

Geographical patterns of evolution in Neotropical Lepidoptera: differentiation of the species of *Melinaea* and *Mechanitis* (Nymphalidae, Ithomiinae)*

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ABSTRACT. Biosystematic analysis incorporating abundant new field data from many parts of the Neotropics has led to an ordered revision of the mimetic ithomiine genera *Melinaea* and *Mechanitis*. The various polytypic species of these genera probably served as prime movers for the differentiation of other mimetic butterflies in Quaternary forest refuges. The revisions are presented in the form of supplements to the works of Richard M. Fox on these genera, with analyses based on his divisions. Seven species (or monophyletic species-groups) and sixty-three well-differentiated geographic subspecies (six of these described here for the first time) are recognized in *Melinaea*. Specimens are illustrated which demonstrate intergradation between refuge-derived subspecies. Five species and fifty-two differentiated subspecies are recognized in *Mechanitis*, whose members are more abundant and gregarious, more plastic, and apparently more vagile than those of *Melinaea*, resulting in fewer clear-cut mimetic associations, more extensive blurring of differentiation patterns, and apparently fewer incipient biological species in this genus than in *Melinaea*.

Introduction

The mimetic tropical butterfly species in the genera *Melinaea* and *Mechanitis* (Nymphalidae, Ithomiinae) have a confused history of systematic arrangements, due primarily to their apparent plasticity of colour-pattern and monotony of morphology (d'Almeida, 1951; Fox, 1949). The speciation patterns in these two genera were analysed by Forbes (1924, 1927, 1948), d'Almeida (1951) and Fox (1960, 1965, 1967); all three studied a limited number of specimens. Fox's genius is amply demonstrated by the fact that he succeeded in reaching a profound understanding of these

very difficult groups without ever having studied any of the species alive in nature.

Unfortunately, it is not always practical to effect a reliable analysis of the relationships between named forms in these genera without extensive field work in many different regions. The plasticity of the patterns observed in these species is probably in part due to extensive recent recombination of genes arising from past differentiations in isolated forest refuges (Brown *et al.*, 1974; Brown, 1976a). Large samples must thus be obtained from a wide variety of localities before any consistent differentiation patterns become apparent. Fortunately, most of the members of the genera are common Müllerian models for mimicry rings. Thus, it is possible to obtain long series in many areas, showing the limits of local polymorphic variation and intergradation between named taxa; and at least a few specimens may be captured almost

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anywhere, helping to suggest the levels of gene flow between imperfectly isolated geographical races.

As these widespread and common species have recently been implicated as prime movers in the differentiation of other mimetic Lepidoptera (Brown & Benson, 1974; see also Kaye, 1907), it is especially important that there exist a complete and detailed understanding of their geographical variation, incorporating as much data as possible from the field and from museum collections. The present analysis attempts to bring up to date the systematic ordering of the groups presented by Fox (1960, 1965, 1967), in the light of recent field data from many areas, museum specimens not examined by Fox, analyses made by d'Almeida, and a modern understanding of the bases for animal differentiation in the Neotropics. It is not claimed that this represents a final taxonomic revision, as much field, insectary, genetic, cytological, physiological, and biochemical work must still be undertaken before a complete and definitive comprehension of these groups can be achieved. Rather, the interpretations are presented in the light of the patterns discovered in the previous analyses of probable Quaternary refuges in the Neotropics (Brown *et al.*, 1974; Brown, 1976a), which are then used to suggest solutions for some especially difficult cases.

A discussion of the philosophy used in subspecies designation in relatively sedentary polytypic continental species is presented in the previous paper in this series (Brown, 1976a). That paper also includes a map of the probable Neotropical refuges operative in the last Quaternary dry cycle (and in some cases, probably still operative today), in the differentiation of heliconians and ithomiines; a somewhat revised map (incorporating extensive data collected in 1975–76) accompanies this paper. Methodology for species analysis in difficult mimetic groups has been presented with relation to the silvaniform *Heliconius* (Brown, 1976b).

The demography and ethology of the Ithomiinae have been discussed by many authors (see especially Kaye, 1907; Collenette & Talbot, 1928; Fox, 1967; Gilbert, 1969; Brown & Benson, 1974; Brown & Vasconcellos Neto, 1976), and are probably very important

in their systematics. *Melinaea* and *Mechanitis* species are notable for highly localized occurrence and dramatic fluctuations in population levels. Many populations of *Melinaea* seem to be absent during parts of the year, but reach high levels under certain select conditions. In a 1 ha 'ithomiine pocket' recently studied in southern Brazil (Brown & Vasconcellos Neto, 1976), mark-recapture experiments indicated that the population level of *Mechanitis polymnia casabranca* varied over several powers of ten in a period of but 3 months. In the same study it was shown that this species can move rapidly over reasonable distances (at least 2 km). Many similar investigations support a picture of general demographic instability (Brown & Benson, 1974), and reasonably great dispersion ability between sharply physically bounded populations, for the more strongly coloured, mimetic ithomiines. Thus, it is not surprising that many polymorphic populations are known in these genera, with traits appearing in local colonies which apparently have immigrated from regions as much as thousands of kilometres away. The narrow ecological tolerances of ithomiines have undoubtedly contributed to rapid differentiation during dryer periods, when the colonies would be widely separated by large and essentially impassable areas of dryer vegetation, and also to the maintenance of these differentiations in the present day. Moreover, the dispersal abilities of many of the mimetic species, especially evident at dawn and dusk and on cloudy or very humid days, would permit a mixing of complex colour-pattern elements of the evolved races with consequent production of confusingly variable local populations. These factors are probably the source of much of the difficulty in the systematics of these groups. This problem will be examined more carefully in some of the cases discussed in the following sections.

Differentiation of the species of *Melinaea*

The following analysis of species and races is based on the papers of Fox (1960, 1965), to which this constitutes a supplementary revision. Names within the section headings refer to the separate species recognized by Fox, in the order established by him, except that the first name represents the oldest, to be applied

to the species as redefined in this analysis. The papers of Fox should be read in parallel with the present discussion, as here only important new information will be specifically mentioned, and only relevant specimens illustrated (many additional *Melinaea* have been figured by Brown & Benson, 1974). A complete list of the new ordering of the taxa, with references to Fox's revisions, is given in the Appendix.

