area or in front of their perch. In sparse populations, these territories may be quite large, and promenading males may be found over 50 m. from the food-plant; in dense populations, the areas defended by males are correspondingly smaller.

In spite of this apparently marked home-range behavior and the extremely localized nature of *tales* colonies, the phenotypic composition of Amazonian populations of *tales* indicates that, at least at some times, the males and/or females range widely, creating effective gene-flow across large rivers and over several thousand kilometers of forest. On the north and south banks of the Rio Negro at Manaus, width about six Km. from forest to forest, populations are found of three *Heliconius* species *(erato, demeter*, and *aoede)*, which are rather sedentary and strongly restricted to shady forest, whose phenotypic compositions indicate essentially no gene-flow of color-pattern elements across the river. More powerful flyers in the same genus *(egeria, burneyi*, and *numata)* show appreciable geneflow across the river; and *E. tales* populations are also much hybridized to the north and south of the river, indicating that the species is capable of crossing this distance of open water. Similarly, down-river in Óbidos (north bank of the Amazonas) and Santarém (south bank), the populations of *tales* demonstrate the existence of considerable gene-flow across the river. This is shown, on the north bank, by the form aquilifer STICHEL, 1903 (Figure 12), with the yellow forewing pattern of *pythagoras* but the hindwing of *tales*, and by the presence of occasional rayed individuals; and, on the south bank, by the form zernyi NEUSTETTER, 1928 (Figure 13), with the *tales* forewing pattern and a *pythagoras* hindwing, and by the presence of individuals with reduced expression of the rays. Both here and in Manaus, populations on both riverbanks show variable development of the rays, while farther north away from the banks, rays are always absent, and farther south, always present. In Óbidos-Santarém as in Manaus, the river is an effective barrier for *aoede* and the dennis-rayed (more forest-restricted) forms of *erato* and *melpomene;* however, the more open-country-adapted red-banded forms of the latter two species can cross the Amazon in a variety of areas between Itacoatiara and Santarém, appearing on both banks of the river.

The west Amazonian phenotype with a reduced yellow forewing band (elimination of yellow in the cell) may be found in populations over two thousand kilometers downriver in Manaus (Figure 5); the condensed square forewing band of *cognatus* may be found one thousand kilometers downstream at Barcelos, or far south in Rondônia. These data indicate appreciable expansion of these forms since their first formation, to occupy today much of the upper Amazonian aera (see Map). In this case, as the forest is continuous today over much of this area, the correspondending phenotypes of *erato, melpomene, aoede,* and other heliconians have also expanded to occupy similar areas. However, the *cognatus*-like *erato reductimacula* has not crossed the Colombian llanos, being replaced in them and westward to the Andes by the red-banded *erato hydara*. The appearance of *cognatus* and even *pythagoras* (as form barcellinius in the llanos and as far as the slopes of the eastern Colombian cordillera, and of similar-appearing subspecies of *tales* in other parts of Colombia and Venezuela well away from the Hylaea, indicates a tolerance by *tales* of dryer and more open habitats, which is not shared by Amazonian forms of *erato* and *melpomene*.

GENETICS

The compositions of the hybrid populations produced where two or more subspecies of *tales* meet and mingle (see Map) permit some predictions to be made on the nature of the major color-pattern characters of this species, which may correspond to principal genes. Experimental work in crossing has not yet been performed, however, and the following discussion is necessarily rather speculative.

D e n n i s. The red base of the forewing is probably controlled by a single gene, possibly not homologous to those operating in the Ama-

