Geographical patterns of evolution in Neotropical Lepidoptera. Systematics and derivation of known and new Heliconiini (Nymphalidae: Nymphalinae)

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ABSTRACT

Analysis of the known and recently discovered differentiation patterns of 58 forest butterfly species (of the total 66) in the tribe Heliconiini, including over 300 races and forms, has led to the drawing of a map of core areas for evolution in the group. The majority of these are not isolated by any obvious modern physiogeographic barriers to dispersal of these butterflies, and probably correspond to forest refugia during the two or three most recent Quaternary dry periods. The map is in good accord with the results of similar studies in other groups of animals (forest vertebrates and invertebrates) and in forest trees, but indicates a larger number of significant operative refugia (38) than other analyses. Bases for the understanding of differentiation patterns in polytypic continental species are developed, in accord with the refuge theory and using intensive and extensive data on local monomorphic populations and secondary contact zones between differentiated forms. The known forms discussed include: *Dione juno miraculosa* Hering, *Eueides libitina* Staudinger, *Heliconius xanthocles explicata* Stichel, *H.eleuchia* (Hewitson) and *H.leucadia* Bates together with a supplementary revision of the tribe giving information published since 1972. The following new forms are described: *Eueides emsleyi* sp. n. and nine new subspecies of *Heliconius*: *H.aoede philipi*, *H.wallacei araguaia*, *H.pardalinus orteguaza*, *H.p.butleri*, *H.hecale australis*, *H.h.barcanti*, *H.clysonymus tabaconas*, *H.congener aquilionaris*, *H.sapho candidus*. Geographical details of the refugia are given in Appendix I, and in Appendix II the heliconians are assigned to the postulated refugia.

INTRODUCTION

Heliconian butterflies (Lepidoptera : Nymphalidae, Nymphalinae) have historically attracted much attention through their gaudy colours, participation in local Müllerian mimicry rings, and pattern plasticity in zones of secondary contact between differentiated forms. Whereas such classical and ecological aspects of heliconian biology still merit much field study, these organisms have today become laboratory animals, widely employed in investigations of genetics, biochemistry, physiology, ethology, and evolutionary mechanisms. Concomitantly, this surge of attention has resulted in the collection of much fascinating and new information in the wild, on the ecology, ecological genetics, natural behaviour, dispersal, differentiation and hybridisation of these versatile and

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usually common Neotropical insects. To support all these studies, it has become necessary to develop a firm systematic base for the understanding of the differentiation patterns observed in the various species. The classical revisions of Emsley (1963, 1964, 1965) laid the foundations for the modern understanding of the taxonomy of the group; recent additional publications by Turner (1966, 1967, 1968, 1972), Holzinger & Holzinger (1969, 1970, 1971, 1972, 1974), Brown & Mielke (1972), Brown (1973), Brown & Holzinger (1973), and Brown & Benson (1974) have represented supplements to Emsley's work. Further papers on the rare species *hecalesia* (= *longarena*) and *hermathena*, on the very complicated silvaniform *Heliconius*, and on new forms from Venezuela, are in preparation or in press (Brown & Benson, 1975*a,b*, 1976; Brown, 1976; Brown & Fernández Yépez, 1976).

The present paper grew out of an invitation to this author, whose information on heliconians has been gained largely in the field, to visit the collections of the British Museum (Natural History) (BMNH), extended by the trustees of that institution and aided by a grant from the Royal Society/Conselho Nacional de Pesquisas cooperative programme. At the time of this visit (July, 1974), the collection of Heliconiini was nearing the final stages of a comprehensive recuration, undertaken over a two-year period by Messrs P.R.Ackery and R.L.Smiles. The union of all Heliconiini material into a single assemblage, and its near-complete reorganisation by these lepidopterists, presented ideal conditions for the discovery of new information in this vast (more than 40 000 specimens) collection. The following data derive principally from this very profitable exploration into the excellent material deposited by British and other lepidopterists in the BMNH. A visit was also made to the American Museum of Natural History (AMNH) in New York, en route to London, where much valuable information and a number of new forms were discovered in the very well-organised Heliconiini collection. A small amount of supplementary data from recent field work, which cast light on important systematic aspects in the tribe, are also reported. Much additional important data is now in press, as an illustrated catalogue of heliconian types in the BMNH, prepared by the above-mentioned scientists.

A BASIS FOR THE UNDERSTANDING OF HELICONIAN SYSTEMATICS

The confusion of named forms in the Heliconiini represents a major barrier to correctly understanding the evolution of the group (Emsley, 1964, 1965; Turner, 1972; Brown, 1976). Many of the names represent aberrations, genetic recombinants, and minor intrapopulational variants. Furthermore, a reasonable number of well-isolated taxonomic entities have not received names, due to a praiseworthy reluctance of modern systematists to add new taxa to a poorly defined or ill-understood group in which available names may be found to be applicable to newly discovered or differentiated populations.

Fortunately, recent field work in both well-known and little-explored parts of the Neotropics, and extensive genetic experiments in the insectary, have provided enough data on the distribution and variation of heliconian taxa to permit a reasonably confident decision to be made as to the correct systematic status of each known name. Furthermore, analysis of the emerging patterns of distributions of monomorphic races and of secondary contact zones has led to the discovery of a striking parallel between these differentiation patterns and those recognised to occur in other Neotropical forest organisms, from trees

and insects to birds, lizards, and mammals (Haffer, 1967, 1969, 1970, 1974*a,b*; Vanzolini & Williams, 1970; Vanzolini, 1970; Vuilleumier, 1971; Müller, 1972, 1973; Spassky *et al.*, 1971; Winge, 1973; Lamas Müller, 1973; Prance, 1973; Brown, Sheppard & Turner, 1974). According to current interpretations, these parallel differentiation patterns observable in such diverse organisms, are ascribable in part to Quaternary climatic cycles (Turner, 1964, 1971) which promoted appreciable fluctuations in the area of forest in the Neotropics. In extremely dry periods, the now near-continuous tropical forest was reduced in extent, leaving a number of isolated moist refugia, in which local evolution could occur with the formation of species, subspecies and other differentiated forms. These have today spread out to meet in well-defined zones of secondary contact, where overlap and/or hydridisation may occur, depending upon the degree of reproductive isolation of conphyletic forms.

A preliminary analysis of a number of relatively common and sedentary forest butterfly groups in the Neotropics, including the Heliconiini (Brown, Sheppard & Turner, 1974), has led to the mapping of probable refugia which operated on these organisms in the most recent major dry cycle (probably over 12 000, but possibly only 3000 years B.P.; see Vanzolini, 1973; Müller, 1973). A refined version of this map, including new data collected in the AMNH and BMNH in 1974 on heliconians and ithomiines, is included here, with suggestions for names to be stabilised for the 38 refugia recognised; the map is discussed more fully in Appendix I. A more extensive work (Part IV of this series) will detail the present-day distributions of 150 species in the Heliconiini and Ithomiinae, and give more precise definition of probable refuge limits and effectiveness. The third paper in the series will deal with the systematics and differentiation of the larger mimetic Ithomiinae. The relationships between the new taxa described below and the proposed refugia will be detailed in the respective paragraphs.

The important point to note is that Map 1 of probable refugia (or core areas for evolution) is useful in a variety of correlated studies. It permits predictions to be made as to expected differentiated forms, perhaps still undiscovered (or unrecognised due to superficial similarity), derived from widespread species or complexes, to be encountered in the various 'centres of evolution and dispersal' (Müller, 1972, 1973; Haffer, 1974*b*). It is probable that most forest organisms which survived in isolation within each refuge underwent differentiation governed by local selective pressures (Brown & Benson, 1974). In some cases, this differentiation resulted in easily visible changes in standard taxonomic characters in the respective groups, making the analysis of modern patterns relatively straightforward. In other cases, cryptoraces were most probably formed, not corresponding in their differentiation to well-defined systematic aspects of the group to which they belong, and thus remaining unrecognised. As most butterflies are classified by wing colour and pattern, and this is often easily modified by a few genes (Turner, 1972) and subject to rapid evolution in mimetic environments, the differentiation of many mimetic Lepidoptera is easily recognised. The pattern differences of these have been, in large part, already crystallised into appropriate formal taxa; in the case of mimicry-selected butterflies these taxa probably have a high degree of correlation with real adaptations to the prevailing bioenvironmental conditions. This fact greatly aided in the formulation of the refuge map, using the patterns of differentiation observed in the mimetic Heliconiini and Ithomiinae; the patterns were later discovered in other non-mimetic groups, with a high confidence of correlation. Many cryptoraces may also be expected even in mimetic groups; a few of these are pointed out and named below, in cases where isolation of

populations and consistently recognisable differences are present. Others, of uncertain isolation and unreliable recognition levels, are not judged to be worthy of formal description. The decision in each case is necessarily in part subjective, but the use of the following criteria can bring a reasonably high level of confidence to recognition of valid races in polytypic continental species:

(a) The race should be easily 'spotted' (visually, morphologically, chemically, etc.) in a series of its closest relatives, through recognition of characteristic aspects which correspond to characters of standard usage in the taxonomy of the group.

(b) The race should occur in monomorphic form over a reasonably large area, preferably corresponding approximately with areas of monomorphism in other species and groups (see refuge map).

(c) The type of differentiation observed should be clearly linked to selection by significant and recognised ecological factors in the area of presumed evolution, when these are known.

(d) The recognition of the race should be useful in the understanding of the genetics, physiology, distribution, differentiation, and/or other important aspects in the biology of the species.

The application of these relatively conservative biosystematic criteria to the definition of continental subspecies in widely distributed polytypic organisms is worthy of further comment. The use of the subspecies concept varies widely among taxonomists who deal with different systematic groups. For highly vagile, poorly differentiated organisms it is surely dispensable, except for well-defined insular races. At the other extreme, in highly sedentary and well-differentiated organisms (such as land snails), it could be easily abused, hiding the interest of the ecological genetics behind a smoke-screen of valid but non-useful taxa. The Lepidoptera treated here (Heliconiini, and Ithomiinae in the third paper) represent an intermediate system, in which many recognisable polygenic forms, most of them certainly produced as a result of the natural selection of more favourable phenotypes, occur monomorphically over reasonably large areas, seeming to correspond with past centres of evolution. These forms are conveniently referred to available and/or descriptive race names, properly published in Latin and supported by type-series.

Other forms, of course, represent mere genetic recombinants or intrapopulational variants. If names are available for these, they are best conserved, and written in quotations (not italicised); someday, with more complete biosystematic work, a part of these names may be found to merit revalidation as good subspecies or even species. If the variants are unnamed, they had best remain so until subspecific or specific category can be established, referring to the forms by vernacular descriptors such as 'wide-band form', 'north-eastern phenotype', 'dwarf', 'red-eyed mutant', 'transitional form' (between a and b), 'recombinant' (between genes AB and ab), etc., always giving the pertinent characters and genotype where possible.

A complication in the analysis of patterns through the application of centres of evolution is introduced by the variability in the dispersal abilities and ecological tolerances of different species and races. This results in different positions and widths of secondary contact zones, and in occasional cases leads to complete blurring of subspecies boundaries, at times without concomitant erasure of the original differentiated characters, giving polymorphic populations within core areas (this is especially frequent when only a few genes are involved in the systematic aspects considered; see Brown & Benson, 1974). A general approach in the latter case, common in the Heliconiini, is to recognise the
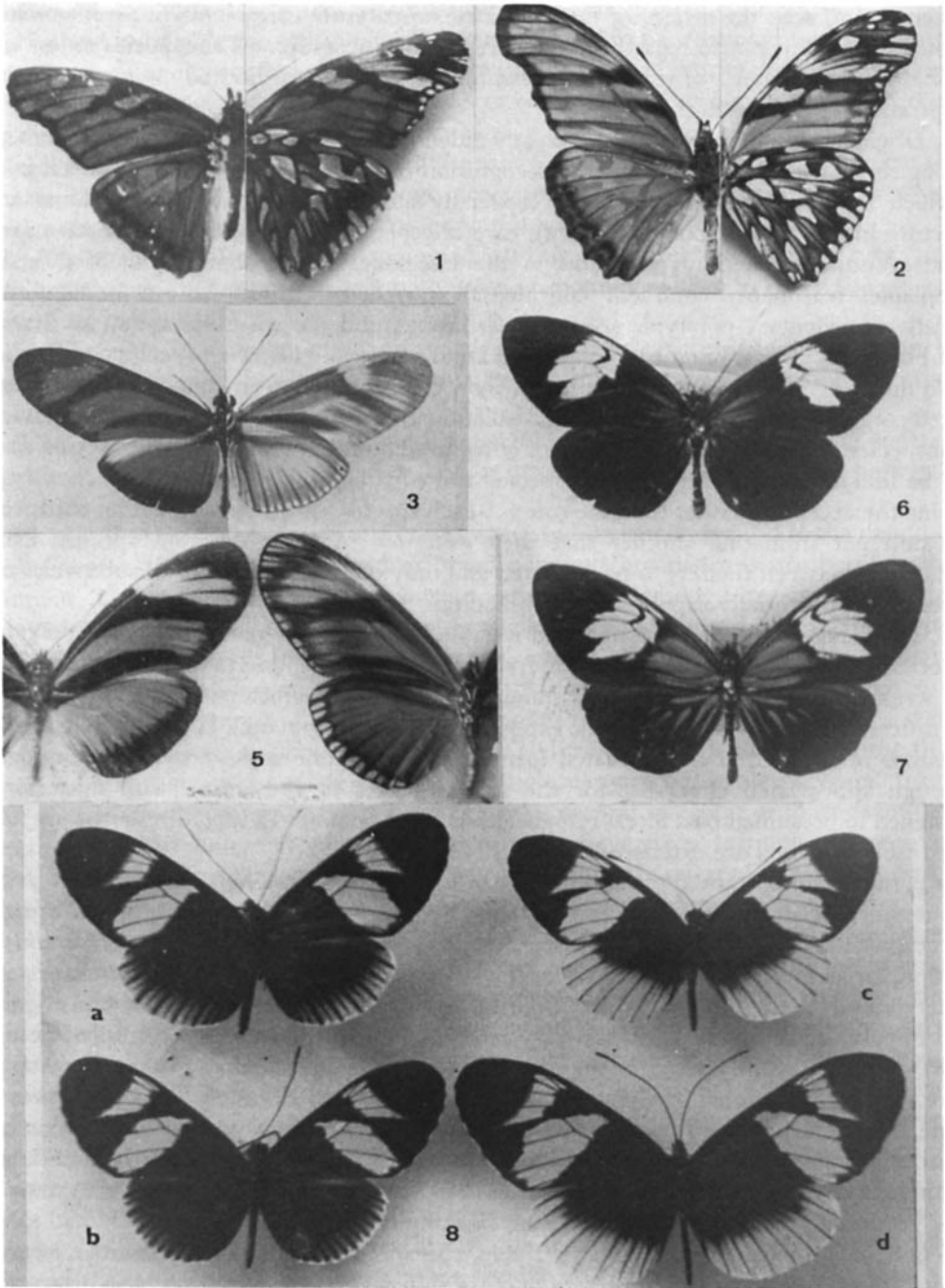
interest, and seek the origin, of the sympatric, apparently conspecific but well-differen-
tiated forms, but not to regard them as present-day geographical subspecies unless they
conform to the criteria of very widespread monomorphism, or limited monomorphism in
a presumed refuge area.