The species are presented here in proposed evolutionary order, though the present data on this sequence are admittedly sparse. The known entities are united into seven groups, each of which appears, from present information, to represent a single polytypic species or monophyletic species-group (insectary test crosses have not yet been possible in *Melinaea*). There are four widespread, well-differentiated Amazonian species; one of these (*mneasias*) is very rare and little known, but well integrated, and includes a splinter subspecies in southern Brazil (*thera*). Each of the other three species (*maenius*, *marsaeus* and *menophilus*) represents a tentative union of a lowland complex with a pair of premontane subspecies; with *maenius* is also placed a recently discovered isolate from the Guianas (*mediatrix*). There is also one poorly-differentiated Amazon-Guiana species (*mneme*). In the two widespread species which enter Central America (*ethra* and *ludovica*), the northern and southern populations have still imperfectly defined continuity through the associated Amazonian subspecies.

Recent karyological work (Brown, Emmel & Suomalainen, in preparation) suggests that reproductive barriers may be found to exist between the lowland and premontane subunits of *marsaeus* as defined here, and between the northern, Amazonian, and southern subunits of *ethra* and *ludovica*. However, the evolutionary unity of these complexes is affirmed here, and in the present work they are treated as species in the phenetic and phyletic, if perhaps not the biological sense.

(1) *Melinaea mneasias* (Hewitson) (including *M.comma* Forbes and *M.lucifer* Bates)

The polytypic species composed of the known taxa *mneasias* Hewitson, *thera* Felder & Felder, *tecta* Haensch, *eratosthenes* Hall,

comma Forbes, *romualdo* Fox, *lucifer* Bates, *lutzi* Fox, and *eryx* d'Almeida is represented by so few specimens *in toto* (only *comma* and *lucifer* are moderately frequent in collections) that it is not strange that the assemblage was regarded as three separate species by Fox. The Andean subspecies (*comma* and *romualdo*) lack the characteristic series of submarginal spots present in all the others. The west Amazonian (*lucifer*) and east Amazonian (*mneasias*) types were not known to intergrade; Fox remarked that 'on distributional grounds there would be little objection to combining the two as a single species, but the pattern in *lucifer* is strongly modified' (1960:165). Recently discovered specimens, however, which include three new subspecies and three important transitional elements, permit a fuller picture to be drawn of this very widespread but rarely encountered, presumably relict *Melinaea*. In size and colour-pattern, *mneasias* looks more like a member of the genus *Hypothyris*, where indeed some early authors placed it. It can be separated from other *Melinaea*, and from *Hypothyris* as well, by the shape of the forewing comma-mark which extends basad from the margin along vein Cul. It is regarded as a proto-*Melinaea*, well separated from all other members of the genus, though some important colour-pattern affinities with the *Melinaea ethra* complex can be seen and are mentioned below.

The south Brazilian subspecies *thera* (Fig. 1) has been captured in southern Espírito Santo (Negro and the Itabapoana area) and western São Paulo (Araçatuba). Only six specimens are known to this author, who has never seen the subspecies in 10 years' intensive field work in southern Brazil, including a number of trips directed specifically at relocating it as well as the sympatric and similarly 'lost' ithomiine *Hyalyris fiametta* (Hewitson). Its close resemblance to the abundant and co-occurring *Hypothyris ninonia daeta* (Boisduval) may cause it to be overlooked by collectors. No transitions between *thera* and adjacent subspecies are known, but its affinities with *mneasias* are evident. The strange disjunct distribution and extreme rarity of *thera* today strongly suggest that it differentiated in the Rio de Janeiro refuge in the past (probably not in the most recent dry cycle, but in a previous one), and has been displaced from the

area in modern times by more aggressive species, occurring locally only in peripheral habitats. Similar disjunct distributions are known in other rare and/or relict Lepidoptera (Fox, 1949; Brown & Benson, 1975), and may be useful to define refuge limits. A corresponding race, possibly derived from the Bahia refuge farther north on the Brazilian coast, has yet to be discovered if indeed it exists at all.

The east Amazonian *m. mnasias* (Fig. 2) has turned up fairly frequently in recent collections from Pará and western Maranhão, and is probably a product of the Belém refuge. On the north coast of South America occurs a somewhat modified, less yellow-transparent phenotype, which possibly differentiated in the Roraima refuge and bears the subspecific name *tecta*. The highlands in the interior of Amapá and the Guianas, and south-central Venezuela, are inhabited by the mimetic phenotype described as *eratosthenes* (Fig. 3), with a black hindwing typical of many species associated with the Manaus/Guiana and Ventuari refuges. The very few known specimens of *tecta* and *eratosthenes* suggest that they may be partly sympatric today in western Guyana, though they probably originally differentiated in allopatry.

Intergradation southwestward from *mnasias* to the last of the three new subspecies described below is evident in a *tecta*-like specimen from Itaituba, on the Rio Tapajós, in the collection of R. Diringshofen of São Paulo (Fig. 4); this may eventually merit a name as a Tapajós-derived subspecies. Westward, a clear intergrade between the characters of these two and *lucifer* (which probably evolved in the Loreto refuge) can be seen in a specimen from Tefé, deposited in the Museu Nacional in Rio de Janeiro (Fig. 5), which may also merit a name if and when a series becomes available. Transition between *lucifer* (Fig. 6) and the north Peruvian *lutzi* (Ucayali refuge?) can be seen in a specimen from southeast of Benjamin Constant in western Brazil (Fig. 7, from the Rio Javari). While *eryx*, from the Alto Rio Jurua farther south, still preserves a dark hindwing (Fig. 8), the forewing pattern is much modified toward that of *romualdo*, derived in the Inambari refuge; *eryx* may be a locally derived race, or a mere transitional form. A much more interesting specimen, with a dorsal

hindwing much like that of *comma* and a forewing only differing from that of this Andean subspecies by the retention of the Amazon Basin submarginal spot series, is in the Museu Nacional from 'San Felippe' = Eirunepé on the middle Juruá (Fig. 9). The transitional series terminates with *comma* (Fig. 10), probably derived in the Chanchamayo refuge.

Three new subspecies of *mnasias* have now been discovered occupying the northwest, north-central, and south-central peripheries of the known range of the species, and are described here.

Melinaea mnasias abitagua subsp.n.

Female (Fig. 11)

FW 40 mm. Similar to *M.m.comma* (Fig. 10), but possessing a much narrower yellow postmedian band and united discocellular spots on the forewing as in *lucifer* and *lutzi*, reduced black submarginal elements on the hindwing, and a darker ground-colour.