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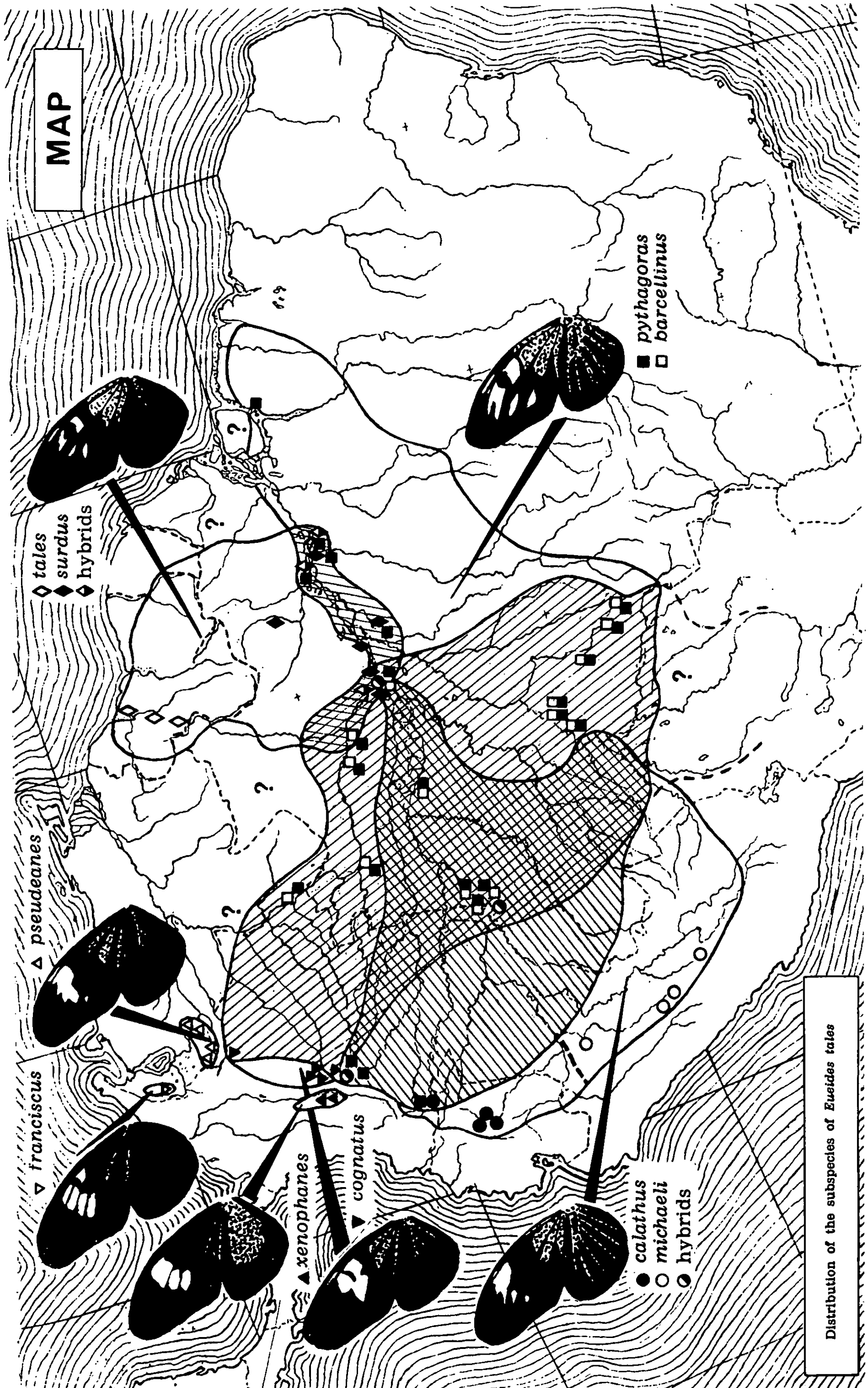
EXPLANATION OF THE MAP

The distribution of each of the seven subspecies of *tales* in the northern half of South America is indicated by an area enclosed by a heavy dark line; anywhere within this area where, suitable habitat and food-plants exist, the illustrated subspecies may be expected to occur. Known localities for the various subspecies and forms are indicated by a variety of symbols, which are assigned to names beside the respective illustrations. In cases where two or more subspecies meet and intermingle, cross-hatching – single, double, or triple (near Manaus) – defines the regions where mixed forms are to be expected: 45° for *calathus* mixture, 135° for *cognatus* mixture, and 80° for *tales* mixture with the central subspecies *pythagoras*.

ERKLÄRUNG DER KARTE

Die Verbreitung jeder der sieben Subspezies von *tales* in der nördlichen Hälfte Südamerikas ist durch eine das Gebiet umfassende starke schwarze Linie gekennzeichnet; überall innerhalb dieses Gebietes, wo in einem geeigneten Biotop die Futterpflanze vorkommt, ist die abgebildete Subspezies zu erwarten. Bekannte Fundorte für die verschiedenen Subspezies und Formen werden durch verschiedene Symbole gekennzeichnet; diese sind mit dem zugehörigen Namen der entsprechenden Abbildung beigefügt. Wo sich zwei oder mehr Subspezies treffen und kreuzen, ist das Gebiet, in dem Mischformen zu erwarten sind, durch Schraffierungen – einfach, doppelt oder dreifach (bei Manaus) – definiert: 45° für Mischpopulationen von *calathus*, 135° für solche von *cognatus* und 80° für die von *tales* mit der zentralen Subspezies *pythagoras*.



Distribution of the subspecies of *Eueides tales* zonian forms of *Heliconius erato* and *melpomene*. Probably simply modified to the reduced form shown by *cognatus* and *pseudeanes;* the extreme reduction to a double red line in *xenophanes* and *franciscus* is likely to be a different allele.

R a y. The unique red ray pattern over the hindwing veins of *tales* is surely controlled by several genes, and probably is not linked to dennis; the continous development of the rays in hybrid populations, and the great variability in almost all populations, precludes the hypothesis of a single dominant gene, as in *erato* and *melpomene* (SHEPPARD, 1963; TURNER and CRANE, 1962; TURNER, 1971). The rayed phenotype is nearly confined to the south and west of the Amazonas and Negro rivers, except for occasional crossings as discussed above.