Obviously, any analysis will be greatly aided by the availability of abundant material
(long series from key transects), the recognition of appropriate secondary contact zones
(which are often heavily collected, especially along Amazonian rivers, leading to a
picture biased toward polymorphism), carefully planned field work in important areas,
and eventually genetic experiments in the insectary. Where some or all of these are
available, reasonably confident continental subspecies definitions can be made for
relatively sedentary polytypic species, bearing in mind the wise orientation of Richard
M.Fox (1968 : 167): "Some lepidopterists attempt to avoid using subspecies names where
two different populations are connected by a clinal gradation in colouring and pattern,
preferring to demonstrate geographic isolation between populations of what they call
subspecies. However, the possibility of clinal gradation between subspecies seems to me
to be inherent in the definition of species and of subspecies, with geographic isolation
being the exception rather than the rule . . . each species [of *Tithorea*] includes subspecies
so different from one another that they were described as different species. Clinal
gradation between them is to be expected and only demonstrates that all subspecies of a
species are potentially capable of interbreeding."

The refuge theory gives a new and reliable basis for systematic analysis of polytypic
species, and is especially useful in the frequent cases where, due to high dispersal ability
or weakened selective pressures on standard taxonomic characters, the clear boundaries
of differentiated forms have become extensively blurred. Appendix II presents a complete
analysis of recognised differentiated forms in the Heliconiini (representing an updated
though abbreviated check-list for the forest species in the tribe), with most forms
assigned to presumed past forest refugia (Map and Appendix I), including some probable
past isolates which are extensively diluted today.

A further important application of the refuge map is in the obtaining of high-quality
monomorphic stock for genetic experiments, by sampling populations in central areas of
larger, well-separated refugia. The map should also be useful in selecting areas for conser-
vation, so as to ensure the survival of the largest possible number of threatened species;
inter-refugial areas are usually very poor in endemic forest forms of plants and animals.

Finally, a cautionary note: the very large number of presumed Neotropical refugia
(38) which apparently acted in the differentiation of heliconians and other Neotropical
forest butterflies probably include some areas which are effectively isolated in present
time, even though the majority now appear to be connected by zones of secondary
contact of differentiated subspecies, across which the species are continuously distributed.
Although obvious modern physiogeographic barriers are not evident between many of
the proposed refugia, some students of Neotropical zoogeography believe that subtle
barriers (edaphic conditions, broader rivers, climatic or seasonal discontinuities, vegeta-
tional transitions) exist in the present and are sufficient to account for all the patterns of
race formation observed. Such persons would substitute the word 'area' for 'refuge' in all
contexts in which the latter is employed in this paper, and indeed should do so in order
to appreciate and apply the results of the analyses presented, whose fundamental impli-
cations are independent of which theory is advanced for the origin of the differentiation
patterns observed.

Figs. 1–8. All insects life size except in Fig. 8 (about 0·75 life size). (1) *Dione juno miraculosa* Hering, male, dorsal (left) and ventral (right) wing surfaces, Lima, Peru (Henry Edwards coll.), AMNH. Black, brick-red, cream, and silver. (2) *Dione juno andicola* (Bates) × *miraculosa*, male, dorsal (left) and ventral (right) wing surfaces, Santo Domingo de los Colorados, western Ecuador, collection of the author. Black,

As present-day barriers are subject to experimental observation and verification, it should be possible to determine which refugia are indeed still operative in the present. Solid support for the refuge theory should come with detailed pedological and palynological studies in a large number of areas within the Neotropical forest. At present, these have been barely initiated, mostly in marginal or nonforest habitats. Data for the ecological barrier hypothesis will depend upon extensive ecological field work throughout tropical America. Both endeavours are worthy of extensive interest and support, since it is probable that both hypotheses (past *vs.* present differentiation) carry some part of the truth.

COMMENTS ON KNOWN SPECIES

Dione juno miraculosa Hering, 1926

This was placed (still unexamined) as a 'possibly good species' in the earlier revision (Brown & Mielke, 1972). Several specimens of both sexes have now been examined in the AMNH (fig. 1), the BMNH, and the Museu de Zoologia (São Paulo). These show

Fig. 4. *Eueides libitina* Staudinger, lectotype male, internal aspect of left genital valve (left) and distribution of androconial scales on hindwing veins (right).

orange, cream, and silver. (3) *Eueides libitina* Staudinger, lectotype male, dorsal (left) and ventral (right) wing surfaces, Cayenne, in the Berlin Museum. Black and orange; ventral submarginal spots cream. (5) *Eueides lineata* Salvin & Godman, females, dorsal (left) and ventral (right) wing surfaces, Santa Rita, near Colón, Panamá (southern limit of range; morphologically identical to Guatemala specimens); males have the postmedian band on the fore wing narrower and oranger, nearly concolorous with the basocubital area. Collection of the author. Black, orange, and ochre; ventral submarginal spots white. (6) *Heliconius xanthocles explicata* Stichel, male in the BMNH, dorsal, Mocoa, upper Rio Putumayo (1° 9′ N, 76° 37′ W). Black, yellow, and red. (7) *Heliconius xanthocles flavosia* Kaye, male from near Villavicencio, Meta, Colombia, in the BMNH. Black, yellow, and red. (8) Four specimens of *Heliconius eleuchia primularis* Butler × *H.e. eleusinus* Staudinger, from Paramba, 3500 ft (Imbabura, 0° 49′ N, 78° 21′ W), north-west Ecuador, iv.1897, dry season (*Rosemberg*) (Rothschild collection, BMNH): (a, b) form 'deflava' Joicey & Kaye, with a fore wing near that of *primularis* and a hind wing closer to that of *eleusinus*; (c, d) with hind wing like that of typical *primularis* and a fore wing closer to that of *eleusinus*. Blue-black and yellow.

morphology identical to that of *Dione juno* (see Emsley, 1963) of which *miraculosa* should be considered a reddened southern subspecies. Intergrading specimens with the west Ecuadorian *D.j.andicola* are known from a broad transition zone in north-western Peru and south-western Ecuador (fig. 2). The typical form occurs in the Lima area and southward to Arequipa (type-locality), in a very dry area where its principal foodplants today (according to G.Lamas Müller, pers. comm., 1975) are *Passiflora suberosa* and the cultivated *P. edulis* (*juno* is known to be a serious pest of the latter in many areas). Information on the Henry Edwards (Lima) specimens in the AMNH indicates larvae feeding on *Tacsonia* sp.; as this subgenus of *Passiflora* occurs only in the very high Andes, it may be presumed to have been a cultivated plant in Lima (where *P.(T.)mixta* is often grown), or a misidentification.

The subspecies flies together with a similar, also reddened endemic subspecies of *Agraulis vanillae*, named *A.v.forbesi* by Michener (1942).

Eueides libitina Staudinger, 1885

This species was described from but three specimens, two males and a female, all reportedly captured in Cayenne (Guyane Française), and to the best of knowledge has not been seen since. However, as it is extremely similar to the common *Eueides lybia*, it could easily be passed over by collectors who would quickly become 'saturated' with the latter species.

Through the courtesy of Dr H.J.Hannemann of the Zoologisches Museum der Humboldt-Universität (Berlin), I was able to examine and dissect one male from the syntypic series of *libitina*; this specimen has been designated as lectotype of the name (fig. 3). The morphology of this specimen (fig. 4) places it between *Eueides lineata* from Central America (fig. 5) and the widespread *E.vibilia*, and indicates that it should be regarded as a distinct species. Collectors in the area influenced by the Oyapock refuge (principally Guyane and Amapá) should be on the lookout for unusual-appearing or -behaving *lybia*, as *libitina* should still be found in the area today.

The male (fig. 3) may be easily recognised by the very broad light costal area on the dorsal hind wing, and the broad black anal stripe on the ventral fore wing. Both sexes
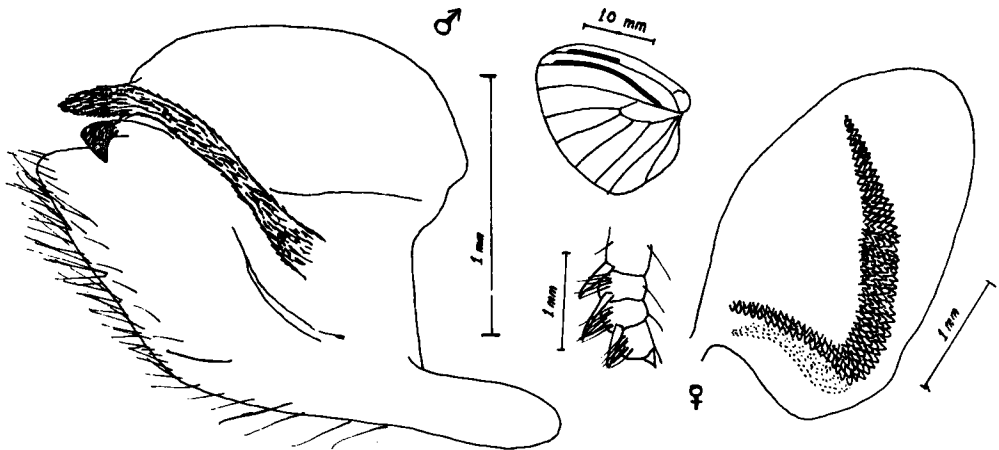

Fig. 10. *Eueides emsleyi* sp. n., holotype male, internal aspect of left genital valve and androconial distribution on hind wing veins (left, upper); paratype female in BMNH, fore tarsus and bursa copulatrix (right, lower).

possess well-defined and paired light marginal spots on the ventral wing surface (especially on the hind wing), and share with only *lybia* in the genus the presence of red basal spots on the hind wing.

Heliconius xanthocles explicata Stichel, 1923 (fig. 6)

This is a most unusual and little-known subspecies which flies with locally endemic *H.erato dignus* and *H.melpomene bellula* (with red fore wing bands and yellow hind wing stripes) in the upper Rio Putumayo near Mocoa, Colombia (see Brown & Mielke, 1972 : 8). This subspecies is represented by a single male (figured) in the BMNH; the female, which apparently has a narrower yellow band on the fore wing, was designated *para-nympha* earlier on the same page. The name *explicata* is here validated for the endemic Putumayo-refuge subspecies of *xanthocles*, which is very different from the neighbouring *flavosia* Kaye (fig. 7) in the Villavicencio refuge area, and from *melete* Felder & Felder from lower elevations in eastern Colombia and north-western Brazil (Imerí refuge), principally in the reduction and near elimination of the red basal 'dennis' area on the fore wing and red hind wing rays.

Heliconius eleuchia (Hewitson, 1854)

This species was suggested, in the earlier revision, to include the west-Colombian form *eleusinus* Staudinger, which intergraded through 'ceres' Oberthür to west-Ecuadorian *primularis* Butler (see Brown & Mielke, 1972). The types of 'ceres' are in the BMNH collection, as are many true intergrades between *eleusinus* and *primularis* from extreme northern Ecuador (Paramba, Cachabé). The obsolescent hind wing border of 'ceres' is white, not yellow, suggesting that it results from mixture of *eleuchia* rather than *primu-laris* genes with *eleusinus*; this is supported by its collecting locality ('Cali'). Similar specimens, with either partly confluent or near-separate, white or cream-coloured fore wing bands, and variable white scaling in the hind wing marginal region, can be captured today in the Anchicayá Valley west of Cali. *H.e.eleuchia*, a very wide-ranging and mass-breeding species, probably originally derived in the Nechí area, is sporadically abundant in the upper Cauca Valley near Cali, and certainly should be expected to occasionally flow over the low passes (about 1400 m) to the western slopes (Anchicayá area), there mixing with the locally common *eleusinus* (Chocó-derived), producing the 'ceres' type of pattern. The true integration to Chimborazo-derived *primularis* is seen in the previously mentioned (Brown & Mielke, 1972) forms from extreme south-western Colombia, and intergrades from extreme northern Ecuador (including form 'deflava' Joicey & Kaye; see fig. 8), with confluent or separate fore wing bands and reduced yellow scaling in the hind wing marginal area.

The association of *eleusinus* with *eleuchia* rather than with *sapho* is supported by the above-mentioned intergrading series, the occurrence of yellow pigment in *eleusinus* (missing from all known *sapho* forms), and the recent discovery of a Chocó-derived new subspecies of *sapho* sympatric with *eleusinus* in western Colombia (Brown & Benson, 1975*b*).

Heliconius leucadia Bates, 1862

This species has been captured sparsely in very widely separated areas of the Amazon Basin, principally as the form *pseudorhea* Staudinger, which lacks the white marginal markings on the hind wing and closely resembles *H.sara thamar* (Hübner) (= *Papilio*

rhea Cramer, an invalid homonym). Although the two species are closely related morpho-
logically and can only be distinguished with certainty by the red basal spots on the ventral
surface of the hind wing (the anterior dot in *leucadia* being greatly elongated), they are
probably quite different in biological and ecological parameters. The dorsal character
most often used for separation—presence (*sara*) or absence (*leucadia*) of a yellow spot
below vein *Cu*2 of the fore wing—has been observed to fail to correctly identify many
Colombian and Venezuelan *sara* ('magdalena'-types resulting from intergradation of
s.sara and *s.thamar*, with reduced fore wing yellow bands), and at least one Manaus
leucadia (with a full band extending well below *Cu*2; captured by W.W.Benson in July,
1974).

The species is high-flying and much harder to capture than *sara,* preferring deep,
heavy woods and occurring very locally. However, specimens are now known from
essentially all well-collected points in the Amazonian Hylaea, within a broad oval
bounded by the Atlantic Ocean, western Maranhão, northern Goiás, central Mato
Grosso (Ilha do Bananal in the east, Rio Jaurú in the west), northern Bolivia and eastern
Peru to reasonable elevations in the Andes, central Ecuador (Abitagua highlands,
headwaters of the Rios Napo and Pastaza to over 1000 m elevation), south-eastern
Colombia (both upper Rio Putumayo and Villavicencio areas), southern Venezuela
(Amazonas and southern Bolivar), and central (perhaps coastal) Guianas. It is often
frequent when found.