Male

Unknown, but probably identical in colour-pattern.

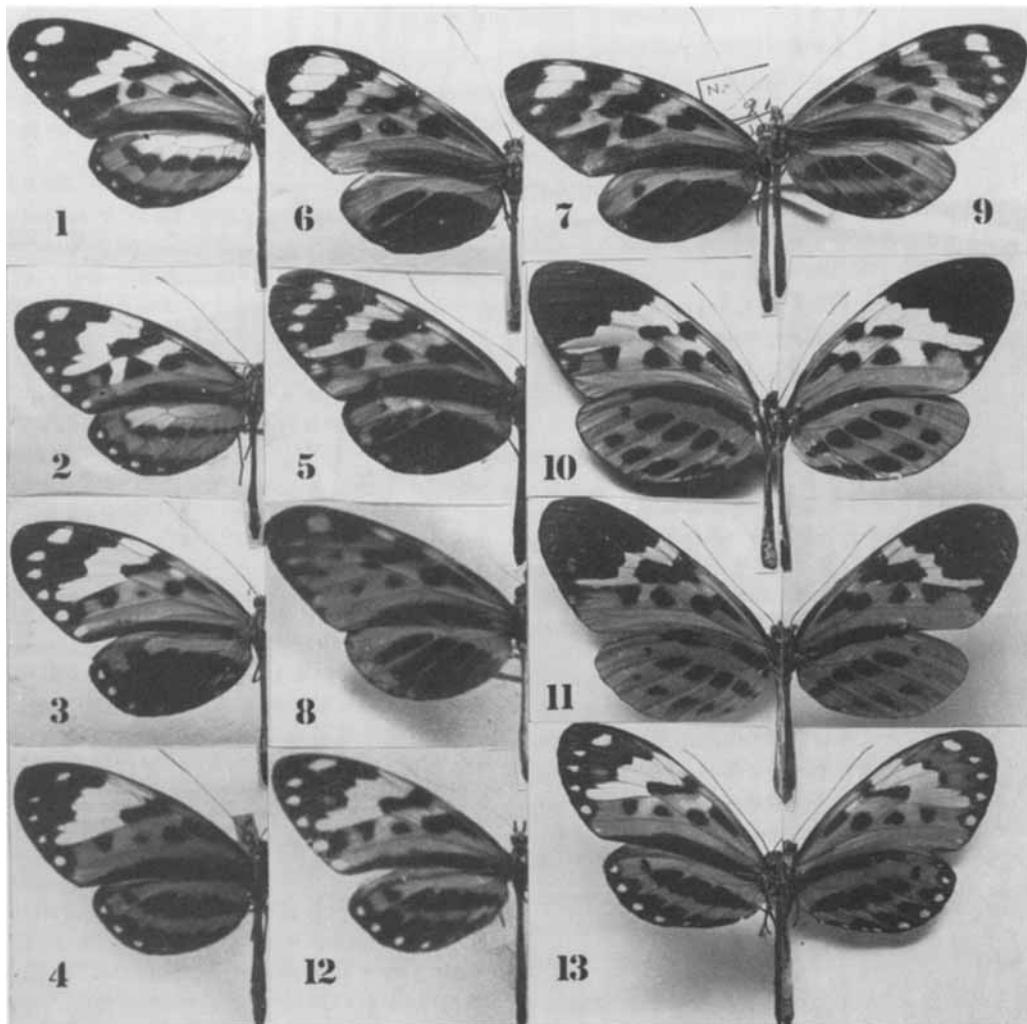
Holotype ♀, ECUADOR: Oriente (Napo-Pastaza), Km 43 of the Puyo-Napo road, near Santa Clara ($1^{\circ} 16' S$, $77^{\circ} 52' W$), 600 m, 9.xii.71 (K. S. Brown, Jr), donated to the Museu Nacional, Rio de Janeiro.

This subspecies almost certainly evolved in the Abitagua refuge, though it may eventually be found further east in the Putumayo and Napo areas also.

Melinaea mnasias neblinae subsp.n.

Male (Fig. 12)

FW 38 mm. Similar to *M.m.tecta* but more heavily marked, the black spots on the FW larger and the hindwing median and marginal black areas broad, barely separated by a narrow orange stripe. Single intervenal yellow submarginal dots prominent on forewing and on hindwing to space Cu1–Cu2. Yellow band on forewing not extending discally into cell or space Cu1–Cu2. Ventral surface essentially identical in colour-pattern to dorsal.



FIGS. 1–13. *Melinaea mnasias*. All 0.9 × life size, black, yellow and orange. (1) *M.m.thera* Felder & Felder, male, dorsal, Araçatuba, São Paulo (Museu Nacional, Rio de Janeiro, no. 13/850). (2) *M.m.mnasias* (Hewitson), male, dorsal, Km 64 Estrada Pará–Maranhão, Mun. Ourém, Pará, 17.iii.64 (MN-Rio, O. Mielke leg.). (3) *M.m.eratosthenes* Hall, male, dorsal, Serra do Navio (ICOMI), Amapá, Brazil, 7.iii.63 (MN-Rio, Roppa & Mielke leg.). (4) *M.m.* subsp., male, dorsal, Itaituba, Rio Tapajós, Pará, i.62 (R. Diringshofen). (5) *M.m.(mnasias X lucifer)*, male, dorsal, Tefé, Amazonas, Brazil (MN-Rio, no. 16/624, coll. Arp – ‘flavosignata hicetas’). (6) *M.m.lucifer* Bates, male, dorsal, Benjamin Constant, Amazonas, VIII/947 (MN-Rio, Parko leg.). (7) *M.m.(lucifer X lutzi* Fox), male, dorsal, Rio Javari above Benjamin Constant, Brazil/Peru border, 11–16.ix.40 (MN-Rio, Parko leg.). (8) *M.m.eryx* d’Almeida, holotype male, dorsal, Alto Rio Juruá, Acre (MN-Rio, no. 14/001). (9) *M.m.(lucifer X comma)*, male, dorsal, ‘San Felipe, Acre’ = Eirunepé, Amazonas, middle Rio Juruá (MN-Rio, no. 13/767 – ‘*M.hicetas* – d’Almeida det.’). (10) *M.m.comma* Forbes, female, dorsal (right) and ventral (left), La Merced, Chanchamayo, Peru, v.63 (KB, L. & G. Harris leg.). (11) *M.m.abitagua* nov., holotype female, dorsal (right) and ventral (left) (left side has a large tear in forewing cell M3-Cul), near Santa Clara, Km 43 of Puyo–Napo Road, east Ecuador, 9.xii.71 (MN-Rio, KB leg.). (12) *M.m.neblinae* nov., holotype male, dorsal, Cerro Neblina, norte Brasil, 1500 m, 25.iv.64 (Facultad de Agronomía, Maracay, Venezuela, J. & B. Bechyne leg.). (13) *M.m.rondonia* nov., holotype male, dorsal (left) and ventral (right), near Riozinho, Rondônia, 7.vii.72 (MN-Rio, KB leg.).