The suppression of the rays on the ventral surface of the hindwing in surdus may be a single semi-dominant gene, as it affects populations of *pythagoras* across the river, and has nearly eliminated rays from all populations of *tales tales* except for a few in the Guianas.

F o r e w i n g b a n d. The normal *pythagoras*-type band can be modified (probably more than one gene) by reduction of size of the inner and outer elements, to give the type seen in *tales* and surdus. A further reduction of all elements, with essential disappearance of the spot in the cell, occurs in the Óbidos area and gives the form reducta NEUSTETTER, 1931 (Figure 14). The *cognatus*-type constricted band, produced formally by widening of the elements in M3 and Cu1 and their dislocation toward the cell, may be a separate allele, also possibly present in modified form in *franciscus* n. ssp.; its presence can be detected as far east as Barcelos and Manaus, and as far south as Rondônia, in Brazil. The outer band of *calathus* may prove to be a very distinct character; when it interacts with the *cognatus* or the *pythagoras* band, forms appear (Figure 5) in which only a small yellow spot remains, beyond the cell on the forewing. However, a specimen of *pythagoras* from Benjamin Constant in the Museu Nacional has only a partial reduction of the cell element, as if intermediate to *calathus*. This phenotype has spread north as far as La Macarena in Colombia, and east south of the Negro as far as Manaus, from its center in eastern Ecuador and Peru; it also seems to be present in a somewhat modified from in *xenophanes* and *pseudeans*. Further reduction of the forewing band in the Huallaga valley gives the form michaeli ZIKÁN, 1937 (Figure 4), which also tends to have stronger and more orange hindwing rays, like other sympatric heliconian species.

A b e r r a t i o n s. EMSLEY, 1965 mentioned specimens from Santarém with the dennis and ray „stone-colored" rather than red. The Museu Nacional in Rio has similar aberrations in a number of species of heliconians, in which the red pigment is completely replaced by a flat greyish-beige. This color change is probably produced by a single environment-conditioned biochemical malfunction in the synthesis of the red pigment.

The Museu Nacional also contains an unusual surdus from Óbidos in which the yellow spot-band on the forewing has been enlarged to cover the entire median area, with fuzzy edges; this is apparently an individual aberration of unknown, but probably genetic, origin.

JUVENILE BIOLOGY

The early stages of *Eueides tales* have been seen and studied in four widely separated areas, representing the northeastern, northwestern, and southwestern extremes and the center of the species' range; no gross regional or subspecific differences were apparent.

The first discovery was on January 6, 1971, on the steep humid escarpment between Atkinson Field (the Georgetown, Guyana airport) and the valley of the Demerara river, less than a kilometer from the airport installations. A female of *t. tales* was observed repeatedly investigating and laying eggs under older leaves of a large vine in the *Passiflora laurifolia* group, which remained unidentified (no flowers were discovered). Careful subsequent inspection of all branches of this vine, which was also being visited by a female of *Heliconius numata numata*, disclosed four eggs, two first-stage and a third-stage larvae of *tales*, all under older leaves, in addition to an egg and a mature larva of *numata* on younger growth. There was also discovered a most singular mature heliconian caterpillar, similar to that of *numata* but with far longer scoli and yellower final abdominal segments. In spite of its unique appearance (Figure 21), this larva was presumed to belong also to *tales*, a guess which was later confirmed by rearing up various larvae to maturity.

In October 1971, eggs and larvae of *t. pythagoras* were discovered and reared partly through in Riozinho, Rondônia, the opposite extreme of the species' range. The foodplant was once again a species in the *Passiflora laurifolia* group, probably undescribed but near to *P. nitida* and *P. guazumaefolia*. Further early stages were discovered and reared, across the Rio Negro from Manaus in October-November 1971 (hybrid population, *t. tales — t. pythagoras — t. calathus)* on a species very near *P. laurifolia* and on *P. nitida;* and in La Macarena in eastern Colombia in February 1972 (hybrid population, *t. pythagoras — t. cognatus — t. calathus*), on a species very near to *P. laurifolia,* also being fed upon by *Heliconius numata* larvae.

The egg of *E. tales* is similar to that of many other members of the genus (small and whitish), and the early larval stages likewise resemble those known for other species of *Eueides,* though somewhat darker in overall coloration. However, the late fourth- and fifth-instar larvae substitute, for the traditional *Eueides* color-pattern, a strikingly different appearance almost identical to that of the larvae of *Heliconius numata* (Figure 23) and *Heliconius melpomene* (Figure 24), which frequently feed upon the same vines as *tales* larvae. This radical departure of the mature *tales* larva from the normal *Eueides* larval color-pattern, to adopt a much more visible white-spotted-with-black coloration, can best be rationalized as a well-marked instance of *Müllerian mimicry in caterpillars* (see also TURNER, 1968, and CARPENTER, 1913). The same phenomenon can also be observed in the larvae of *Passiflora*-feeding Dioptid moths of the day-flying genus *Josia*, which strongly resemble, except for the lack of scoli, all known *Eueides* larvae *(aliphera, pavana, vibilia, isabella,* and *lybia)* except *tales*. The other *Eueides* larvae possess a generalized longitudinally striped pattern, far more cryptic and disruptive than that of *tales*, and several of them live gregoriously or semi-gregariously and adopt coordinated aggresive behavior when disturbed, patterns not seen in *tales*. The larvae of Heliconiini are probably at least as distasteful as the adults, sequestering alkaloids, saponins, and/or cyanogenic glucosides from the passifloraceous host-plants (K. BROWN, work in progress) to which they are totally restricted. Thus, a solitary but non-aggressive larva of a highly localized species such as that of *tales* would acquire appreciable protection against predators, by resembling larvae of microsympatric, abundant and widespread heliconians such as those of *melpomene* and *numata*.