H.leucadia is but one example of a number of extremely widespread but apparently
very poorly differentiated blue-and-yellow mimetic *Heliconius* (others are *metharme,
doris* (blue morphs), *wallacei, sara,* and *antiochus,* the last with white rather than yellow
bands over much of the Amazon Basin). It seems highly significant that all of these
species have been shown to have gregarious larvae (except for *leucadia* which is still
unknown but presumed to be similar, as the female abdomen is short and thick and
expressed eggs are not fertile). Essentially all have been found, with minimal differentia-
tion of a colour-pattern nearly unique to *Heliconius* (not mimetic of other distasteful
groups, but mimicked by a few presumably non-distasteful Papilionidae, Pieridae, and
Nymphalinae), in areas corresponding with the refugia denominated Oyapock, Belém,
Tapajós, Araguaia, Guaporé, Rondônia, Madeira, Yungas, Inambari, Ucayali, Napo,
Abitagua, Tefé, Loreto, Putumayo, Villavicencio, Imerí, Parima, Roraima, Imataca, and
Manaus/Guiana on the Map. It is possibile that the relative constancy of the blue-and-
yellow pattern of these species is due to a form of 'autoselective stabilisation', caused by
the inevitable simultaneous presence of large numbers of genetically similar individuals
in any one place at a given time, prescribed by the gregarious-larvae habit, and in the
absence of other consistently common distasteful butterflies with similar colour-patterns.
This would be presumed to represent a powerful force for maintenance of colour-pattern
consistency, with diverging individuals being rapidly eliminated by negative predatory
selection; the differentiation of these species in refugia might perhaps be detectable in
enzymes, behaviour, or juvenile characteristics. That the gene-complement of these
species is no more inherently conservative than that of others in the tribe is supported by
the many striking aberrations which have been captured, and the existence of occasional
local mimetic subspecies like *sara brevimaculata* (of *erato chestertonii* in the Cauca Valley)
and *wallacei elsa* (of abundant white-banded *antiochus* in the Roraima area); thus evolu-
tionary potential is apparently not restricted. Another explanation, such as that above
('selection for stability') must be sought for the non-divergence of these relatively non-

mobile forest organisms (an exception is *doris*, which is migratory and widely poly-morphic; it has been suggested to be a Batesian mimic (Benson, 1971)), in the refugia.

Further additions to the previous revision

(a) Brazilian Amazonian heliconians, predicted to invade the upper Paraguay River basin in central Mato Grosso (Brown & Mielke, 1972) and now confirmed to do so, are the following: *Philaethria dido* (Barra do Bugres area), *Eueides lybia lybia* (same, and upper Rio Cabaçal), and *Heliconius doris doris* (São Vicente, east of Cuiabá; also very near Paraná Basin in central Goiás, Iporá). *H.burneyi* has now been confirmed in the Barra do Bugres area and the upper Rio Cabaçal; in the former area, *H.melpomene* is found as the central Bolivian subspecies *amandus* Grose Smith & Kirby, with occasional individuals transitional to *m.burchelli*; in the latter area, *H.melpomene penelope* and hybridised *H.erato* (*phyllis* × *venustus*) were found. Substantially pure colonies of *H.erato phyllis* and *H.e.venustus* have now been found but 20 km apart near Uirapuru, farther north-west. However, the four 'Cuyabá-Corumbá River System' species (*astraea*, *elevatus*, *demeter* and *ricini*) have not yet been discovered in central Mato Grosso; only a sight record of the first of these is available, on the road between Cuiabá and Cáceres.

(b) For a discussion of *Heliconius numata*, of which 'silvana' is but a supergene-morph, see Brown & Benson (1974).

(c) For a discussion of *Agraulis vanillae lucina*, *Dryas iulia titio* (= *i.iulia* auctorum), and four new subspecies of *Heliconius demeter* (with an analysis of differentiation patterns in this species), see Brown & Benson (1975*a*).

(d) For a discussion of *Heliconius hecalesia* == *longarena*, including analysis of differentiation patterns in this species and in *H.sapho*, see Brown & Benson (1975*b*).

(e) For a discussion of *Heliconius hermathena* and *Philaethria pygmalion*, and comments on present-day evolution in Amazonian non-forest refugia, see Brown & Benson (1976).

A total of 66 species may now be recognised in the tribe, three having been eliminated (*Agraulis lucina*, *Heliconius longarena* and *H.silvana*) by recombination, and three added (*Philaethria pygmalion*, *Eueides libitina* and *E.emsleyi*, below) to the 1972 list.
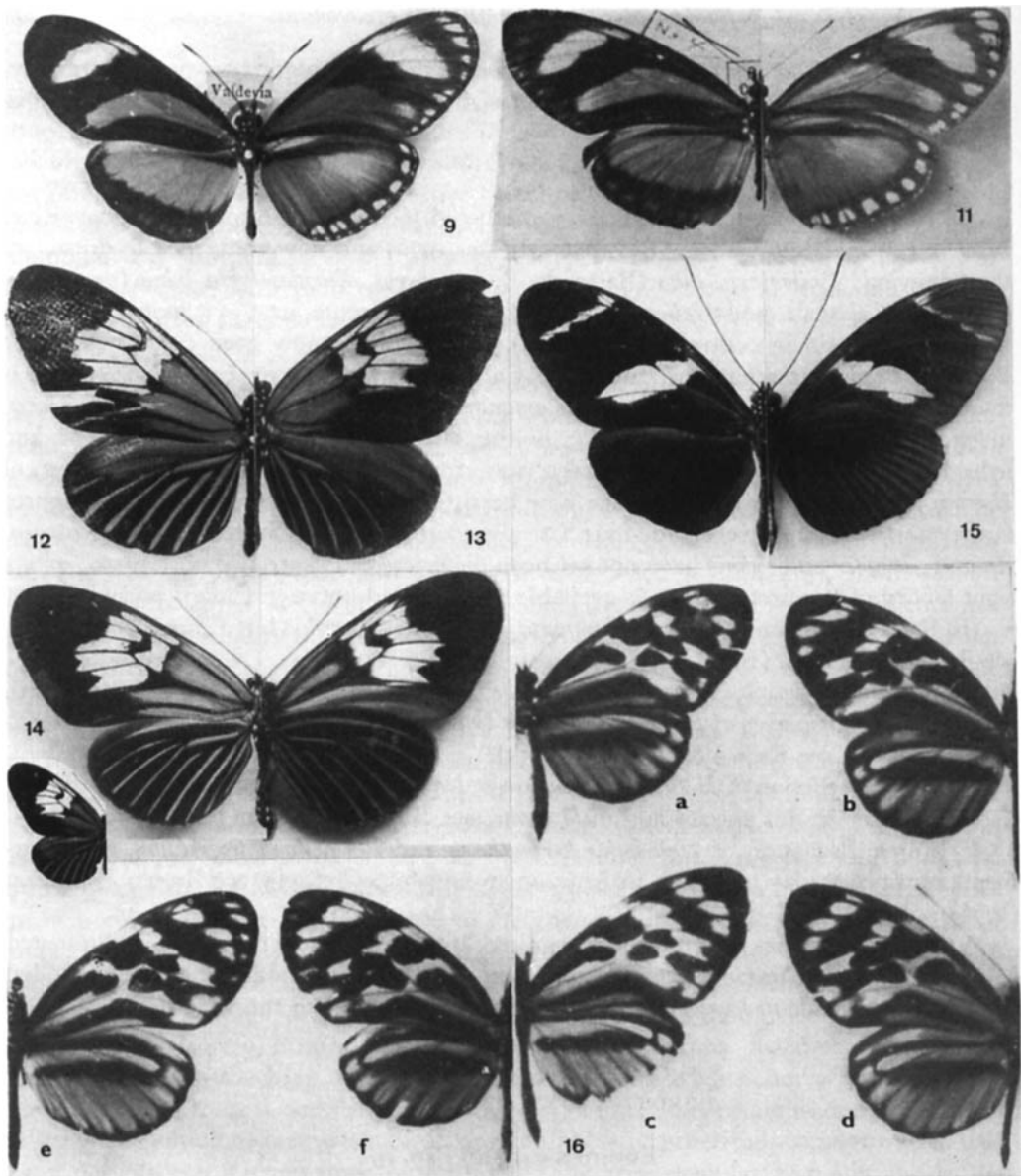
DESCRIPTIONS OF NEW FORMS

Eueides emsleyi sp. n.

In his revision of the genus *Heliconius* (in which he included *Eueides*), Emsley (1965 : 198) placed the following note under *H.(E.)vibilius* [*sic*]:

"In the AMNH there is a single female specimen recorded from La Lechera, Rio Opon, north of Tunja, Boyaca, Colombia, which has typical *vibilius* morphology and ventral alary colour pattern, but which is dorsally similar to *H.lybius olympius*. There is a similar specimen in the BM from La Chima, which is in western Ecuador. Both localities have aberrant material in other series, so further specimens must be obtained before the distribution can be confirmed."

Two more specimens have now appeared of this unusual and evidently very rare species: a male in the Joicey collection (BMNH) from Valdivia, in northern Colombia (fig. 9), and a very large female in the Museu Nacional in Rio de Janeiro from the

Figs. 9–16. All insects about life size except insert at left of figure 14 (0·4 ×) and figure 16 (0·85 ×). (9 and 11) *Eueides emsleyi* sp. n., dorsal (left) and ventral (right) wing surfaces, black, orange, and ochre; ventral spots white: (9) holotype male; (11) paratype female, 'Bogota' MN(Rio). (12) *Heliconius aoede philipi* nov., holotype ♂, dorsal, black, yellow, and orange. (13) *Heliconius aoede lucretius* Weymer, male, dorsal, Mitú, Vaupés, eastern Colombia, collection of the author. Black, yellow, and orange. (14) *Heliconius aoede* nr. *philipi*, presumably transitional to *eurycleia* Brown, female, dorsal (left) and ventral (right) wing surfaces, Todos Santos, Chapare, north of Cochabamba, Bolivia, in the collection of the author; and male (lower left inset), dorsal, same locality, in the collection of H.Holzinger, Vienna. Black, yellow, and orange. (15) *Heliconius wallacei araguaia* ssp. n., holotype male, dorsal (left) and ventral (right) wing surfaces. Black and yellow (no blue iridescence). (16) *Heliconius pardalinus orteguaza* ssp. n. dorsal: (a–e) data as holotype: (a) holotype; (b–d) three paratype males; (e) paratype female; (f) paratype female, Caucayá, Putumayo, 10.xii.1948, in the AMNH. Black, yellow, and orange-brown.

generalised locality 'Bogotá' (fig. 11).* These four specimens constitute the type series of the taxon, which is dedicated to Dr Michael G.Emsley of Fairfax, Virginia, USA, who first recognised its distinctness and interest.

Male (fig. 9)

FW 34 mm. Dorsal fore wing black with a 3 mm-wide orange cubital bar from base to within 2 mm of outer margin, and an equally wide postmedian cream-coloured band from very near the costal margin to a tapered point on vein Cu_1, 2 mm from outer margin; this divided by black scaling over the radial vein, with the superior element projecting basally 2 mm more than the rest of the band, producing a marked triangular black 'bite' from the band at the radial; inner and outer margins of the band otherwise near parallel, smoothly curved. Dorsal hind wing with an inconspicuous light area near costal margin, a black basocostal triangle, and an orange median area with a broad (5 mm along veins M_3 to $2A$) black border, presenting faint lighter spots corresponding to ventral white spots. One yellow basal spot in the humeral region. Ventrally similar, with orange areas darker red-brown; much cream scaling in the fore wing cubito-submarginal area and hind wing median area (above vein M_3); fore wing anal black bar missing, the area being red-brown like that above it. Two series of paired intervenal white spots, a very small marginal group (near obsolescent on the fore wing) and a large submarginal group (fused and elongated in fore wing apical area, fused and compressed in hind wing medio-apical region). Fore wing costal line red; hind wing costal stripe yellow, wide; hind wing subcostal line black, reaching to apex; one yellow basal dot on hind wing between cubital and anal veins.

Genital valve (fig. 10) intermediate between and distinct from those of *Eueides vibilia* (Godart) and *E.procula* Doubleday (with both of which *emsleyi* is sympatric); also similar but not identical to that of *E.lampeto* Bates (allopatric, but unlikely to be conspecific due to fundamental differences in important minor colour-pattern elements).

Female (fig. 11)

FW 35-40 mm. Very similar to male, with a longer black subcostal stripe on the dorsal hind wing, and darker anal and costal areas on the ventral fore wing. Fore tarsus fore-jointed, signa on bursa copulatrix large, wide, and slightly asymmetrical (fig. 10).

Holotype ♂, COLOMBIA: Antioquia, Valdivia ('Valdevia'), (7° 11′ N, 75° 27′ W), (BMNH, Joicey Bequest, 1934–120).

Paratypes (all ♀). La Lechera (Quebrada), Rio Opon region (7° 3′ N, 73° 53′ W, Santander), 750–1000 m, N of Tunja, Boyacá, Colombia, (*E.Richter*), (AMNH, Frank Johnson donor); 'Bogotá', No. 4/472, Museu Nacional, Rio de Janeiro (very large, specimen figured); and La Chima (Rio de las Juntas, near Bahahoyo, Provincia Los Rios, near 1° 15′ S, 79° 15′ W), western Ecuador, (*M.de Mathan*) (BMNH, Levick Bequest, 1941–83).

The species is probably to be looked for at moderate elevations in central Colombia and western Ecuador, and must be presumed to be either extremely rare and local or very high-flying, to have so consistently escaped collectors' nets. In museum series it

* Three further specimens, not regarded as paratypes, are in Museum national d'Histoire naturelle, Paris, and Zoologisches Museum der Humboldt-Universitat, Berlin. Two of these were collected in Santo Domingo de los Colorados, western Ecuador (Turner, J.R.G., pers. comm., 1975).

should be looked for among *Eueides lybia lybioides* Staudinger (not among *lybia olympia* which has a white rather than a cream-coloured postmedian band on the fore wing); *lybia* has no white submarginal spots on the ventral surface of the wings.

Heliconius aoede philipi subsp. n.

Male (fig. 12)

FW 38 mm. Similar to the northern subspecies *H.a.lucretius* Weymer (fig. 13), differing principally in the expansion and continuity of the fore wing square yellow patch, due primarily to an increase in the size of the element in the distal third of the discal cell, uniting with the red-orange basal dennis area (which is also increased distally) and the yellow extracellular band; and the longer and more numerous red rays on the hind wing, which include a streak in cell $Rs–M_1$ and reach almost to the outer margin (these are shorter, narrower, and lacking more costal elements in *lucretius*). The over-all appearance of the insect is thereby appreciably different from that of *lucretius*.

   Holotype ♂, BOLIVIA: La Paz, Sarampiuni (as 'Salampioni'), on the Rio Challana above Guanay, about 600 m, 15° 25' S, 68° 7' W, (BMNH, Joicey Bequest, 1934–120).

   It is surprising that very few *aoede* have been captured in Bolivia, although the species is commonly found in various parts of south-western Brazil: in Mato Grosso as *eurycleia* Brown, 1973; in Rondônia as *faleria* Fruhstorfer, and in Acre as *bartletti* Druce. The very few known Bolivian specimens, other than the holotype male, come from Todos Santos, Chapare, north of Cochabamba, and have a large black spot in the middle of the fore wing yellow patch (at the end of the discal cell) (fig. 14); otherwise, they are similar to *philipi*, but are not designated as paratypes. I propose here that these are actually transitional specimens; that the true Yungas-derived form of *aoede* no longer exists in the core area where it evolved; and that *philipi* has evolved and may still be found in the transitional area between the Yungas and Inambari refugia, under selection by hybrid populations of other *Heliconius*, which if true would represent a most unusual situation in *aoede*.