Female

Unknown, but probably identical in colour-pattern.

Holotype ♂, BRAZIL: Amazonas, Pico Neblina, 1500 m (as 'Cerro Neblina') ($0^{\circ} 46' N$, $66^{\circ} 04' W$), 25.iv.64 (J. & B. Bechyne), Facultad de Agronomía, U.C.V., Maracay, Venezuela.

Paratypes. One ♂, same data as holotype, and one ♂, same data except 24.iv.64, in the same collection.

This subspecies probably evolved in the Imerí refuge, and may be looked for elsewhere in northwestern Brazil. The high altitude of the capture is exceptional, possibly representing an altitudinal variation of the marginalization phenomenon general in this species.

Melinaea mnasias rondonia subsp.n.*Male* (Fig. 13)

FW 36–38 mm. Similar to *m. mnasias* but somewhat larger, with the forewing strongly orange, possessing a narrower yellow postmedian band, a somewhat reduced commar-mark, and much anteapical orange coloration ventrally. Hindwing median and marginal black areas wider; no yellow on hindwing. A full series of single intervenal submarginal yellow spots present on both wings, dorsally and ventrally.

Female

Unknown, but probably identical in colour-pattern.

Holotype ♂, BRAZIL: Rondônia, near Riozinho, in woods north of Km 489 of the Porto Velho-Vilhena Highway ($11^{\circ} 31' S$, $61^{\circ} 20' W$), 300 m, 7.vii.72 (K. S. Brown, Jr), donated to the Museu Nacional, Rio de Janeiro.

Paratypes. One ♂, same data as holotype, retained in the collection of the author; one ♂, same locality, 5.vii.72, in the collection of W. W. Benson (Campinas, São Paulo).

This subspecies probably evolved in the Rondônia refuge, on whose southeastern margins it was captured, and may be expected to appear rarely in various parts of the territory today. The scrubby woods ('cerradão') in

which it was captured, along with twenty other species of Ithomiinae, have since been destroyed.

Further races of *mnasias* may be predicted to occur in areas marginal to the Putumayo, Napo, and Huallaga refuges, and some or all of those mentioned above may prove to be good subspecies rather than transitional forms, associated with the Tapajós, Tefé, and Madeira refuges. The species seems to be everywhere mimetic and very rare, and though it obviously has a very extensive distribution, many gaps remain to be filled. Most of the known specimens have been captured in localities peripheral to supposed refuges, flying with transitional or hybridized populations of more common species, which strongly suggests that *mnasias* has been subjected to strong, probably competitive dislocatory phenomena by its relatives, in many areas (see Fox, 1949 and Brown & Benson, 1975).

(2) *Melinaea ethra* (Latreille) (including *Melinaea liliis* Doubleday, *M. scylax* Salvin, *M. mnemopsis* Berg, *M. maelus* (Hewitson), *M. maeonis* Hewitson, and *M. maenius* (Hewitson) (sensu Fox, part)).

The three allopatric species *liliis*, *scylax*, and *ethra* were recognized by Fox (1960: 118) as closely related, forming a superspecies within *Melinaea*. As all of the pattern characteristics of *scylax* (Fig. 14), except for its characteristic unmarked hindwing, are represented in the adjacent and allopatric subspecies related to *liliis*, *imitata* Bates and *parallelis* Butler (these two intergrade in west-central Panamá; an excellent transitional series from Cerro Campana exists in the collection of Gordon Small, Fig. 15); and as the three form a Central American triad assignable to differentiation from a single stock, under mimetic pressure, in the Quaternary refuges designated Chiriquí, Guatemala, and Darién, respectively (the Mexican *flavicans* Hoffmann, Fig. 16, is apparently a north-peripheral isolate), it seems best to regard *scylax* as a subspecies of the widespread and polytypic *liliis*-group, in spite of the morphological differences reported (Fox, 1960).

The pattern elements in the southern *M. ethra* (Fig. 17) are considerably different from those of *liliis*-group races. This butterfly has recently been found far into the interior

of southern Brazil (upper Rios São Francisco and Grande) and may be very widespread if rather sparse over extra-Amazonian Brazil. In view of the wide geographic separation between *ethra* and *lilis* (all of the Amazon Basin, at least 3000 km), it becomes necessary to identify associated races in the intervening area in order to propose that the two may be regarded as conspecific. The logical candidates are the members of the *M.maelus* complex, which are closely related and allopatric to, and possess many pattern elements in common with *lilis* and *ethra*.

Colour-pattern elements of *maelus* and *ethra* as well as of the *lilis*-group races are conspicuously present on both fore- and hind-wings of *M.mnemopsis* from northern Bolivia (Fig. 18), which should thus form part of this polytypic species also.

Melinaea dodona Hopffer was named from an apparently unique specimen from 'Bolivia'. Its description strongly suggests that it is a member of the *lilis*-group, where it was placed by Fox (1960). Indeed, its colour-pattern suggests that it should occur in Colombia and not Bolivia, as it combines characters of *messatis* (Hewitson) with those of *erica* Bargmann or *ezra* Fox, both of which should intergrade at the peripheries of the central Colombian valleys with *messatis*. The author captured in December 1971 a male apparently very near *dodona* on the Rio Anchicayá above Buena-ventura, on the west coast of Colombia. Four recent specimens from the same area, in the Facultad de Agronomía, Maracay, Venezuela, include two essentially identical to *dodona* (Fig. 19), with the forewing postmedian band broken into separate spots. These considerations suggest that *dodona*, rather than *erica*, is the typical Chocó race of *M.ethra*, identical to west Colombian phenotypes; *erica* would then be a transitional form to *messatis* in the central Colombian valleys. It seems extremely unlikely that an isolated subspecies of the *lilis*-group with typical Colombian colour-pattern characters, should occur in Bolivia more than 4000 km to the south, where no similar specimens have been captured in the last hundred years, and which is inhabited by another conspecific race. It is noteworthy that one of the five specimens in Hewitson's type series of *messatis*, essentially identical with the others, is also labelled 'Bolivia' (Fox,