DESCRIPTION OF EARLY STAGES

Egg. (Figures 15, 16): a creamy white ovoid truncated at bottom, about 0,80 mm. in diameter and 1,05 mm. in height, with 8—10 horizontal ridges (irregular on hemispherical top) and 16—17 vertical ridges. Placed under an older leaf of a *Passiflora* in the subgenus *Granadilla*, series *laurifoliae.* On the day before hatching, the cap of the egg turns very dark (Figure 16). Duration two to seven days (normally five to six days if fertilized only when laid).

Larva translucent whitish, with a black head and very prominent dark setae, about 1,5 mm. long when hatched. Eats by rasping the undersurface of the leaf; tolerant of other caterpillars but not gregarious. Passes through a banded phase at the end of the first instar (Figures 17 and 18), with alternate green, black, and white, occasionally with reddish, narrow rings around the thorax and abdomen. Length at end of first instar, about 4,0 mm.; duration of instar two to seven days, often much prolonged on older or tougher leaves.

Second instar (Figure 19) essentially all black, armed with approximately equal scoli (1,5x height of head capsule) on the head, thorax, and abdomen. Maximum length near 7 mm.; duration two to five days.

Third instar (Figure 20) still very black, but with a yellow head and a yellow-orange patch covering the dorsal half of the eighth and ninth abdominal and anal segments. All scoli black; thoracic scoli relatively very short; head scoli 3—3,5x head height, very prominent; abdominal scoli about 2,5x head height. A few whitish spots appear on the abdomen by the end of the instar. Maximum length about 11 mm.; duration two to four days, prolonged on older leaves.

Fourth instar initially dark as third, rapidly becoming lighter with the progressive deposition of white pigment during the instar; by the end, almost like the fifth-instar larva. All scoli dark; head scoli 3,5—4x head height (about 6 mm.), abdominal scoli up to 4 mm.; head light yellow, final abdominal segments capped with yellow-orange. Maximum length about 18 mm.; duration three to five days.

Fifth instar (Figure 21) white, with dark pigment spots in a pattern nearly identical to that of the mature larvae of *Heliconius numata* (Figure 23) and *H. melpomene* (Figure 24); underparts dark; head, and dorsal parts of eighth and ninth abdominal segments and anal segment, bright yellow-orange. Ocelli and all scoli black; head scoli 4,5x head height (up do 14 mm. long, or nearly half of the overall length of the larva); abdominal scoli up to 8 mm. long; prolegs yellow-brown. Maximum length about 30 mm.; duration near 7 days. Curls up double for a day, under a horizontal surface (generally a leaf), before pupation.

Pupa (Figure 22) as illustrated by TURNER, 1968, strongly bowed at eighth abdominal segment, to lie horizontally under the leaf surface. Color strong yellow with a few darker markings, especially paired large dorsal spots on 7AB and between 8AB and 9AB; short recurved unbranched head appendages; unbranched paired subdorsal spines on 3AB and 4AB (5 mm.), 5AB (2 mm.), and 6AB (1,5 mm.), with short pointed tubercle-like spines on 2TH, 3TH, 2AB, and 7AB. Length 18 mm.; duration 10—14 days.

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SUMMARY

The mimetic heliconian species *Eueides tales* may be recognized by the ventral surface of the hindwing, which bears at least partial red rays overlying the veins, and a double row of paired intervenal submarginal white spots. It occurs as seven well-marked subspecies and a further six recognizable forms, over much of the Amazon Basin and Guianas, Venezuela, and Colombia; however, it is very local. The northwest Venezuelan subspecies, known so far from only one locality in the Sierra Perijá, is previously undescribed. The four Amazonian subspecies meet and intergrade over large areas; hybridized populations on the banks of the Amazon and Negro rivers indicate appreciable mobility for the species, and the occurrence of isolated subspecies in Venezuela and Colombia reveals its tolerance for dryer non-forested habitats. The juvenile forms are mostly similar to those of other *Eueides* species (these and many other criteria indicate good generic status for *Eueides*, separate from *Heliconius*), except for the coloration of the mature larva, which converges strongly on the appearance of the larvae of *Heliconius numata* and *H. melpomene*, common and widespread microsympatric feeders on *Passifloras* of the *laurifolio* group, to which *tales* larvae also seem to be restriced; this appears to be a well-marked case of Müllerian mimicry in caterpillars.