   The Sarampiuni area, and indeed the lower Nor Yungas of La Paz in general, do not conform in vegetation morphology to the usual aspect of refuge areas visited in other parts of the Neotropics. Indeed, the area still includes today large patches of 'cerrado' (dry scrubby grassland with a typical, if depauperate, flora and fauna) and poor forest, even during an apparent wet period, indicating that it was unlikely to have operated as part of a forest refuge during past dryer periods. The higher Nor Yungas, on the other hand, possess a very rich humid cloud forest, which extends as dense rain forest at lower elevations over the Sur Yungas, much of the Yungas area north of Cochabamba, and a large lowland area in central Bolivia where the Rios Chapare, Ichilo, Piray, Yapacani and Grande join to form the Rio Mamoré. It is proposed that this region, very rich today in endemic plants and animals, was once the true Yungas refuge (Map), covering an altitudinal range of 200 to 3000 m but not including the Yungas north of La Paz below 1800 m, if indeed even the higher parts of these.

   The heliconians show an odd pattern of differentiation in these areas. Whereas some apparently Yungas-derived forms are well distributed and monomorphic over the region, the typical mimetic *H.erato venustus* and *H.melpomene penelope*, with a square yellow band on the fore wing and much reduced and reddened dennis and rays, exist only in hybridised populations over much of the presumed original refuge area. They apparently

have been successfully dislocated from their centre of evolution by ecologically adaptable red-banded subspecies from the south-east, *H.erato phyllis* (Fabricius) and *H.melpomene amandus* Grose Smith & Kirby. Reasonably pure Yungas-type colour-pattern populations now exist only in the Guaporé refuge area to the north-east (where, however, they are also hybridised eastward, indicating non-derivation there), and in the Yungas of La Paz, where they still show some gene infusion from *phyllis/amandus* and also from Inambari-derived forms to the north-west. The corresponding mimetic form of *aoede, a.eurycleia,* is found today only in north-eastern parts of the Guaporé refuge; farther to the north-west it intergrades through *lucretius*-like individuals, still satisfactory mimics but possessing much more extensive and oranger dennis and rays, to *faleria* in south-eastern Rondônia (see Brown, 1973). It is proposed that it also intergrades across the former Yungas refuge area, now occupied by polymorphic hybridised populations of *erato* and *melpomene* having relatively little value in the formation of a useful mimetic environment for *eurycleia,* giving the further *lucretius*-like forms (fig. 14) before meeting pure *philipi* populations in extreme north-western Bolivia and south-eastern Peru.

The origin of *philipi* is thus problematic. It does not much resemble the sympatric and abundant (and presumably dislocated) *H.erato venustus* and *H.melpomene penelope* in the Guanay area (visited in late 1974, without rediscovery of *philipi*). It does look very much like some forms of *erato* and *melpomene* which occur in the south-eastern-most parts of the Inambari region, similar to the Bolivian subspecies but with a full orange dennis and rays. These in turn seem to be hybrid populations, resulting from the meeting of *H.e.lativitta* Butler and *H.m.aglaope* Felder & Felder, with a full orange dennis and rays but a reduced extracellular fore wing yellow band, with the higher elevation *H.e.amphitrite* Riffarth and *H.m.euryades* Riffarth, lacking dennis or rays but possessing a very enlarged, fully compacted square red fore wing band in the same position as the yellow patch of *philipi.* A number of *erato* and *melpomene* are known from the southern-most parts of Peru (Rio Inambari) which possess a full orange dennis and rays like *lativitta* and *aglaope,* but also a large square yellow band on the fore wing. It seems possible that these form local populations occupying an area between the narrow yellow-banded forms to the north-east, the wide red-banded forms to the south-west, and the reduced, reddened-dennis-ray forms in Bolivia—roughly the Peru/Bolivia border north of Lake Titicaca—which served as a mimetic environment for the formation and stabilisation of the very similar *philipi,* which would thus have been derived in an interrefugial area. Only further collecting in this little-explored region will serve to resolve this question; it is of interest, however, that the few known collections from this border region (in the BMNH) include some endemic forms of ithomiines.

Even if the phenotype with the black spot inside the square yellow fore wing band should prove to be the typical form of *aoede* over all of northern Bolivia, the new sub-specific name *philipi* can be safely applied to all these populations (since the type represents a part of these). Bolivian *aoede* are separated by several thousand kilometres from the superficially similar *lucretius* on the upper Rio Negro and Rio Vaupés (Imerí-derived), without evidence for genetic continuity in the intervening area, and are easily distinguished from the northern subspecies by the extent of the dennis and rays, even when the fore wing band is not continuous (figs. 13, 14); thus, they are in need of a separate name. In such a case, though, the subspecies would be best ascribed to the Yungas refuge.

The new taxon is dedicated with gratitude to Dr Philip M.Sheppard of the Depart-

ment of Genetics of the University of Liverpool, who has greatly advanced our know-
ledge of the distribution, differentiation, genetics, ecology and evolution of heliconiine
butterflies, and who not only first set this author to working on the refuge theory as
demonstrated in the heliconians, but provided ideas and materials for innumerable key
experiments and projects in heliconiine biology.

Heliconius wallacei araguaia subsp. n.

Male (fig. 15)

FW 38 mm (small for this species). Similar to *H.w.flavescens* Weymer and *H.w.wallacei*
Reakirt, but with the yellow median band on the fore wing intermediate between these,
narrower and more pointed at both ends than that of *flavescens*, and somewhat fuller
than that of *wallacei*; with a distinct yellow line over the dorsal fore wing cubitus, very
faint or absent in other subspecies; and with complete absence of any blue or green
iridescence on the flat brownish-black dorsal wing surface. The last character occurs
occasionally in other populations of *wallacei* (e.g. Leticia, Colombia, 1971; J. Glassberg),
but in combination with the other characters and the geographically restricted and
peripheral range of *araguaia*, serve to characterise the new subspecies. The ventral
surface is very washed-out, with poorly developed red basal spots. The taxon probably
developed in the Araguaia refuge in west-central Goiás, and may be found uncommonly
or locally over much of the dry south-eastern Amazon today, in western and northern
Goiás and extreme eastern Mato Grosso; typical *H.w.flavescens* is common from the
Xingú drainage south-westwards, in the moister, more continuously forested parts of
central and western Mato Grosso.

Female

Not seen, but probably identical as in other subspecies.

    Holotype ♂, BRAZIL: Rio Araguaia (as 'Araguaya'), 'Provincia' (= state of) Goiás (as
'Goyaz'), vi.1906 (*G.Baer*) (BMNH, Rothschild Bequest, 1939–1).

    Paratypes. 3 ♂, same data as holotype; 2 ♂ 'Araguaya R.', (*E.Reynolds*), (BMNH
90–58); 2 ♂, Tocantins, 1910, (BMNH, ex Grose Smith, Joicey Bequest, 1934–120);
2 ♂, Ilha do Bananal, Nos 25/928–9, Museu Nacional, Rio de Janeiro, ex May collection.

Heliconius pardalinus orteguaza subsp. n.

Male (fig. 16a–d)

FW 40–44 mm. Dorsally similar to *H.p.dilatus* Weymer, especially on the hind wing
which bears a very narrow black median band widely separated by orange from the
narrow, deeply dentate black border; however, majority of fore wing, and hind wing
above median band, predominantly suffused with yellow, leaving only a variable but
minimal amount of orange scaling near the base of the fore wing and between the black
areas of the hind wing. In the type of *dilatus*, from central Peru, the orange is greatly
predominant, leaving yellow only in the fore wing subapical spots; other specimens are
known from southern Ecuador to central Peru which also bear a yellow postmedian
band (specimen from the Rio Santiago in the AMNH, for example), or even have
extensive yellow in the fore wing median area (form 'colorata' Stichel), but none approach

the extreme yellow suffusion typical of *orteguaza*. Fore wing apical area with one or rarely two rows of four yellow dots; black transverse spot-band in median region variably broken or fused; heavy black anal bar and cell dagger on fore wing; comma-mark a broad paraboloid leaving a yellow submarginal spot, as in other *pardalinus* forms; hind wing with two to four diffuse large yellow subapical spots in the orange region, and ventrally bearing a large diffuse red basal spot between the cubital and anal veins, as in other *pardalinus*.

Female (fig. 16e–f)

FW 41–45 mm. Identical to the male except in the lack of the light area in the costal region of the dorsal hind wing; tending to have the yellow colour more washed out, at times infused with orange scaling basally.

Holotype ♂, COLOMBIA: Caquetá, the Rio Orteguaza, near 1° N, 75° W, 14.ix.1947 (*L.Richter*) (AMNH, Frank Johnson Bequest).

Paratypes. 11 ♂, 2 ♀, same data as holotype except viii–ix.1947; 1 ♂ 10.xii.1948 and 1 ♀, 13.xii.1948, Caucayá, Putumayo (near 0°, 75° W) (all in AMNH); 1 ♂, identical to Rio Orteguaza specimens, from the Rio Guayabero, La Macarena, Meta, Colombia (2° 36' N, 72° 47' W) (coll. Dr E.W.Schmidt-Mumm, Bogotá).

A single paratype male from the Rio Orteguaza is heavily infused with orange, appearing intermediate to the subspecies described next. As most *pardalinus* populations are at least dimorphic (probably due to a large dispersal ability of the species), it is not unexpected that occasional individuals in Colombian populations should show genes from populations farther downriver.

The subspecies probably differentiated in the Napo refuge, and may be sought in northern Peru and eastern Ecuador at higher elevations than the following race, as well as in southern Colombia.

Heliconius pardalinus butleri subsp. n.

The heavily marked, very orange-washed subspecies of *H.pardalinus* Butler, which occurs commonly in north-eastern Peru, between the dark mahogany and yellow nominate subspecies (from western Brazil) and the lightly marked *dilatus* and *tithoreides* Staudinger from farther west and south (as well as the above-described subspecies from farther north-west), has usually been referred to the name *radiosus* Bates. However, the type of the latter name, from Villa Nova (today called Parintins) on the lower middle Amazon, belongs to a very distinct subspecies occurring between Manaus and Santarém only, similar to but far from identical with the north-east Peruvian race. Due to this widespread misapplication of Bates' name, the common Peruvian subspecies lacks a name; it is here designated in honour of A.G.Butler, who greatly contributed in the last century to our knowledge of Amazonian and other heliconians.

Male (fig. 17, upper)

FW 40–42 mm. Dorsally similar to *H.p.dilatus*, especially on the fore wing which is heavily printed in black over orange, with yellow restricted to the four subapical spots and faint scaling in the costal part of the postmedian band, and which bears orange streaks in the subapical region. The hind wing, however, is very heavily marked with black, leaving only a series of intervenal orange spikes between the median and marginal dark

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areas, poorly joined across the veins in the anal region, at times nearly obsolescent leaving most of the hind wing black. Ventrally similar to *p.tithoreides*, with extensive orange scaling in the fore wing apex (practically eliminating black areas), but with hind wing heavily marked in black both in median and marginal regions as on dorsal surface, not heavily suffused with orange marginally as in *tithoreides*. Parabolic midspace black comma mark in fore wing cell Cu_1–Cu_2, heavy cell-dagger and anal bar, and large red basal spot between cubital and anal veins of ventral hind wing, as in other *pardalinus* forms.

Female (fig. 17, lower)

Very similar to male, without broad light area in costal region of dorsal hind wing, and with the orange-brown and yellow colours more diffuse and muted, producing a 'washed-out' effect common in female silvaniforms.

   Holotype ♂, PERU: Loreto, Caballococha (as 'Cavallo-Cocho'), 3° 55′ S, 70° 30′ W, 'Amazonas', v–vii.1884 (*M.de Mathan*) (BMNH, Levick Bequest, 1941–83).

   The paratypic material is restricted to representatives from principal localities, in the long series in the BMNH; typical examples can be found in almost all major collections from the Loreto refuge area, between São Paulo de Olivença and Yurimaguas, especially around Iquitos: 1 ♂, same data as holotype; 2 ♀, Pebas, 'Amazonas', Loreto, 3° 10′ S, 71° 49′ W, Peru (*M.de Mathan*), (BMNH, Levick Bequest, 1941–83); 1 ♂, Rio Chambirayacu (as 'Chambireyacu près Yurimaguas, Huallaga'), San Martin, near 6° S, 76° W, Peru, vi–viii.1885, same collection; 1 ♂, viii.1931 and 1 ♀, viii.1932, Iquitos, Loreto, 3° 46′ S, 73° 15′ W, Loreto, Peru (*G.Klug*) (BMNH, Rothschild Bequest, 1939–1); 1 ♀, Rio Pacaya, lower Ucayali, Loreto, 5° 9′ S, 74° 7′ W, Peru, viii–ix.1912, (BMNH, Joicey Bequest, 1934–120).

   The fact that this subspecies lacked a name was apparently first recognized by N.D.Riley of the BMNH, when he recurated the heliconian collection several decades ago.

   The subspecies is presumably a product of the Loreto refuge, which might be considered as an eastern subregion of the Napo refuge of Haffer (1969), but which has produced a reasonable number of endemic forms in north-eastern Peru. The true Napo refuge apparently was centred farther north-west, and was responsible for many divergent forms, including probably the above-described and very different-appearing *pardalinus orteguaza*.

Heliconius hecale australis subsp. n.

Male (fig. 18)

FW 42–46 mm. Similar to *H.h.melicerta* Butler (fig. 19), differing from this common Panamanian and Colombian subspecies (Nechí-derived) in the much narrower hind wing dark border (5–6 mm wide, versus 7–10 mm in *melicerta*), with a consistently smooth inner edge (usually broken in *melicerta*), giving a much cleaner and brighter-coloured look to *australis*.

   Holotype ♂, WEST ECUADOR: Manabi, Palmar, 200 m, 0° 14′ S, 79° 20′ W, 13.iv.1941 (AMNH).

   Paratypes. 2 ♂, same locality as holotype, 13 and 16.iv.1941 (AMNH); 1 ♂ (fig. 18), Quevedo, Los Rios, W. Ecuador (*W.Buchward*) (BMNH, Rothschild Bequest, 1939–1).

Female

Unknown, though probably very similar to male.

It is surprising that so few specimens of this subspecies have been taken in the very heavily collected areas of western Ecuador. It must be supposed to be very rare and/or localised, in sharp distinction to the abundance of *melicerta* farther north. This could be explained by the fact that it is a south-western peripheral population in the range of the species, possibly existing under unfavourable conditions such as scarcity of larval foodplant (we have seen very little *P.vitifolia*, the typical *melicerta* foodplant, or indeed any other well-known *hecale* foodplant in western Ecuador). Thus, in spite of efficient mimetic association with the common sympatric *H.ismenius metaphorus* Weymer, *australis* may be unable to build up in numbers or to disperse to areas where the larval foodplant is infrequent or unavailable for use.

The subspecies was probably differentiated in the Chimborazo refuge, which is discussed more fully under *H.sapho candidus*.

Heliconius hecale barcanti subsp. n.