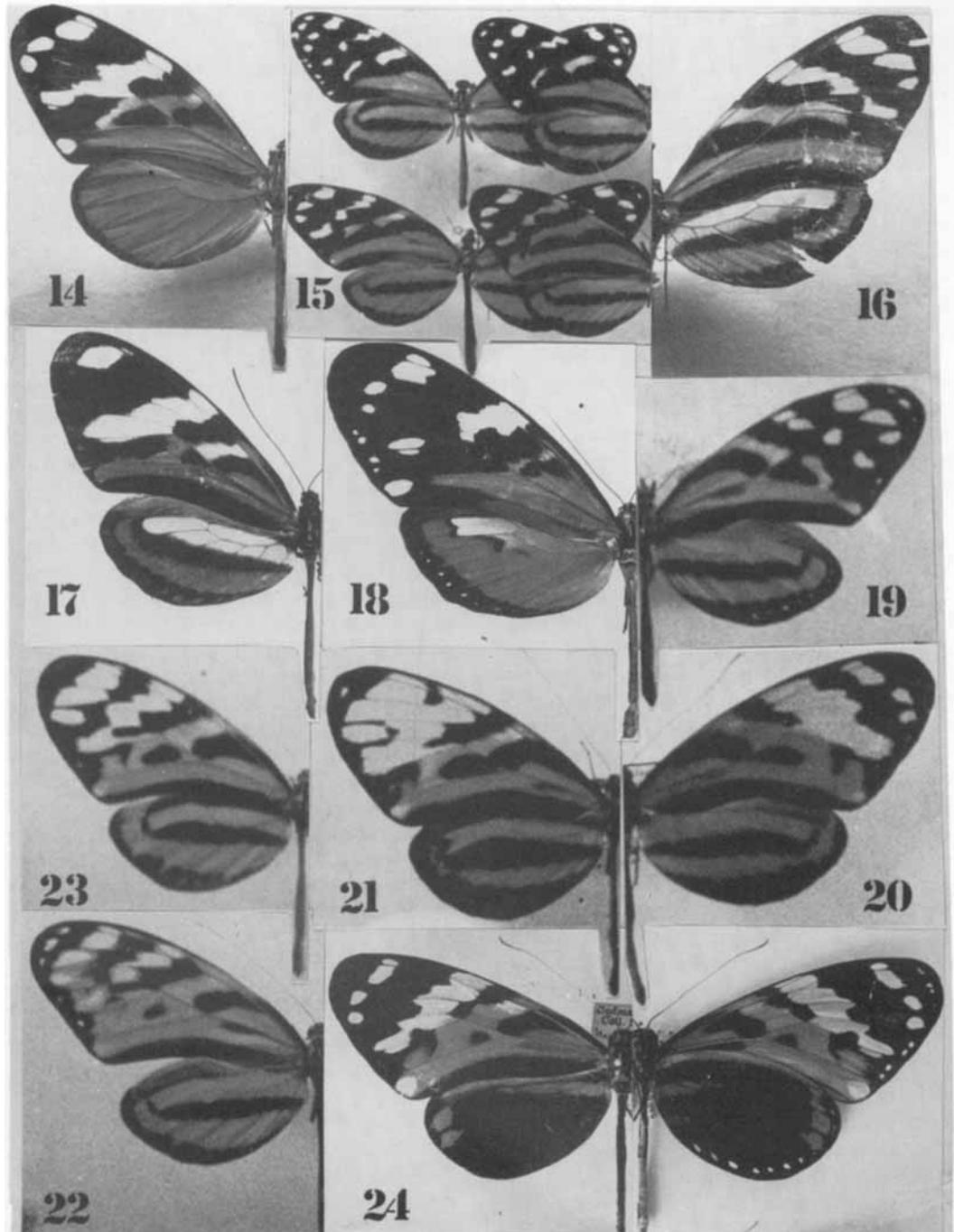
1965); such mislabelling with generalized localities was quite common in early material from South America, and often introduced great confusion into nomenclature until the respective taxa could be relocated in their proper ranges.

Melinaea lilis limitata Hall (Fig. 20) was correctly synonymized by Fox (1960) with *sola* Kaye from Trinidad and represents an endemic Sucre/Trinidad subspecies. The types of *limitata* are from the Cumaná area in extreme northeastern Venezuela, and recent specimens are available from Caripe. *M.l. lateapicalis* Hall (Fig. 21) is entirely different in appearance and represents a good geographically defined subspecies from northwestern Venezuela. It has not been relocated in recent collecting, which has produced an *ezra* (described from the Santa Marta range in extreme northern Colombia) from the Sierra Perijá (Fig. 22). Moreover a single transitional specimen (Fig. 23) between *lilis* (northcentral Venezuela, Rancho Grande refuge) and *lateapicalis* has been taken in Barinitas, where the probably conspecific *zamora* (see below) also occurs very rarely. More specimens are needed from this region to define the transition between Venezuelan races of *ethra*. Pure *lateapicalis* should be sought in the southern part of the Catatumbo refuge, west of Mérida on the northern slopes of the Andes.

An additional undescribed and mimetic subspecies of the *lilis*-group has been discovered in the collection of the British Museum (Natural History):

Melinaea ethra kayei subsp.n.