ZUSAMMENFASSUNG

Die mimetische Heliconiinen-Art *Eueides tales* ist durch die zumindest auf der Hinterflügel-Unterseite teilweise vorhandenen und im Gegensatz zu allen anderen vergleichbaren Arten auf den Adern liegenden roten Strahlen, sowie durch eine doppelte Reihe paarweise in den Aderzwischenräumen der Hinterflügel-Unterseite stehender weißer Submarginalpunkte gekennzeichnet. Diese Art ist in sieben deutlich unterschiedenen Subspezies und weiteren sechs kennbaren Formen über den größten Teil des Amazonas-Gebietes und Guayanas, wie auch in Venezuela und Columbien verbreitet, tritt jedoch ziemlich lokal auf. Die Subspezies aus Nord-Venezuela, nur von einer einzigen Lokalität in der Sierra Perijá bekannt, war bis jetzt unbeschrieben. Die Verbreitungsareale der vier Amazonas-Unterarten überschneiden sich, so daß über große Gebiete Mischformen auftreten; Hybridpopulationen an den Ufern des Amazonas und Rio Negro deuten auf eine beträchtliche Beweglichkeit der Art, und das Vorkommen isolierter Unterarten in Venezuela und Columbien läßt auf eine vergleichsweise größere Toleranz der Art gegenüber trockeneren waldlosen Biotopen schließen. Die Jugendstadien (eines der vielen Kriterien für den Status von *Eueides* als gutes, von *Heliconius* getrenntes Genus) sind sehr ähnlich denen der anderen *Eueides*-Arten mit Ausnahme der Färbung der erwachsenen Raupe; diese gleicht im Aussehen stark denen von *Heliconius numata* und *H. melpomene*,

häufigen und weitverbreiteten, mikrosympatrisch an Passifloren der *laurifolia*-Gruppe fressenden Arten (auch die Raupe von *tales* scheint an diese Futterpflanze gebunden zu sein); es muß dies als ein gutes Beispiel für den selten bekanntgewordenen Fall einer Müller'schen Mimikry bei Raupen angesehen werden.

KEY

DEFINITION OF *EUEIDES TALES:* A Nymphalid Lepidopteran with a simple recurved humeral vein on the hindwing, and on the ventral surface of the hindwing complete or reduced red rays overlying the veins (especially anally), and two distinct rows of paired intervenal submarginal white spots.

SYNOPSIS OF NAMED SUBSPECIES AND FORMS:

1. a. Forewing with basal red marks restricted to one or two narrow lines near the anal margin — 2.
   b. Forewing with a well-developed basal red area, extending at least halfway distad in the cell — 3.
2. a. Dorsal surface of the hindwing with a large red basal patch, covering nearly or more than half the wing, serrate distad but not giving rise to distinct rays (central-west Colombia, very local in the Magdalena valley) (Figure 7) — *xenophanes* FELDER (= *crystalina* HALL)
   b. Hindwing with very restricted red on the dorsal surface; forewing with a continuous yellow band outside the cell and a smaller square patch within it (Sierra Perijá, Venezuela) (Figure 10) — *franciscus* n. ssp.
3. a. Forewing yellow area roughly quadrangular, compact, centered over the end of the cell which bears a black triangular mark, otherwise unbroken by black streaks (northeastern Andes of Colombia, east through the llanos to the upper Rio Vaupés, possibly northern Bolivia also) (Figure 6) — *cognatus* WEYMER
   b. Forewing yellow area either exclusively extra-cellular, or broken into a number of separate spots by black veins, not squarish or compacted — 4.
4. a. Hindwing with very restricted red markings dorsally, usually only a few small streaks baso-anally, not reaching into the outer two-thirds of the wing — 5.
   b. Hindwing with moderately to well developed red rays dorsally and ventrally, reaching into the distal two-thirds of the wing, in extreme cases fused laterally into an antesubmarginal red line — 6.
5. a. Forewing yellow band continuous, extracellular, and triangular, pointing towards the inner angle; red basal area reduced to three lines, strongly divided by black veins Cu and 1A (southeastern slope of Venezuelan Andes in Barinas and Táchira) (Figure 9) *pseudeanes* BOULLET & LECERF

b. Forewing yellow area composed of a number of separate spots, usually including an element within the cell, or if only a single spot beyond the cell, this very small and restricted to above vein M3 (Guianas south to the Amazon and Negro rivers, west to the Rio Branco) *tales* CRAMER

i. Forewing yellow area restricted to outside the cell.

i-a. A single spot only or a relatively compact area above vein M3 (Manaus) unnamed form

i-b. A series of separate spots (Óbidos) (Figure 14) f. reducta NEUSTETTER

ii. Forewing yellow area including a spot in the distal end of the cell.