In his recent book, 'Butterflies of Trinidad and Tobago', Malcolm Barcant (1970), a long-time and assiduous Trinidad collector, illustrated a unique specimen of '*Heliconius hecali* (Plate 5, No. 1, p. 96), captured in August 1951 by Michael Rodriguez near Rio Claro, in the southern part of the island. This specimen represents a colour-pattern unlike that of any known subspecies of *H.hecale*, though related to that of the east Venezuelan *H.h.clearei* Hall. Much further searching by Mr Barcant and this author in the very interesting swamp forests near Rio Claro did not reveal the presence of a colony of this presumably new, possibly Trinidad-endemic subspecies. However, a number of examples of this form have now been found in public collections; all were taken on the Paria Peninsula in extreme north-eastern Venezuela, whence the Trinidad specimen was probably a stray. The subspecies is normally present and has been recently collected in north-eastern Sucre state, and represents the farthest north-western extension of melanic *hecale* into Venezuela; it still lacks 500 km, however, to meet the eastern-most population of orange *melicerta* and *anderida* types near Caracas.
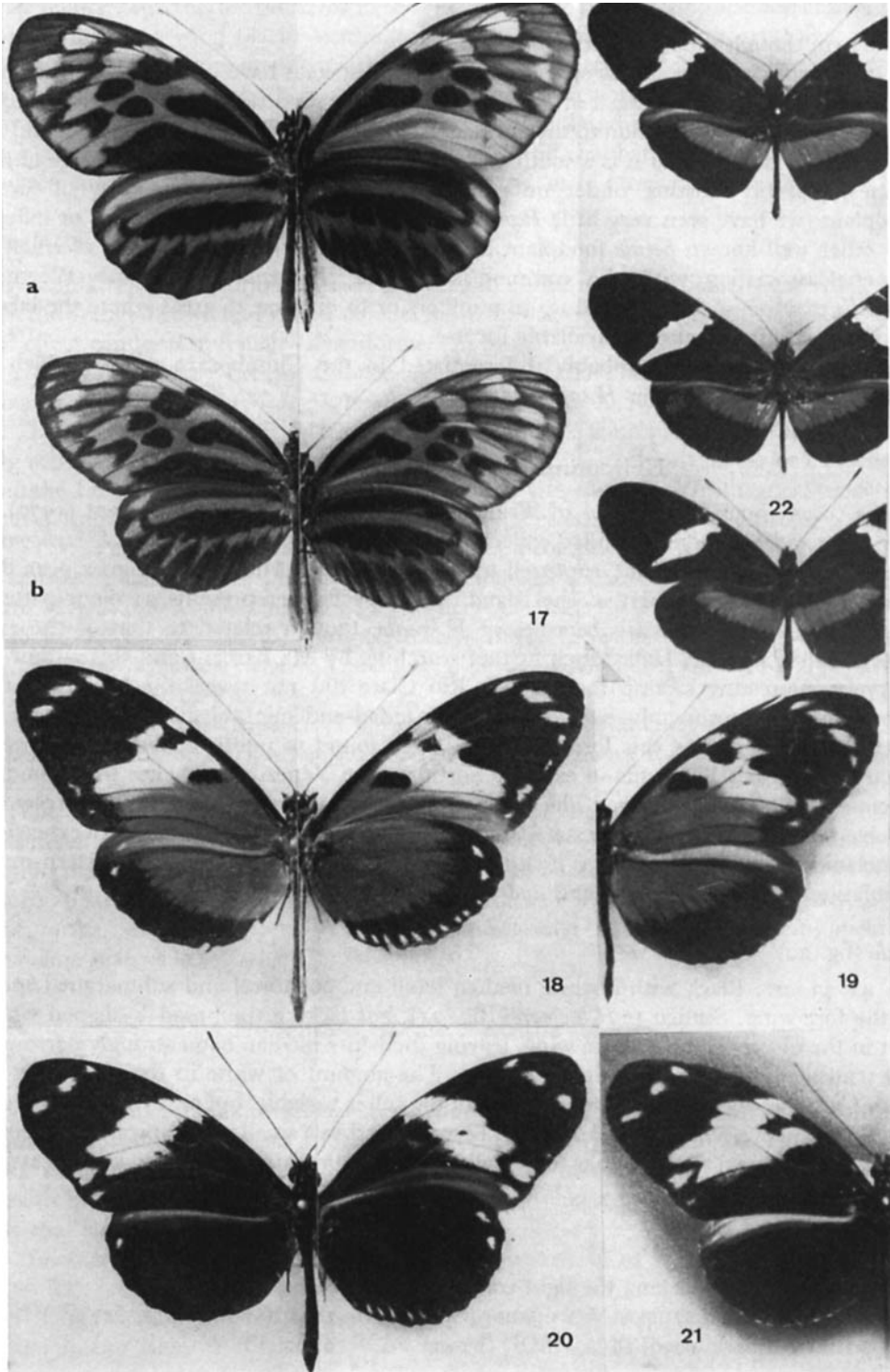

Male (fig. 20)

FW 41–43 mm. Black with a white median band and subapical and submarginal spots on the fore wing. Similar to *H.h.clearei* (fig. 21), but lacking the broad V-shaped white spot in the discal cell of the fore wing, leaving the white median band strongly narrowed and truncated costally on its inner margin. The amount of white in the inner part of space $Cu_1–Cu_2$ and the lower outer corner of the cell is variable, but always very reduced. Hind wing with a small white apical dot dorsally, and two small white apical dots, paired intervenal marginal white streaks (especially in the anal region) and a yellow costal stripe ventrally.

Female

Similar to male, but lacking the light costal area on the dorsal hind wing.

Holotype ♂, VENEZUELA: Carupano (Sucre), xii.1891 (*C.W.Ellacombe*) (BMNH, Rothschild Bequest, 1939–1).

Paratypes. 2 ♂, same data as holotype (BMNH); 1 ♂, 1 ♀, Rio El Chorro, Sucre, near 11° N, 63° W, Venezuela, 27.vi.1937, pinned but unspread material (AMNH); 1 ♂, Rio Claro, southern Trinidad, viii.1951 (*M.Rodriguez*) (in the M.Barcant collection, now conserved intact by the Angostura Bitters Co. of Trinidad); 1 ♀, Maraval, near Irapa, Sucre, 22.vii.1974 (coll. Facultad de Agronomia, Maracay, Venezuela).

This represents one of the very few heliconians which was apparently derived in the Sucre subset of the Sucre/Trinidad refuge (though such forms are common in other butterfly groups). It is a well-differentiated form, separated geographically from the nearest populations of *H.h.clearei* by the grassy delta of the Orinoco River.

Heliconius clysonymus tabaconas subsp. n.

H.clysonymus Latreille is a wide-ranging, submontane species which, perhaps because it can cross high mountain passes, has produced clearly differentiated forms only in near-isolated peripheral regions of its range: *c.hygiana* (Hewitson) from west-central Colombia to western Ecuador, and *c.montanus* Salvin in the Chiriquí area of Panamá and Costa Rica. *H.hortense* Guérin-Meneville, occurring from southern México to Nicaragua, may be a further, still interfertile peripheral isolate of *clysonymus*; putative intergrading specimens have now been seen in the AMNH and the BMNH, from northern Costa Rica, but insectary crossing behaviour should be studied before these (semi)species can be united.

At the extreme southern frontiers of its range in the Marañón Valley of northern Perú, *clysonymus* also presents a visible if minimal differentiation, with respect to 'typical' Colombian and Venezuelan specimens. As this is also a peripheral population, corresponding to a presumed refuge (Marañón), and as the slightly modified colour-pattern converges in its differentiation on that of a common endemic heliconian of the same refuge, the Peruvian *clysonymus* are judged to be worthy of formal description.

Male (fig. 22, centre)

FW 40 mm. Nearly identical to *H.c.clysonymus* (fig. 22, upper, from eastern Ecuador), but easily distinguished dorsally by the undulate and 'chopped' distal border to the slightly narrower red basal bar on the hind wing (produced by black scaling, invading mostly along the veins), giving an appearance very much like that of *H.(erato?) himera* Hewitson, endemic to southern Ecuador and northern Perú in the upper Rio Marañón area over to the western slopes of the Andes.

Figs. 17–22. All insects life size except in figure 22 (about 0·75 × life size). (17) *Heliconius pardalinus butleri* ssp. n. (a, b) dorsal (left) and ventral (right) wing surfaces: (a) holotype male; (b) paratype female, Pebas, Loreto, Peru. Black, yellow, and orange-brown. (18) *Heliconius hecale australis* ssp. n., paratype male, dorsal (left) and ventral (right) wing surfaces, Quevedo, Los Rios, west Ecuador. Black, yellow, and bright orange; ventral submarginal spots white. (19) *Heliconius hecale melicerta* Butler, male, dorsal, northern Colombia, in the MN(Rio). Black, yellow, and orange. (20) *Heliconius hecale barcanti* ssp. n., holotype male, dorsal (left) and ventral (right) wing surfaces. Black and white, ventral costal stripe yellow. (21) *Heliconius hecale clearei* Hall, paratype male, dorsal, Mabaruma, extreme north-west Guyana, Allyn Museum. Black and white. (22) *Heliconius clysonymus clysonymus* (upper), male, dorsal, Alpayacu, Rio Pastaza, east Ecuador; and *H.c.tabaconas* ssp. n., holotype male (centre), and paratype female (lower), Rio Tabaconas, north Peru. Black, yellow, and red.

Female (fig. 22, lower)

FW 40 mm. Very similar to male, but lacking the light area in the costal region of the dorsal hind wing.

    Holotype ♂, N. PERU: Charapi (as 'Charape'), Cajamarca, 5° 25′ S, 78° 59′ W (BMNH, Joicey Bequest, 1934–120).

    Paratypes. N. PERU: 1 ♀ Charapi, 1 ♂, 1 ♀, Rio Tabaconas, Cajamarca, 5° 19′ S, 79° 19′ W (BMNH, Joicey Bequest 1934–120).

    Peruvian specimens have not been seen in other museums. Although *tabaconas*-like individuals appear with some regularity in the Rio Pastaza populations of *clysonymus* in east-central Ecuador, the name is restricted to specimens of undoubted south Ecuadorian and north Peruvian origin, in the region where *himera* occurs. The subspecies was probably differentiated in the Marañón refuge and may be presently found in that region, though apparently rarely.

Heliconius congener aquilionaris subsp. n.

The small number of specimens of *H.congener* Weymer known from the eastern cordillera of Colombia are consistently different in both size and markings from those captured in the area of the type-locality, the Abitagua Highlands of eastern Ecuador. It is probable that this observed differentiation (which while small is none the less appreciable in terms of known race differences in blue-and-yellow *Heliconius*) represents a result of past isolation of Colombian from Ecuadorian populations, in the Villavicencio and/or Putumayo versus Abitagua refugia, respectively, and for this reason the Colombian populations are judged to be worthy of description.

Male (fig. 23, upper)

FW 40–45 mm (considerably larger than Ecuadorian *c.congener*, 32–40 mm). Dorsally iridescent blue with two yellow bands on the fore wing, very similar in pattern to the nominate subspecies (fig. 24), being separated by the wider and longer yellow median band on the fore wing, extending nearly to the anal angle through a large, V-shaped element between the cubital and anal veins, and expanded distally in spaces M_3-Cu_1 and Cu_1-Cu_2 to give a bulbous projection. Ventrally with red costal lines on the fore and hind wings, yellow line over the radius of the fore wing, and five medium-sized red basal spots on the hind wing, as in the nominate subspecies.

Female (fig. 23, lower)

Essentially identical but best distinguished from the male by the darker anal region of the ventral fore wing.

    Holotype ♂, COLOMBIA: Medina, Ost-Colombia, Cundinamarca, 4° 30′ N, 73° 21′ W, 1500 m (*Fassl*) (BMNH, Joicey Bequest, 1934–120).

    Paratypes. 2 ♂, 4 ♀, same data as holotype, BMNH except 1 ♂, 1 ♀ (BMNH, Roth-schild Bequest, 1939:1); 1 ♂, Colombie, env. Bogotá (BMNH, Joicey Bequest); 2 ♂, 1 ♀, same data, Frère Apollinaire-Marie, 1918 (BMNH, Levick Bequest, 1941–83); 1 ♂, Villavicencio, Meta, 4° 9′ N, 73° 37′ W, and 2 ♂, 'Rio Chili, Cauca Valley' (Tolima, 4° 7′ N, 75° 16′ W, but probably an erroneous label), ii.1916 (Kaye Collection, in the Allyn Museum of Entomology, Sarasota, Florida, 1967–5); 1 ♂, Villavicencio (Museu

Nacional, Rio de Janeiro); 1 ♂ (small), 'Jacula, Pacifico' (probably captured in the upper Rio Putumayo) (Instituto Oswaldo Cruz, Rio de Janeiro); 1 ♂ from above Florencia, Caquetá, Colombia, 22.iii.1967 (in coll. Ernesto W.Schmidt-Mumm, Bogotá); 2 ♂ (one small), 'Muzo' (a generalised Colombian locality; probably captured near Villavicencio), ex coll. LeMoult (coll. H.Holzinger, Vienna).

Latin *aquilionaris* = 'northerly'.

Heliconius sapho candidus subsp. n.

The west Ecuadorian form of *Heliconius sapho* Drury, frequently over the last 120 years referred to the nominate subspecies, is in fact separated from this Colombian race by 700 km of area uninhabited by *sapho* (central-south Colombia), or 1000 km of area (the west coast of Colombia) inhabited by very sparse populations of a new mimetic subspecies different from both the nominate and the Ecuadorian races (see Brown & Benson, 1975*b*). This isolation is accompanied by a significant differentiation, producing in the west Ecuadorian race a broad, clear white hind wing border, easily distinguishable from the narrow, black-streaked border of the nominate (Colombian) subspecies.