The prominent black-hindwing mimicry ring of the Potaro area of (formerly British) Guyana (Kaye, 1907) includes four known species in the genus *Melinaea*: *M.mneme mneme* (Fig. 33), *M.maenius mediatrix* (Fig. 35; see below), *M.ludovica crameri* (Fig. 43; long confused with *mneme* due to Cramer's erroneous figure of this species), and *M.mnasias eratosthenes* (Fig. 3; very rare, mixed with *m.tecta*). In view of this diversity already present, it was a great surprise to discover mixed among the *mneme* from Guyana in the British Museum (Natural History) three examples of a fifth mimetic species of *Melinaea*. These were, once



FIGS. 14-24. *Melinaea ethra*, *lilis*-group and southernmost races. All life size except 15 (0.65 X), black, yellow (or white, in 15 upper left), and orange. (14) *M.e. scylax* Salvin, male, dorsal, Potrerillos, Chiriquí, Panamá, 31.xii.65 (KB, G. B. Small leg.). (15) *M.e. (imitata) X parallelis*, transitional series (upper left, female near *parallelis* Butler, others males, lower right near *imitata* Bates), dorsal, Cerro Campana, Panamá (G. B. Small). (16) *M.e. flavicans* Hoffmann, female, dorsal, Santa Rosa Comitán, Chiapas, México, vi.66 (KB, T. Escalante leg.). (17) *M.e. ethra* (Latreille), male, dorsal, Baixo Guandu, Espírito Santo, Brazil (KB, P. C. Elias leg.). (18) *M.e. mnemopsis* Berg, male, dorsal, Colonia Hardeman, norte de

recognized, easily distinguished from all other sympatric ithomiines by the great extent and shape of the black area on the hindwing. Minor elements of colour-pattern, especially the fused discocellular bar on the forewing (shared only with *M.ethra sola*, Fig. 20, and some races of *M.mnasiás*), suggest that this new race is closely allied to the *lilis*-group, representing the farthest southeastern extension of this fundamentally northwestern complex.

Male (Fig. 24)

FW 37–42 mm. Similar to *M.m.mneme* (Fig. 33), but immediately distinguishable from this species and from *M.maenius mediatrix* (Fig. 35) by the extensive black suffusion on the hindwing, reaching the costal margin in the median region and cutting off a narrow orange basicostal dagger both dorsally and ventrally. Distinguished from sympatric *M.ludovica crameri* (Fig. 43) by the shape of this orange dagger (in *crameri*, a basal block) and by the full dark anal bar and fused discocellular spots on the forewing; and from sympatric *M.mnasiás eratosthenes* (Fig. 3) by the lack of single yellow intervenal submarginal spots on the hindwing. Forewing discocellular spots united into a short, irregular, narrow bar, and a narrow black stripe under the forewing cubitus, both of these characters occurring only in other subspecies of *ethra* (*lilis*-group) and *mnasiás* (Figs. 1–13, 20–22). Paired submarginal white spots well developed ventrally.

Female

FW 43 mm. Very similar, without the dark streak under the forewing cubitus.

Holotype ♂, GUYANA: Quonga (probably about 6° 30' N, 59° W) (H. Whitley), in the BMNH (Rothschild Bequest, 1939–1).

Paratypes: one ♂ and one ♀, same data and collection as holotype.

M.m.mneme and *M.maenius mediatrix* from the same locality (Quonga) are illustrated in Figs. 33 and 35. This represents a most unexpected geographical and mimetic expansion of the *lilis*-group of *M.ethra*.

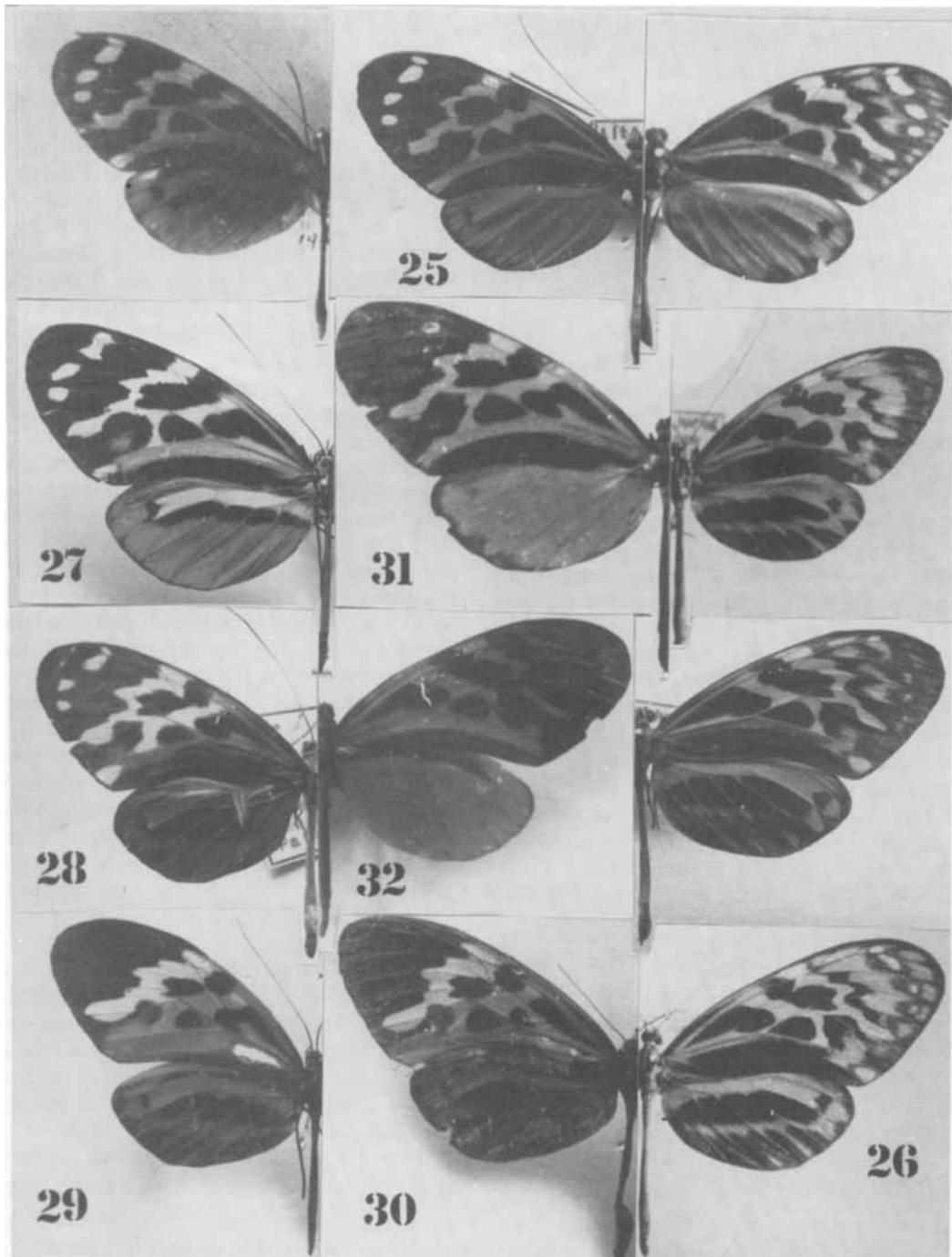
Fox's species *maelus* and *maeonis* show many related aspects of colour and pattern, and are essentially allopatric except for *zamora* Haensch, the unique type of which bears a generalized locality label (Ucayali). The southwestern Brazilian entity *brunnea* Riley (Fig. 25) represents in fact an intergrading series between *maelus cydon* Godman and Salvin and *maeonis* patterns, specifically a new *maeonis*-group subspecies described below. Other intergrading patterns, closer to *cydon*, are represented by the specimens in Fig. 26.