ii-a. Ventral hindwing with well-developed red rays (western Guianas) (Figure 1) *tales* f. typ.

ii-b. Ventral hindwing with very poorly developed or no red rays (north Brazil).

ii-b-1. Extracellular area of the forewing broken up into small, subequal spots (Figure 3) f. surdus STICHEL

ii-b-2. End-cellular and anterior extracellular spots large, the latter much elongated distad into two points (Figure 12) f. aquilifer STICHEL

6. a. Forewing yellow area exclusively extracellular, usually triangular, pointing towards the anal angle (eastern Peru, Ecuador, and Colombia, occasionally eastward as far as Manaus) *calathus* STICHEL

i. Forewing yellow area limited to a small spot distad to the end of the cell (La Macarena, Manaus, and other blend areas) (Figure 5) unnamed forms

ii. Forewing yellow area larger, usually subtriangular, with elements present in M3-Cu1 (always) and in Cu1-Cu2 (frequently).

ii-a. Hindwing red rays not well developed; forewing yellow area relatively larger, extending to a point in space Cu1-Cu2 (eastern Ecuador to south-central Colombia) (Figure 4 a) *calathus* f. typ.

ii-b. Hindwing rays oranger and well-developed, sometimes even fused into a submarginal line; forewing yellow area smaller and usually lacking a spot in space Cu1-Cu2 (eastern Peru) (Figure 4 b) f. michaeli ZIKÁN

b. Forewing yellow band including a small to large spot in the end of the cell (southern and western Amazon area from Belém to Barcelos, southern Venezuela, northeastern Colombia, eastern Peru, Arce, and Rondônia) *pythagoras* KIRBY (= *heraldicus* STICHEL)

i. Forewing band broken up into small separate spots (blend areas near Amazon and Negro rivers: Santarém, Manaus, Barcelos) (Figure 13) f. zernyi NEUSTETTER

ii. Forewing band containing an elongated rectangle in the cell, and a long single yellow spot distad to the end of the cell, with two additional spots posterior to this in spaces M3-Cu1 and Cu1-Cu2.

ii-a. The spot distad to the cell extending into two long points, and the spots below it relatively small (all of southern and western Amazon area) (Figure 2) *pythagoras* f. typ.

ii-b. The spot distad to the cell quadrangular, not extending into two long points, and the spots below this larger, sometimes nearly fused (northwestern blend areas with *cognatus*, Rondônia, occasionally in the rest of the range) (Figure 11) f. barcellinus ZIKÁN A lectotype of this name is designated in this paper (see explanations of Figures).

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PLATE I

All butterflies are black, yellow, and red or orange, and are illustrated in life size.

Figure 1. CRAMER's original figures of *Papilio tales*, dorsal (left) and ventral (right) surfaces.

Figure 2. HÜBNER's original figures of *Nereis festiva thales*, now known as *Eueides tales pythagoras*, male (a) and female (b), dorsal (left) and ventral (right) wing surfaces.

Figure 3. *Eueides tales tales* f. surdus, Óbidos, Pará, dorsal (left) and ventral (right) surfaces (Museu Nacional, Rio).

Figure 4. *Eueides tales calathus*, Sarzayacu, Oriente Ecuador, dorsal (a), (compared with holotype in the collection of the Naturhistorisches Museum, Vienna), and *Eueides tales calathus* f. michaeli (compared with holotype in the Instituto Oswaldo Cruz), Tingo Maria, Peru, dorsal (b) (collection K. B., Rio).

Figure 5. *Eueides tales calathus* × *pythagoras* × *tales*, Ponta Negra, Manaus, Amazonas, dorsal (a), and *E. t. calathus* × *cognatus*, Vista Hermosa, La Macarena, Colombia, dorsal (b) (collection K. B., Rio).

Figure 6. *Eueides tales cognatus*, Rio Negro, Meta, Colombia, dorsal (collection K. B., Rio).

Figure 7. Syntype of *Eueides tales crystalina* HALL, 1921, synonym of *E. t. xenophanes* FELDER, Crystalina, west Colombia, 1200 ft., dorsal (Allyn Museum of Entomology, Sarasota).

Figure 8. Holotype of *Eueides eanes* f. lucretius ZIKÁN, 1937, regarded here as an extreme example of *E. tales pythagoras* f. barcellinus, São Gabriel, upper Rio Negro, ventral (a female, in the Instituto Oswaldo Cruz, Rio, No 27.585). A nearly identical specimen was captured by E. W. Schmidt-Mumm of Bogotá in the upper reaches of the Rio Sarare, near Pamplona in northeast Colombia.

Figure 9. *Eueides tales pseudeanes*, Barinitas, Barinas, Venezuela, male (a) and female (b), dorsal (collection K. B., Rio).