Male (fig. 25, upper)

FW 33–40 mm. Dorsally iridescent blue with a broad white fore wing median band (element in the discal cell variable) and hind wing border; ventrally with red costal stripes on the fore and hind wings and five large red basal spots on the hind wing. Similar to nominate subspecies (fig. 26), being distinguished by the wider white border of the hindwing (5–6 mm, rather than 2–4 mm), with much reduced black scaling over the veins and obsolescent intervenal spikes.
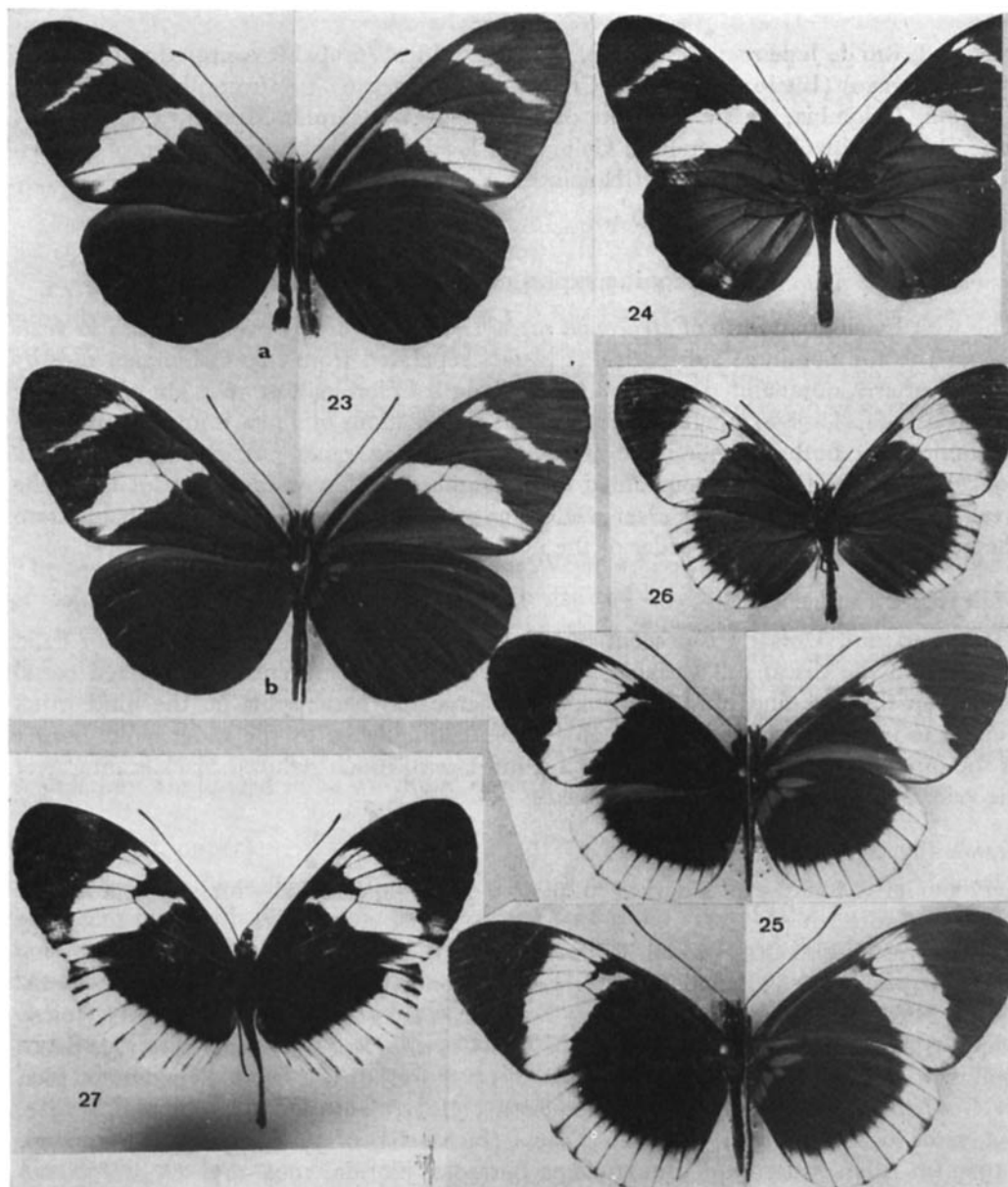
Female (fig. 25, lower)

Very similar to male, with a darker costal area of the dorsal hind wing and anal area of the ventral fore wing.

Holotype ♂, ECUADOR, ex coll. Riffarth (BMNH, Joicey Bequest, 1934:120).

Paratypes. 2 ♂, 1 ♀, Ecuador (BMNH, Hewitson coll., 79–69); 1 ♂, Ecuador (*Fruhstorfer*) (BMNH, Joicey Bequest); 1 ♀, Ecuador, 1910 (*Grose Smith*) (BMNH, Joicey Bequest); 1 ♀, Angamarca, Ecuador (BMNH, Crowley Bequest, 1901–78); 1 ♂, Santo Domingo de los Colorados (Pichincha, 0° 15' S, 79° 9' W), west Ecuador, x.1893 (*W.Goodfellow*) (BMNH, Rothschild Bequest); 5 ♂, 1 ♀, Santo Domingo, 900 m, i.1969, 1 ♂, same locality, v.1969, 1 ♂, Rio Toachi (Pichincha, 0° 39' S, 79° 19' W), 1000 m, i.1969 (in Allyn Museum of Entomology, Sarasota, Florida, 1969–11); 2 ♂, 1 ♀, Santo Domingo, iv and xi.1972, 3 ♂, 1 ♀, Alluriquin, Pichincha, xi.1972 and vii.1973 (coll. H.Holzinger, Vienna); 2 ♀, 25.i.1971, 2 ♂, 28.i.1971, 1 ♂, 10.iv.1972, 2 ♂, 20.iv.1972, 1♀, 15.iv.1972, 2 ♂, 1 ♀, 6.vi.1973, 1 ♂, 7.vi.1973, Santo Domingo (in author's coll.).

This species forms a mimetic pair with *H.cydno alithea*, white form 'haenschi' (fig. 27), in the north-western part of Ecuador. Other sympatric heliconians include the closely related *H.eleuchia primularis*§ (fig. 8) which forms a mimetic pair with yellow *H.cydno alithea*§, *H.sara sprucei*§, *H.clysonymus hygiana*§ and *H.hecalesia eximius*§ (these two mostly at higher altitudes on the steep west Andean slopes), *H.charitonia bassleri* × *peruvianus*§, *H.erato cyrbia*§ and *H.melpomene cythera*§ (mimetic pair), *H.hecale australis*§, *H.ismenius metaphorus*§, *H.(ethilla?)atthis*§, *H.doris aristomache*§/*viridana*/*eratonius* (blue/

Figs. 23–27. All insects about life size. (23) *Heliconius congener aquilionaris* ssp. n., (a, b) dorsal (left) and ventral (right) wing surfaces: (a) holotype male; (b) paratype female, data as holotype but Rothschild Bequest. Blue-black and yellow, ventral basal spots red. (24) *Heliconius congener congener* Weymer, male, dorsal, Rio Topo, east Ecuador, collection of the author. Blue-black and yellow. (25) *Heliconius sapho candidus* ssp.n., (a, b) dorsal (left) and ventral (right) wing surfaces: (a) holotype male; (b) paratype female, Hewitson collection. Blue-black and white, ventral basal markings red. (26) *Heliconius sapho sapho* Drury, male, dorsal, Victoria, Caldas, Colombia, in the collection of the author. Blue-black and white. (27) *Heliconius cydno alithea* Hewitson, form *haenschi* Riffarth, male, dorsal, Santo Domingo, west Ecuador, collection of the author. Blue-black and white.

green/red trimorphic population), *Eueides isabella huebneri* × *ecuadorensis*§, *E.edias eury-saces*§, *E.emsleyi*, *E.vibilia vicinalis*§, *E.aliphera cillenula*§, *Dryas iulia moderata*§, *Dione juno andicola*§ (near fig. 2, but lighter), *D.moneta butleri*, *D.glycera*, *Agraulis vanillae forbesi*§ and *Podotricha euchroia straminea*§. Those subspecies marked § are, like *candidus*, presumably derived from the Chimborazo refuge, a region of heavy moist forests extending seaward from the high volcano of this name, and most are essentially endemic to the area today.

According to Professor Calaway Dodson of the University of Miami's field station at Rio Palenque, near Quevedo, Los Rios, W. Ecuador, the preferred larval foodplant of *H.sapho candidus* is *Passiflora* (*Astrophea*) *gigantifolia*, an enormous leaved bush endemic to western Ecuador, whose closest relatives are the unusual *Passiflora* trees of the higher Andes.

Latin *candidus* = 'whitened'.

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APPENDIX I

Brief comments on the refugia as mapped

Four previous authors have presented reasonably detailed maps of proposed Neotropical Quaternary refugia for forest organisms. The high level of agreement between these maps and that presented in this paper indicates that at least the principal centres of evolution in the Neotropics have been identified with a reasonable degree of probability; which of these acted during dry cycles in the past, and which are still acting, remains to be determined.

The 38 refugia of the map are described in some detail below, in an attempt to narrow down the most probable 'core areas' within the broader regions of high endemism. Only half of the areas have been personally visited by the author; all present a rather characteristic scene of high and lush forest, abundant ground water and rainfall, and swarms of usually monomorphic and often endemic insect species. Conversations with others who have visited a further 11 refugia indicate that this impression was also created on them by the 'core areas'. However, such areas in modern time do not necessarily correspond to past refugia. In the mapping of the refugia for forest Lepidoptera, a number of objective parameters were taken into account. The areas are all high-rainfall, apparently stable forest regions with no known periods of drying out in the last 50 000 years. They are all areas with sufficient elevation to have avoided flooding during the interglacials, and usually include steep areas exposed to predominant humidity-laden winds today. On detailed maps the areas are often shown as headwaters for an inordinately large number of streams, often flowing in several directions. With relation to the Müllerian-mimetic Lepidoptera species, areas with high indices of polymorphism or apparent hybridisation have been eliminated. Areas with many endemic forms, which are isolated in modern time from nearby forest regions by water or non-forest habitat, are not regarded as refugia but are designated as present-day islands.

The 38 refugia proposed with the application of these criteria are compared in the Table with those proposed by Haffer (1967, 1969, 1974a,b; if indicated on the 1969 map but not named, 'no name'; if indicated in 1969 but not in 1974, numbered and named), Müller (1972, 1973; Amazonian areas very broadly defined), Prance (1973), and Lamas Müller (1973, and manuscript in preparation). An attempt has been made to choose names of local origin but preferably well-known usage, deviating as little as possible from the names previously proposed for the refugia (those of Prance, 1973, had already been harmonised with those of this author). Each refuge is also given in the Table a relative importance (based on analysis of a number of nymphalid groups), which has been adjusted to take into account the average rainfall in the area, the altitudinal range, present and past isolation, probable size at maximum reduction, and amount of study by lepidopterists. The last factor is indicated by a letter, from A (very well studied) to E (almost unstudied); the refugia in the latter category deserve first priority for future studies by Neotropical biologists, for some surely harbour unimagined new forms and phenomena. Many which presently seem to be 'weak' in action may be so only because of the paucity of information available on their endemic forms. The number of differentiated forms considered to be associated with each refuge, in the Heliconiini (Appendix II) and the mimetic Ithomiinae, is also indicated, along with the total number of distinctly different mimetic colour-patterns present in the forms in these two groups presumably derived in each area.

Vanzolini (1970) also proposed a small number of refugia for *Anolis* lizards, which are given in the Table. It is hoped that the Table and the Map, and the following summary descriptions of the refugia and islands, will serve as a working hypothesis for ecological field work and pedological and palynological studies in the future, leading to refinement and new information.

Haffer (1974*b* : 148) discards subspecies as useful categories in the biogeographical analysis of birds, although they constitute the most useful category in the analysis of Lepidoptera which underwent speciation at an earlier stage. The most profitable level of analysis will vary among taxonomic groups, depending upon the evolutionary rate of 'species-characters', and the history of primary differentiation.

NORTH-WESTERN REFUGIA

1. GUATEMALA—Centred on Caribbean slopes of Guatemala highlands. Extends into south-eastern México and western Honduras. Influence felt strongly to north Veracruz and southern Honduras, occasionally to Texas, El Salvador and Caribbean Panamá.

2. CHIRIQUÍ—Pacific slopes of south-eastern Costa Rica and south-western Panamá. Influence apparent to El Salvador and Canal Zone. Strongly isolated even today from Caribbean Costa Rica.

3. DARIÉN—Ridges from just east of Colón and Ciudad de Panamá, Panamá to near Colombian border. Influence strong only in central Panamá, but may be felt from eastern Costa Rica to the lower Magdalena Valley and northern Chocó in Colombia. Often indistinguishable in action from the following refuge.

4. NECHÍ—Northern spurs of all three Colombian cordilleras to near junction of Cauca and Magdalena rivers. Influence strong to central Panamá, and over most of northern Colombia to western Venezuela.

5. CHOCÓ—Pacific slopes of western cordillera of Colombia from north of Quibdó to near Lago Calima, across upper Atrato and San Juan river systems, not to coast. Influence seen as far south as central–west Ecuador, occasional north to central Panamá.

6. CHIMBORAZ—Pacific slopes of west Ecuadorian Andes between about 1° N and 2° S, not to coast. Influence to south-western Colombia and extreme north-western Peru, not in eastern Ecuador.

7. CAUCA—Inner slopes of western cordillera of Colombia from Cali area southward, possibly also on west slopes of central cordillera and in valley; may have a subset north of Cali. Influence to lower Cauca valley and over cordillera to southern Chocó, also south to Nariño. Shows old affinities with northern Venezuela, now severed by the Nechí–Darien link.

8. MAGDALENA—Centred near Tolima drainage on eastern slopes of central cordillera of Colombia, south to dryer upper valley limits, possibly also on east side of central part of valley. Influence very limited to refuge area.

9. CATATUMBO—Venezuelan (eastern) slopes of the Sierra Perijá, probably not southward to high-rainfall area west of Mérida, where influence present but apparently much weaker.

10. RANCHO GRANDE—Coastal Venezuelan mountains from Valencia to just east of Caracas. Influence widespread, from central Colombia to Guyana and north Brazil.
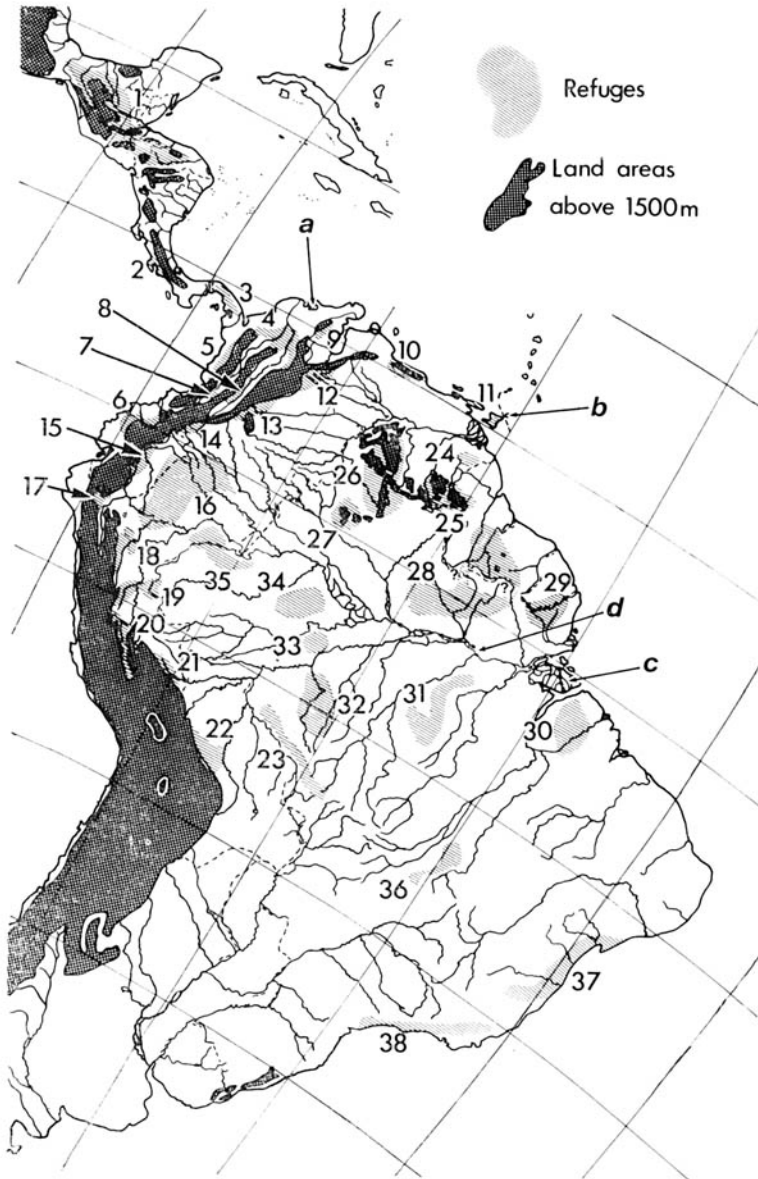
11. SUCRE/TRINIDAD—North-west coast and east tip of Paria Peninsula, Venezuela, and north and south mountain ranges of Trinidad. Occasionally acted as separate subsets. Influence strongly limited.