Zamora suggests by its name a possible origin in southern Ecuador; however, it has never been re-collected in any part of Peru or Ecuador, and its forewing pattern does not correspond with that of Ecuadorian *maeonis*, though the overall colour-pattern might fit in with a predominant mimetic group in the upper Rio Marañón. On the other hand, the type of *zamora*, in the Berlin Museum (Zoologisches Museum der Humboldt-Universität) (Fig. 27), is essentially identical to southwestern Venezuelan specimens of *borealis* Hall (Apure refuge), opening the possibility that the specimen is mislabelled. Forbes (1948) considered the two as synonyms; in this case, *zamora* is the oldest name for the Venezuelan populations, and will be so regarded until specimens of this phenotype are found elsewhere.

Of the other subspecies mentioned by Fox under *maelus*, *flavomacula* Weymer, 1894: 322 (= *madeira* Moulton) (Fig. 28) is a resident of the Madeira refuge area; 'purusana' is a transitional form between *flavomacula* and *maelus* (Tefé refuge); and 'mayi' is treated below under *M.marsaeus*.

It is also evident that *tarapotensis* Haensch (Fig. 29), placed by Fox in *M.maenius*, is in

Santisteban, Santa Cruz, Bolivia, 16.ii.71 (KB). (19) *M.e.dodona* Hopffer, male, dorsal, 'Cali, Colombia' (generalized), 5.viii.70 (FA-Maracay, L. Denhez leg.). (20) *M.e.sola* Kaye (syntype of *M.limitata* Hall), male, dorsal, Campo Alegre, Cumáná, Sucre, Venezuela (British Museum (Natural History), London). (21) *M.e.lateapicalis* Hall, holotype male, dorsal, Mérida, Venezuela (BM-London). (22) *M.e.ezra* Fox, male, dorsal, El Tucuco, Sierra Perijá, Zulia, Venezuela, 21–27.v.71 (FA-Maracay). (23) *M.e.(lilis) Doubleday X lateapicalis*, female, dorsal, El Mijao, Barinitas, Barinas, Venezuela, 1.iii.65 (FA-Maracay). (24) *M.e.kayei* nov., holotype male, dorsal (left) and ventral (right), Quonga, Guyana (BM-London, H. Whitley leg., Rothschild Bequest).



FIGS. 25-32. *Melinaea ethra*, *maelus*-*maeonis* complex. All life size, black, yellow, and/or orange to brown. (25) *M.e.(maelus* (Hewitson) or *cydon* Godman & Salvin \times *lamasi* nov.) (*brunnea* Riley), holotype female (left), dorsal, Boca do Acre, upper Rio Purús, Amazonas, Brazil (BM-London, Rothschild Bequest), and a male and a female (centre and right), Alto Rio Juruá, Acre (MN-Rio, nos. 13/831 and 13/832). (26) *M.e.cydon*, varieties transitional to *lamasi*, three males, dorsal, Alto Rio Juruá, Acre (MN-Rio). (27) *M.e.zamora* Haensch, holotype male, dorsal, 'Ucayali-Zamora' (Zoologisches Museum der

fact a subspecies of the otherwise allopatric *maelus/maeonis* complex of *ethra*; it shows close affinity with only *maelus* in the pattern elements of the forewing median area and hindwing margin, and is associated with and nearly identical to the local race of *Heliconius pardalinus* (*H.p.sergestus*), exactly as are other subspecies of the *maelus* group at lower elevations in Peru and Brazil. A transitional specimen between *tarapotensis* and *cydon* (Fig. 30) was captured by the author near Shapaja, 20 km southeast of Tarapoto, in December 1975.

All *maelus* and *maeonis* related forms show, like many *lilis*-group subspecies, a heavy fusion of the end-cell spots on the forewing, usually toothed on the distal border (this is also present in many *mriasias* subspecies; see Figs. 1–13), and a heavy, strongly angled comma-mark, which usually serve to distinguish them from sympatric races of *M. marsaeus* and *M. maenius*. By these characters, a new subspecies of *ethra* can be recognized and separated from *M. marsaeus clara*, with which it co-occurs in southeastern Peru and southwestern Brazil, and has been confused in the past:

Melinaea ethra lamasi subsp.n.

Melinaea clara, 'female allotype' (no systematic validity as divorced from original description), d'Almeida (1960: 9, Plate 10, Fig. 1).

Male (Fig. 31)

FW 40 mm. Completely orange and black; hindwing clear orange with at most faint black markings marginally; forewing apex completely black; a narrow, jagged orange postdiscal band on the forewing. Otherwise patterned as in *e.maeonis*, though median spots on forewing not fused. Readily distinguished from the superficially similar *marsaeus clara* (Fig. 51)

by the heavy forewing median markings, the discocellular bar being characteristically toothed on its distal (lower) extremity.

Female (Fig. 32)

Essentially identical to male, though lacking the silvery hair-pencil on the costal border of the hindwing, having this replaced by a black bar, as in the majority of *Melinaea* and *Ithomiinae* in general.

Holotype ♂, PERU: Madre de Diós, Iberia (11° 22' S, 69° 35' W), 200 m, 8.ix.75 (José M. Schunke), in the Museo de Historia Natural 'Javier Prado', Universidade Nacional Mayor de San Marcos, Lima, Peru.