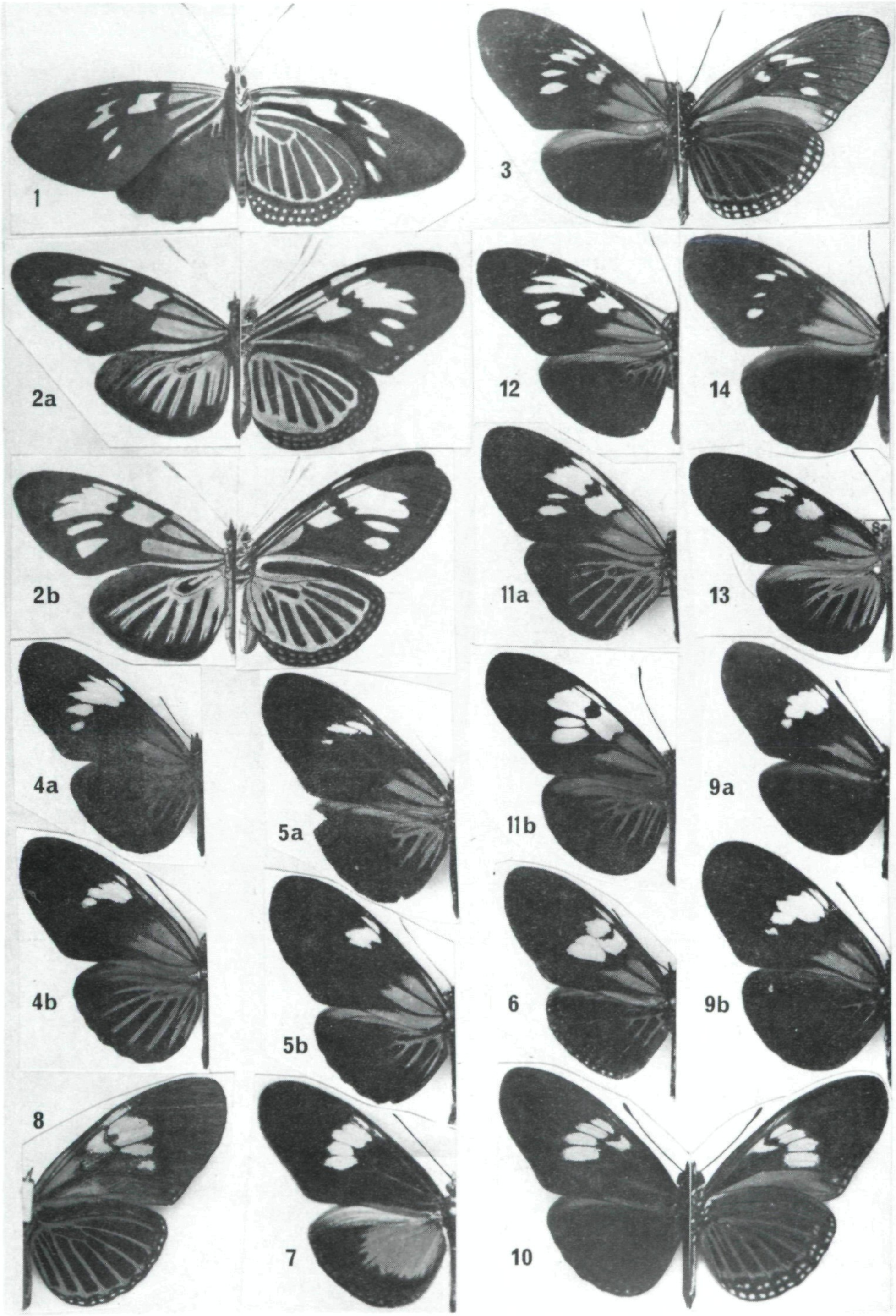
Figure 10. *Eueides tales franciscus* n. ssp., holotype male, dorsal (left) and ventral (right) surfaces, Tucuco, Perijá, Zulia, Venezuela (donated by H. & R. Holzinger to the Facultad de Agronomia, Maracay, Aragua, Venezuela).

Figure 11. *Eueides tales pythagoras* f. barcellinus, Riozinho, Rondônia, female, dorsal (a) (collection K. B., Rio) and a syntype hereby designated lectotype of this name, Barcelos, Amazonas, 31–VII–1927, J. F. Zikán Collection, No 27.578 of the collection of the Instituto Oswaldo Cruz, Rio de Janeiro, labelled by the collector „*Eueides tales* f. *pythagoras* Kirby“, male, dorsal (b).

Figure 12. *Eueides tales* f. aquilifer, Óbidos, Pará, male, dorsal (Museu Nacional, Rio).

Figure 13. *Eueides tales pythagoras* f. zernyi, Santarém, Pará, male, dorsal (Museu Nacional, Rio). The type specimen, in the Naturhistorisches Museum (Wien), is a female and bears somewhat longer rays on the hindwing than the illustrated male.