Table 1. Comparison of Lepidopteran

No.	Suggested name	Strength	Study	Differentiated forms		Mimetic colour-patterns	Haffer
				Heliconiini	Ithomiinae		
NORTH-WESTERN							
1	Guatemala	Average	A	17	11	8	Guatemala
2	Chiriquí	Average	A	10	18	6	Dulce
3	Darién	Average	D	6	8	7	No name
4	Nechí	Strong	C	18	22	15	Nechí
5	Chocó	Average	D	9	8	6	Chocó
6	Chimborazo	Strong	B	20	17	12	1—Chocó (part)
7	Cauca	Average	B	8	5	5	—
8	Magdalena	Average	C	4	7	6	No name
9	Catatumbo	Weak	E	4	2	5	Catatumbo
10	Rancho Grande	Average	B	8	15	9	North Venezuela
11	Sucre/Trinidad	Weak/average	C	6	5	6	—
ANDEAN							
12	Apure	Weak	E	5	4	6	No name
13	Villavicencio	Strong	B	10	21	9	No name
14	Putumayo	Average	E	6	17	9	Napo (part)
15	Abitagua	Strong	B	14	36	15	Napo (part)
16	Napo	Average	B	15	25	9	Napo (part)
17	Marañón	Average	D	4	12	7	—
18	Huallaga	Average	B	7	15	8	East Peruvian (1 of 4)
19	Ucayali	Average	B	11	11	4	East Peruvian (1 of 4)
20	Chanchamayo	Average	B	2	17	7	East Peruvian (1 of 4)
21	Inambari	Average	C	8	18	4	East Peruvian (1 of 4)
22	Yungas	Strong	B	12	30	10	No name
23	Guaporé	Weak	E	3	4	4	—
GUIANA SHIELD							
24	Imataca	Weak	E	3	4	6	—
25	Roraima	Average	D	7	8	7	No name
26	Parima	Weak	E	2	2	3	No name
27	Imerí	Average	D	10	2	3	Imerí
28	Manaus/Guiana	Average	C	14	23	8	Guiana (part)
29	Oyapock	Average	C	9	6	4	Guiana (part)
AMAZON BASIN							
30	Belém	Average	A	9	14	6	Pará
31	Tapajós	Average	D	10	20	6	Madeira-Tapajóz (part)
32	Rondônia	Average	C	5	17	5	—
33	Madeira	Average	D	2	9	4	Madeira-Tapajóz (part)
34	Tefé	Average	C	3	9	3	No name
35	Loreto	Average	B	7	12	5	Napo (part)
BRAZILIAN SHIELD							
36	Araguaia	Weak	E	4	5	8	Goiás
37	Bahia	Average	B	6	15	10	Serra do Mar (part)
38	Rio de Janeiro	Average	A	7	15	9	Serra do Mar (part)

Müller	Prance	Lamas Müller	Vanzolini
1—Central American Rain Forest	—	1—Central American (part)	—
6—Costa Rica (part)	—	2—Costa Rica	—
—	—	—	—
14—Colombian Pacific (part)	2—Nechí + 3—Santa Marta	5—Nechí	—
14—Colombian Pacific (part)	1—Chocó (part)	3—Chocó	—
14—Colombian Pacific (part)	1—Chocó (part)	4—West Ecuador	—
12—Cauca	—	—	—
11—Magdalena	—	—	—
16—Catatumbo	4—Catumbo (sic)	6—Catatumbo	—
17—Venezuelan Coastal	5—Rancho Grande 6—Paria (part)	8—Cordillera de la Costa	Cordillera de la Costa
—	—	—	—
13—Colombian Montane Forest (part)	—	—	—
13—Colombian Montane Forest (part)	—	7—East Colombia	East Andean (part)
13—Colombian Montane Forest (part)	10—Napo (part)	—	East Andean (part)
13—Colombian Montane Forest (part)	10—Napo (part)	9—Napo (part)	East Andean (part)
25—Amazonian (part)	10—Napo (part)	9—Napo (part)	East Andean (part)
28—Marañón	—	10—East Peru (1 of 5)	—
26—Yungas (part)	—	10—East Peru (1 of 5)	East Andean (part)
26—Yungas (part)	14—East Peru (part)	10—East Peru (1 of 5)	East Andean (part)
26—Yungas (part)	—	10—East Peru (1 of 5)	East Andean (part)
26—Yungas (part)	14—East Peru (part)	10—East Peru (1 of 5)	East Andean (part)
26—Yungas (part)	—	11—Yungas	—
—	—	13—Chapada dos Guimar~es (near)	—
22—Guaiana (part)	7—Imataca	—	—
21—Pantepui (part)	—	—	—
21—Pantepui (part)	—	—	—
—	9—Imerí	—	—
22—Guaiana (part)	13—Manaus	15—Guyana (part)	Tumac-Humac
22—Guaiana (part)	8—Guiana (part)	15—Guyana (part)	—
23—Pará	16—Belém-Xingu (part)	16—Belém	—
24—Madeira (part)	—	—	—
24—Madeira (part)	15—Rondônia-Aripuanã	12—Rondônia (near)	—
25—Amazonian (part)	—	—	—
25—Amazonian (part)	12—Tefé (near)	—	—
25—Amazonian (part)	11—Olivença + 10—Napo (part)	—	—
—	—	14—Mato Grosso de Goiás	Mato Grosso de Goiás
33—Serra do Mar (part)	—	—	—
33—Serra do Mar (part)	—	18—Serra do Mar	—

Map 1. Proposed Quaternary Refugia (see Appendix I for numerals and letters).

ANDEAN REFUGIA

12. APURE—Upper Río Apure, principally on south-east slopes of Mérida Andes in Venezuela, and higher flatlands in Táchira and adjacent Colombia. Material mostly from Barinitas, Selvas de San Camilo, and other localities in south-western Venezuela. Influence felt to central Venezuela (Lara) and Boyacá, Colombia.

13. VILLAVICENCIO—Upper Ríos Negro and Guatiguiá in broad valleys north and west of Villavicencio, Meta, Colombia (east slopes of eastern cordillera), south to behind Serranía La Macarena. Influence to north-eastern Colombia, occasionally to upper Putumayo.

14. PUTUMAYO—Upper Ríos Caquetá and Putumayo in Mocoa region, southern Colombia. Shows older affinities with general east Andean elements, and some links to Magdalena Valley. Influence very restricted.

15. ABITAGUA—Upper Ríos Napo and Pastaza, broad valleys and slopes at moderate elevations above Puyo and Macas areas in eastern Ecuador. Influence north to southern Colombia (at times indistinguishable from previous refuge) and at higher elevations south into Peruvian Andes (general Andean fauna).

16. NAPO—Lower-elevation, high-rainfall areas in north-central Peru, extending into south-central Colombia and eastern Ecuador, in regions crossed by middle rivers Caquetá, Putumayo, and Napo, lower Pastaza, and middle Marañón (where joined by Huallaga). Sometimes indistinguishable in effect from previous two and following refugia, as well as Loreto refuge (35). Influence strong, to La Macarena (Colombia), Manaus (central-north Brazil), Rondônia (south-west Brazil), and extreme south-east Peru and northern Bolivia, at 100–300 m elevation.

17. MARAÑÓN—South-east and east slopes of Andes in extreme south Ecuador and north Peru, in valley of Río Marañón above junction with Río Santiago, not in dry valley floor or dryer slopes of upper valley. Influence felt over Abra de Porculla to Pacific slopes, otherwise very limited.

18. HUALLAGA—Western slopes of middle and upper Huallaga Valley above Pongo de Cainarache, central Peru, from above Tarapoto south to above Tingo Maria. Influence felt principally southward over following three refugia, to a lesser extent north-eastward to Loreto area. Shows older affinities with general east Andean fauna.

19. UCAYALI—Serra de Contamana on the Brazil (Acre)/Peru border across the Ucayali River near Pucallpa, Peru and up Pachitea River on lower Andean slopes (possibly restrictable to area west of Río Ucayali). Influence strong, to north Peru and eastern Ecuador, west Brazil, and extreme north Bolivia; not always clearly distinguishable from previous or following two refugia.

20. CHANCHAMAYO—Upper Perene and Apurimac rivers, in broad high-elevation valleys from Tarma and Satipo, Peru south-eastwards. Influence apparent north to Pachitea Valley and Huallaga region, and south across Urubamba and Vilcanota areas to southern Peru.

21. INAMBARI—Upper tributaries of Río Madre de Diós in extreme south-eastern Peruvian Andes. Influence apparent north to area of previous refuge, north-east to Rondônia and Acre (west Brazil), more weakly south-eastward to northern Bolivia.

22. YUNGAS—Higher parts of Nor Yungas of La Paz, across Sur Yungas at moderate elevations to area north of Cochabamba, Bolivia, extending to lowland forests north-west of Santa Cruz. Influence felt far north-west into Peruvian Andes and north-east to south-western Brazil. Sometimes indistinguishable from following refugium.

23. GUAPORÉ—Heavy forests of south slopes of Serra dos Pacaás Novos (Rondônia) and Chapada dos Parecis (Mato Grosso) in south-west Brazil, east to near Barra do Bugres. Influence felt to central Peru and central Bolivia (previous refuge area). Shows old affinities to general Andean fauna of Peru, especially Huallaga, now broken by lowlands of Acre and lower Río Beni.

15

GUIANA SHIELD REFUGIA

24. IMATACA—Slopes of the Sierra de Imataca near the Venezuela/Guyana border, south of the Orinoco Delta. Shows influence west and south to the following refugia, north to Paria Península and east along coastal Guyana, not in interior.

25. RORAIMA—Forested slopes of eastern part of Pacaraima mountains, mostly north and west of present highest area (Mt Roraima) where Guyana, Venezuela and Brazil meet. Influence felt well out into all three countries at higher elevations in forests. Shows older affinities to Colombian Andes, through the following two refugia.

26. PARIMA—Upper Ríos Ventuari, Orinoco, and Uraricoera on the frontier between north-western Brazil and Venezuela, north-west into highlands of southern-central Venezuela. Influence extends north nearly to Orinoco valley in central Venezuela, and well east into north Brazil.

27. IMERÍ—Slopes of the Imerí range north of the upper Rio Negro in extreme north-western Brazil and southern Venezuela (including Pico Neblina, highest non-Andean mountain in South America). Influence felt across previous three refugia into Guyana, west into eastern Colombia, and widely over north-west parts of Brazil, occasionally south of the Amazon River.

28. MANAUS/GUIANA—Two major areas, not distinguishable in present composition or possible past importance, but nearly isolated from one another by the grassy plains of the upper Tumuc-Humac mountains on the Brazil/Guianas border: southern Suriname and south-eastern Guyana; and heavy hilly forests northwest of Manaus as far as the middle Paru in northern Brazil, coming near the Amazon River near Oriximiná and Óbidos. Present and past connections across the broad (100–250 km) western Tumuc-Humac fields undetermined, probably to east with corridors near middle. Influence very strong over the southern Guianas and northern Brazil, sometimes over following refuge area.

29. OYAPOCK—Eastern, forested part of the Tumuc-Humac range on the border of Inini (interior Guyane Française) and Amapá, Brazil, around the upper tributaries of the Oyapock River. Influence strong north-west to Suriname, and south to the Amazon Delta. Older affinities are with the Belém area, not with Guiana or Manaus refugia.

AMAZON BASIN REFUGIA

30. BELÉM—High-rainfall lowland forest south-east of Belém, Pará, Brazil, through the eastern part of the state to the highlands of western Maranhão. Influence over entire area south-east of Amazon and Madeira Rivers, to frontiers of Amazon Hylaea and southern Rondônia, more weakly to extreme western Brazil; often indistinguishable in action from next refuge, sometimes from following one also.

31. TAPAJÓS—Heavy forest around low hills in south-western Pará, Brazil, from south of Itaituba south to the Serra de Cachimbo. Influence as for previous refuge; possibly an alternative to it in many species, but distinctly separate in others.

32. RONDÔNIA—Forests from near the junction of the Rios Madeira and Jiparaná in northern Rondônia, Brazil, south and east over tin-rich hills to the south-eastern part of the territory near the Chapada dos Parecis. Usually distinguishable from previous two refugia, but not always; influence quite restricted, occasional to Santarém and Acre.

33. MADEIRA—Very high-rainfall area between the Rios Madeira and Purús, north of Humaitá, Brazil. Influence restricted, down to Manaus, north-west to following refuge.

34. TEFÉ—Upper Rios Tefé and Coarí, between the lower Purús and Juruá, south of Tefé (= Ega), Brazil. Influence strong over lower Purús and Juruá, central Madeira, and west to north-eastern Peru.

35. LORETO—Heavy forests on both sides of the lower Río Javary, Brazil/Peru border south-west of São Paulo de Olivença and south-east of Iquitos. Wide influence over north-eastern Peru. Sometimes indistinguishable from Napo refuge area (16). May possibly include forests north of the Marañón.

BRAZILIAN SHIELD REFUGIA

36. ARAGUAIA—High-water-table forests from Jataí, Goiás, Brazil north along ridges to central part of the state, possibly also lowland forests north to Ilha do Bananal area. Influence over upper Araguaia area and much of central Brazil.

37. BAHIA—Heavy moist forest on Tertiary tablelands and associated hills from north of Salvador, Bahia into inland northern Espírito Santo, Brazil. Influence north to Pernambuco and south to Rio de Janeiro.

38. RIO DE JANEIRO—Foothill and steep mountain-face forests from south-west of Campos, state of Rio de Janeiro, Brazil, west-south-west between the Rio Paraíba and the coastal plain (Serra dos Ôãrgos) to Angra dos Reis, Serra da Bocaina, Serra de Itatiaia and Serra da Cantareira, possibly to southern São Paulo. Influence from Espírito Santo to Santa Catarina.

ISLANDS

(a) SIERRA NEVADA DE SANTA MARTA—A montane island in northern Colombia, surrounded by scrub forest or other low-elevation and dryer habitats. Heavy premontane forests on seaward and south-eastern sides harbour many endemic forms, but very few are tropical. Differentiated forms are related to colonising stock from moderate to high elevations in the Sierra Perijá, the Mérida Andes, and the northern Colombian cordilleras. Tropical species are mostly undifferentiated, related to Nechí forms.