Figure 14. *Eueides tales tales* f. reducta, Óbidos, Pará, female, dorsal (Museu Nacional, Rio) (compared with holotype in the collection of the Naturhistorisches Museum, Vienna).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3
2a
12
14
2b
11a
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4a
5a
11b
9a
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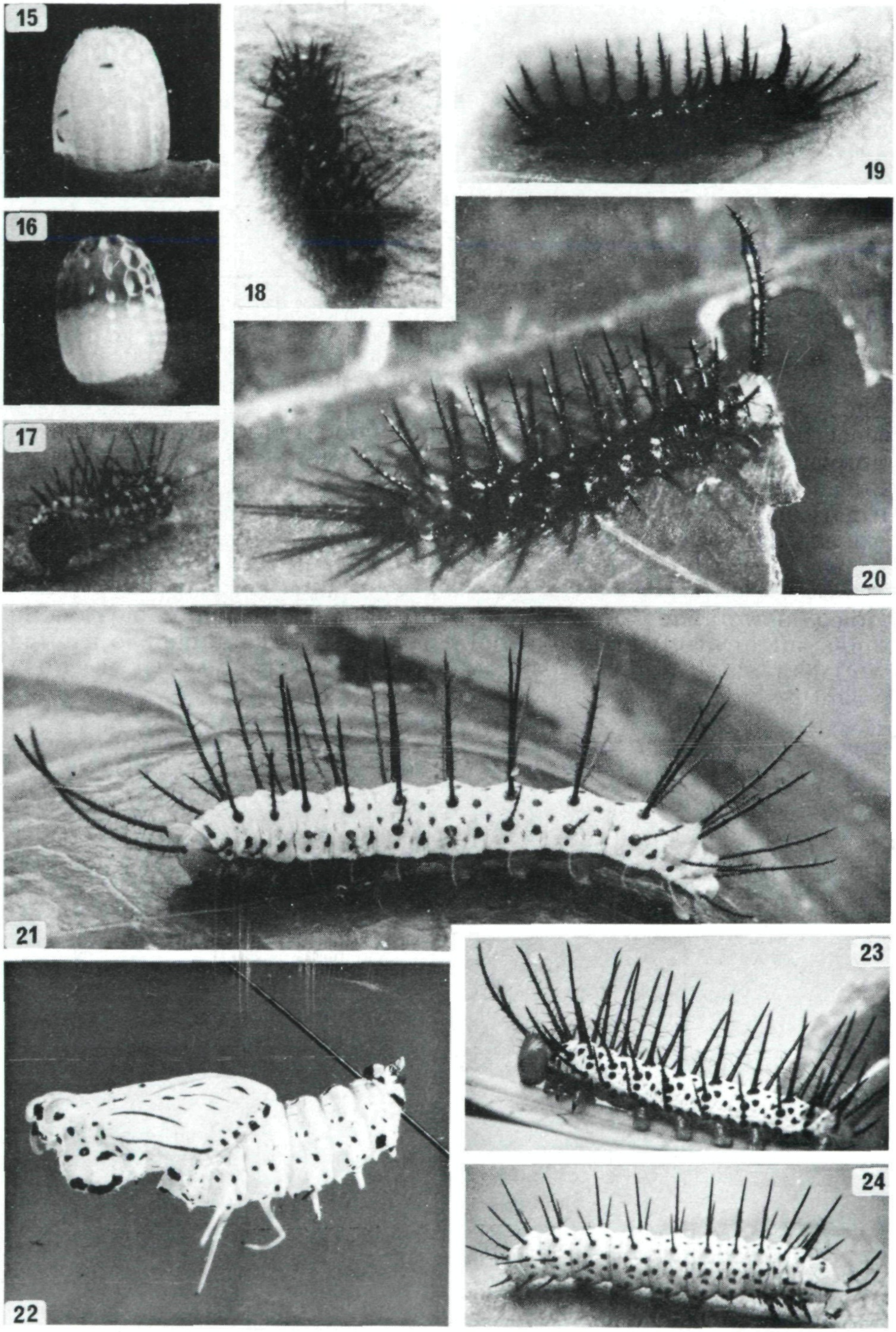
PLATE II

Figure 15. Egg, Manaus, Amazonas, 20× life size.
Figure 16. Egg just before eclosion, Riozinho, Rondônia, 20×.
Figure 17. First instar larva, Georgetown, Guyana, 10×.
Figure 18. First instar larva, dorso-anal, Georgetown, Guyana, 10×.
Figure 19. Second instar larva, lateral, Manaus, Amazonas, 8×.
Figure 20. Third instar larva, latero-dorsal, Manaus. Amazonas, 5×.
Figure 21. Mature (fifth instar) larva, latero-dorsal, Georgetown, Guyana, 2,5× (head scoli foreshortened in this view).
Figure 22. Pupa, latero-dorsal, Manaus, Amazonas, 3×.
Figure 23. *Heliconius numata*, mature larva, lateral, Riozinho, Rondônia, 1,5×.
Figure 24. *Heliconius melpomene plesseni*, larva in molt from fourth to fifth instar, Topo, Rio Pastaza, Ecuador, 2,5× (larvae of other subspecies are essentialy identical).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