(b) TOBAGO—A small forested island near Trinidad, which presents tropical forms slightly to appreciably differentiated from those predominating on the latter island; they occasionally invade the north shore of Trinidad (using prevailing winds), and probably evolved from storm-introduced populations from Trinidad.

(c) EASTERN MARAJÓ—A swampy area at the extreme of the Amazon Delta, with some scrubby forest in which a number of tropical forms have differentiated. The depauperate fauna shows closest ties with Belém, and is separated from that on the western part of the island by a broad belt of field across the centre.

(d) TAPARÁ—Isolated ridges with occasional non-floodable areas in the centre of the Amazon River in front of the mouth of the Tapajós (Santarém). As the few areas which are not covered by high water are near the north shore, the differentiated forms show relationships to the Manaus/Guiana fauna, not that of the Tapajós.

APPENDIX II

Assignment of heliconian forms to postulated refugia

Clearly differentiated forms of heliconians which are presently common and monomorphic in forest areas corresponding to presumed past refugia are the rule. As heli-

conians are almost always collected by amateur lepidopterists, the material available is abundant and covers most known collecting localities in the Neotropics; very few doubts remain as to the ranges of the various forms, and the localisation in secondary hybridisation zones. However, complications are presented by poorly differentiating species; by species with high dispersal abilities; and by occasional superdifferentiated species which differ slightly even in neighbouring populations within proposed centres of evolution. Further complications arise in highly polymorphic species, or species and forms of apparently ancient derivation.

In the following list, any uncertain assignment of a differentiated form to a refuge is indicated by a question mark after the refuge name. Forms of possibly ancient derivation are indicated by a dagger after the refuge name; in these cases, though the area was probably responsible for the differentiation of the form, it may have acted in the very distant past rather than during Quaternary climatic cycles. Weakly differentiated forms, or widespread and diluted isolates, not corresponding to modern subspecies, are indicated by an asterisk after the form name. Other, non-asterisked names are judged to be valid subspecific categories. All 66 species in the tribe are listed in presumed phylogenetic order but only subspecies useful in the refugia analysis are indicated for some of them; non-forest, widespread, or high-altitude forms are designated as such.

Species	Subspecies or form	Presumed Quaternary refuge
Philaethria pygmalion	—	(Non-forest Amazon)
Philaethria wernickei	—	Rio de Janeiro†
Philaethria dido	—	(Widespread)
Dryadula phaetusa	—	(Widespread, non-forest)
Dione juno	*juno*	(Widespread)
	huascama	Guatemala†
	andicola	Chimborazo†
	miraculosa	(Non-forest west Peru)
	suffumata	Araguaia
Dione moneta	*poeyii*	Guatemala†
	butleri	(High-altitude, widespread)
	moneta	Yungas(?)†
Dione glycera	—	(High-altitude)
Agraulis vanillae	*forbesi*	Chimborazo(?)†
	lucina	Napo
	Various others	(Non-forest, islands)
Podotricha euchroia	*caucana*	Cauca†
	mellosa	Chimborazo†
	euchroia	Villavicencio†
	straminea	Abitagua†
Podotricha telesiphe	*telesiphe*	(Widespread, high-altitude)
	tithraustes	Abitagua†
Dryas iulia	Various	(Widespread, islands)
Eueides procula	*asidia*	Guatemala
	vulgiformis	Chiriquí
	edias	Nechí
	eurysaces	Chimborazo
	*umbratilis**	(Santa Marta island)
	procula	Rancho Grande
	browni	Roraima
Eueides pavana	—	Rio de Janeiro†

Species	Subspecies or form	Presumed Quaternary refuge
Eueides vibilia	*vialis*	Guatemala†
	Unnamed subsp.	Nechí
	vicinalis	Chimborazo†
	mereaui	Rancho Grande†
	unifasciatus	Napo†
	vibilia	Bahia†
Eueides lampeto	*amoena*	Abitagua
	acacetes	Napo
	lampeto	Loreto
	copiosus	Manaus/Guiana
	*carbo**	(Widespread, high-altitude)
Eueides emsleyi	—	Nechí†
Eueides lineata	—	Guatemala†
Eueides libitina	—	Oyapock†
Eueides eanes	*eanes*	Napo
	aides	Huallaga (?)
	pluto	Inambari
	heliconioides	Yungas
Eueides isabella	*eva*	Guatemala
	*spoliata**	Darién
	huebneri	Nechí
	ecuadorensis	Chimborazo
	*arquata**	Cauca
	*pellucida**	Villavicencio
	*vegetissima**	Abitagua
	*margaritifera**	Napo
	*hippolinus**	Ucayali
	*personata**	Inambari
	*dissoluta**	Yungas
	*isabella**	Belém
	dianasa	Rio de Janeiro
	Various others	(Mixed, islands)
Eueides tales	*xenophanes*	Magdalena
	franciscus	Catatumbo
	pseudeanes	Apure
	cognata	Villavicencio
	calathus	Napo
	*michaeli**	Ucayali
	tales	Manaus/Guiana
	pythagoras	Belém
	Manuscript subsp.	(Marajó island)
	*barcellinus**	Imerí or Rondônia
Eueides lybia	*lybioides*	Chiriquí
	olympia	Nechí
	Manuscript subsp.	Catatumbo
	Manuscript subsp.	Imataca
	lybia	(Widespread)
Eueides aliphera	*gracilis*	Guatemala†
	cillenula	Chimborazo
	aliphera	(widespread)
Laparus doris	*transiens*	Guatemala
	luminosus/viridis	Chiriquí
	eratonius	Nechí
	obscurus etc.	Cauca

Species	Subspecies or form	Presumed Quaternary refuge
	*aristomache**	Chimborazo
	*metharmina**	Loreto
	*delila**	Tapajós
	*doris, viridanus**	(Widespread)
Heliconius godmani	—	Chocó†
Heliconius metharme	Manuscript subsp.	Parima
	metharme, thetis	(Widespread)
Heliconius aoede	*bartletti*	Napo
	cupidineus	Ucayali
	philipi	(Interrefugial?)
	eurycleia	Guaporé
	Manuscript subsp.	Roraima
	lucretius	Imerí
	astydamia	Manaus/Guiana
	aoede	Oyapock
	faleria	Tapajós
Heliconius hierax	—	Abitagua†
Heliconius hecuba	*tolima*	Nechí
	crispus	Cauca
	crespinus	(Cauca north?)
	hecuba	(Magdalena east?)
	cassandra	Villavicencio
	choarina, etc.	Abitagua
Heliconius xanthocles	*flavosia*	Villavicencio
	explicata	Putumayo
	melittus	Napo
	melior	Ucayali
	meridionalis	Guaporé
	cleoxanthe	Roraima
	melete	Imerí
	xanthocles	Manaus/Guiana
	vala	Oyapock
	paraplesius	Belém
Heliconius wallacei	*kayei*	Sucre/Trinidad
	*elsa**	Roraima
	wallacei	Manaus/Guiana
	araguaia	Araguaia
	flavescens, others	(Widespread)
Heliconius burneyi	*lindigii*	Villavicencio
	huebneri	Ucayali
	ada	Yungas
	catherinae	Manaus/Guiana
	Unnamed subsp.*	Imerí
	burneyi	Belém
Heliconius egeria	*asterope*	Imerí
	egerides	Manaus/Guiana
	egeria	Oyapock
	hyas	Tapajós
Heliconius astraea	*rondonia*	Rondônia
	astraea	Loreto
Heliconius nattereri	—	Bahia†
Heliconius numata	*aulicus*	Rancho Grande
	Manuscript subsp.	Sucre/Trinidad
	peeblesi	Apure

Species	Subspecies or form	Presumed Quaternary refuge
	messene	Villavicencio
	euphrasius*	Putumayo
	lenaeus	Abitagua
	euphone*	Napo
	talboti*	Maranón
	staudingeri*	Huallaga
	arcuella*	Ucayali
	aristiona	(Widespread, high-altitude)
	lyrcaeus*	Inambari
	leopardus	Yungas
	mirus*	Guaporé
	numata	Manaus/Guiana
	silvana*	Belém(?)
	superioris*	Tapajós
	jiparanaensis*	Rondônia
	nubifer*	Tefé
	aurora	Loreto
	mavors*	(Widespread)
	Manuscript subsp.	(Marajó island)
	zobrysi	Araguaia
	ethra	Bahia
	robigus	Rio de Janeiro
Heliconius ismenius	*telchinia*	Guatemala
	clarescens	Chiriquí
	boulleti	Darién
	ismenius	Nechí
	occidentalis*	Chocó
	metaphorus	Chimborazo
Heliconius pardalinus	*orteguaza*	Napo
	sergestus	Huallaga
	dilatus*	Ucayali
	maeon	Inambari
	tithoreides*	Yungas
	radiosus	Tapajós(?)
	lucescens	Madeira
	pardalinus	Tefé
	butleri	Loreto
Heliconius hecale	*fornarina*	Guatemala
	zuleika	Chiriquí
	melicerta	Nechí
	holcophorus*	Chocó
	australis	Chimborazo
	semiphorus*	Catatumbo
	anderida	Rancho Grande
	Near *holcophorus*	Apure
	ithaca/vittatus	Villavicencio
	quitalena	Abitagua
	versicolor*	Huallaga
	sisyphus	Inambari
	felix	Yungas
	barcanti	Sucre/Trinidad
	clearei	Imataca
	hecale	(Coastal Guyana)
	sulphureus	Imeri

Species	Subspecies or form	Presumed Quaternary refuge
	vetustus	Manaus/Guyana
	metellus	(Tapará island)
	novatus	Belém
	paraensis	(Lower Tocantins/Xingu)
	latus	Tapajós
	fortunatus/spurius	(Manaus area downriver)
	nigrofasciatus	Madeira
	ennius	Tefé
	humboldti*	Loreto
Heliconius ethilla	*claudia*	Darién
	semiflavidus	Cauca
	metalilis	Rancho Grande
	ethilla	Sucre/Trinidad
	Near *metalilis*	Villavicencio
	aerotome	Huallaga
	clarus	Ucayali
	nebulosa	Inambari
	tyndarus	Yungas
	chapadensis	(Central-west Brazil)
	hyalina	Roraima
	thielei	Manaus/Guyana
	cephallaenia*	Oyapock
	eucoma	Belém
	numismaticus*	Tapajós
	mss. subsp.	Rondônia
	adela	Loreto
	flavomaculatus	Bahia
	narcaea	Rio de Janeiro
	polychrous*	(South-central Brazil)
Heliconius atthis	—	Chimborazo
Heliconius elevatus	*elevatus*	Napo
	pseudocupidineus	Ucayali
	perchlora	Yungas
	roraima	Roraima
	taracuanus	Imerí
	tumatumari	Manaus/Guiana
	bari	Oyapock
	aquilina	Tapajós
Heliconius luciana	*luciana*	Parima
	watunna	(Rio Caura?)
Heliconius besckei	—	Rio de Janeiro
Heliconius melpomene	*rosina*	Darién
	euryas*	Nechí
	vulcanus	Chocó
	cythera	Chimborazo
	melpomene	Rancho Grande
	flagrans	Sucre/Trinidad
	Unnamed subsp.	(Tobago island)
	bellula	Putumayo
	plesseni	Abitagua
	aglaope	Napo
	amaryllis	Huallaga
	cognatus*	Ucayali
	xenoclea	Chanchamayo

Species	Subspecies or form	Presumed Quaternary refuge
	euryades	Inambari
	penelope	Yungas
	Unnamed subsp.	Roraima
	vicinus	Imerí
	meriana	Manaus/Guiana
	thelxiopeia	Oyapock
	thelxiope	Belém
	Manuscript subsp.	(Marajó island)
	madeira	Tapajós
	amandus	(Central Bolivia)
	burchelli	Araguaia
	nanna	Bahia
Heliconius cydno	*galanthus*	Guatemala
	chioneus	Darién
	cydno	Nechí
	zelinde	Chocó
	alithea/haenschi	Chimborazo
	weymeri/gustavi	Cauca (two subsets?)
	hermogenes	Magdalena
	cydnides	(West cordillera)
	perijaensis	Catatumbo
	barinasensis	Apure
	Near *cydno*	Putumayo
Heliconius heurippa	—	Villavicencio
Heliconius timareta	Various forms	Abitagua
Heliconius pachinus	—	Chiriquí
Heliconius hermathena	various forms	(Non-forest Amazon)
Heliconius charitonia	*vazquezae*	Guatemala†
	bassleri	Nechí†
	peruvianus	Chimborazo
	Various other	(Islands)
Heliconius himera	—	Marañón
Heliconius erato	*petiverana*	Guatemala
	demophoon	Darién
	*guarica**	Nechí
	venus	Chocó
	cyrbia	Chimborazo
	chestertonii	Cauca
	hydara	Rancho Grande
	adana	Sucre/Trinidad
	Unnamed subsp.	(Tobago island)
	dignus	Putumayo
	notabilis	Abitagua
	lativitta	Napo
	favorinus	Huallaga
	emma	Ucayali
	microclea	Chanchamayo
	amphitrite	Inambari
	venustus	Yungas
	Unnamed subsp.	Roraima
	reductimacula	Imerí
	amalfreda	Manaus/Guiana
	erato	Oyapock
	amazona	Belém

Species	Subspecies or form	Presumed Quaternary refuge
	estrella	(Marajó island)
	phyllis	Rio de Janeiro
Heliconius clysonymus	*montanus*	Chiriquí
	clysonymus	Nechí†
	hygiana	Chimborazo
	tabaconas	Marañón
Heliconius hortense	—	Guatemala
Heliconius telesiphe	*sotericus*	Abitagua
	cretacea	Marañón
	telesiphe	(Widespread, high-altitude)
Heliconius hecalesia	*octavia*	Guatemala
	formosus	Chiriquí
	hecalesia	Nechí
	Manuscript subsp.	Chocó
	longarena, * *gynaesia**	(Transitional forms)
	eximius	Chimborazo
Heliconius ricini	—	(Widespread)
Heliconius demeter	*demeter*	Napo
	ucayalensis	Ucayali
	ulysses	Yungas
	zikani	Imerí
	beebei	Manaus/Guiana
	bouqueti	Oyapock
	turneri	Tapajós
	eratosignis	Rondônia
	terrasanta	(Lower Rio Nhamundá)
Heliconius sara	*veraepacis*	Guatemala
	theudela	Chiriquí
	sara	Nechí
	sprucei	Chimborazo
	brevimaculatus (B)	Cauca
	thamar	(Widespread)
	apseudes	Bahia
Heliconius leucadia	*leucadia, pseudorhea*	(Widespread)
Heliconius antiochus	*ocannensis*	Magdalena
	antiochus	Rancho Grande
	aranea	Apure(?)
	salvinii	Imataca
	alba	(Widespread)
Heliconius hewitsoni	—	Chiriquí
Heliconius congener	*aquilionaris*	Putumayo
	congener	Abitagua
Heliconius eleuchia	*eleuchia*	Nechí
	eleusinus	Chocó
	primularis	Chimborazo
Heliconius sapho	*leuce*	Guatemala
	sapho	Nechí
	Manuscript subsp.	Chocó
	candidus	Chimborazo