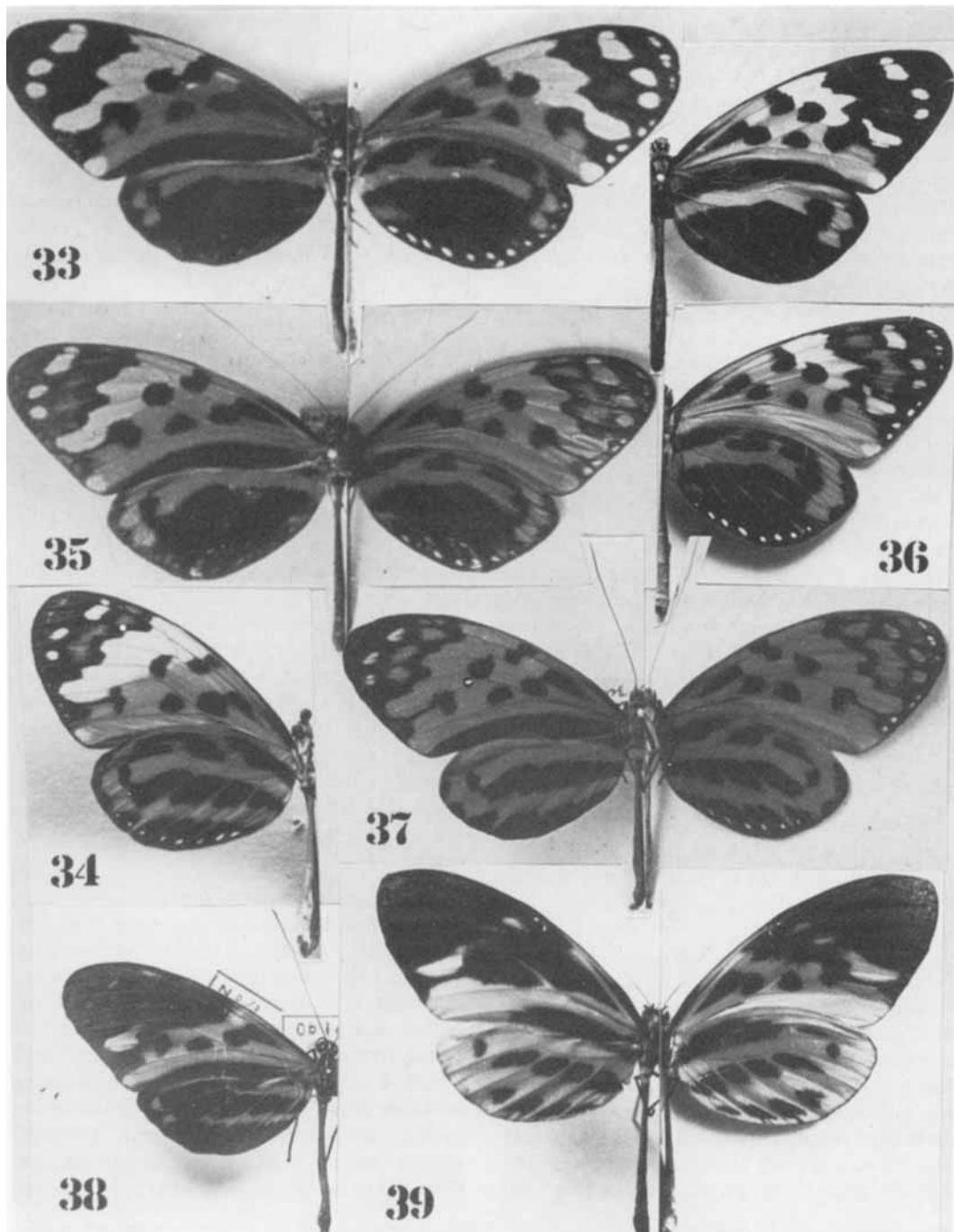
Paratypes: one ♀, BRAZIL: Acre, Xapuri (10° 38' S, 68° 32' W), 190 m (Guinle & Oiticica), in the d'Almeida collection (no. 2979), now in the Departamento de Zoologia, Universidade Federal do Paraná, Curitiba; one ♂, BRAZIL: Acre, Alto Rio Juruá (about 8° 30' S, 73° 50' W), 190 m, in the Museu Nacional, Rio de Janeiro (ex coll. E. May), no. 13/830 (*Melinaea clara*, det. d'Almeida).

This subspecies, which is dedicated to Dr Gerardo Lamas Müller of the Museo 'Javier Prado', was surely derived in the Inambari refuge, and represents a combination of characters from *tarapotensis* and *cydon* to the north (the last connected by 'brunnea' phenotypes) and *mнемопись* to the south of its range.

(3) *Melinaea mneme* (Linné)

The black-hindwing *M.m.mneme* (Fig. 33) is a typical member of the Guyana mimetic complex, as mentioned above. The lighter-hindwing *M.m.mauensis* Weymer is here regarded as a good subspecies, originating south of the Amazon River, though presently found widely in the predominantly black-hindwing northern *m.mneme* populations, probably invading through the Roraima area. The subspecies with a large orange anteapical area (Fig. 34), now also widespread in *mneme*

Humboldt-Universität, Berlin). (28) *M.e.flavomacula* Weymer, male, dorsal, Manicoré, Amazonas, Brazil, X-41 (MN-Rio, no. 1/036, Parko leg.). (29) *M.e.tarapotensis* Haensch, female, dorsal, near Shapaja, Peru, 12.xii.75 (KB). (30) *M.e.(tarapotensis X cydon)*, female, dorsal, near Shapaja, Peru, 12.xii.75 (KB). (31) *M.e.lamasi* nov., holotype male, dorsal, Iberia, Madre de Diós, Peru, 8.ix.75 (Museu Javier Prado, Lima, J. M. Schunke leg.). (32) *M.e.lamasi* nov., paratype female, dorsal, Xapuri, Acre, Brazil (Departamento de Zoologia, Universidade Federal do Paraná, d'Almeida collection, no. 2979, Guinle & Oiticica leg. – 'allotype female of *Melinaea clara*').



FIGS. 33-39. *Melinaea mneme*, *M.maenius mediatrix*, and *M.menophilus* aberration. All life size, black, yellow, and orange. (33) *M.mneme* (Linné), male, dorsal (left) and ventral (right), Quonga, Guyana (BM-London, H. Whitley leg., Rothschild Bequest). (34) *M.m. ca. mauensis* Weymer (new subsp.?), male, ventral, Jaru, Rondônia, 5.viii.75 (KB). (35) *M.maenius mediatrix* Weymer, male, dorsal (left) and ventral (right), Quonga, Guyana (BM-London, H. Whitley leg., Rothschild Bequest). (36) *M.maenius mediatrix* form 'anina' Haensch, holotype male, dorsal (upper) and ventral (lower), British Guiana (ZM-

populations, may have originated in southwestern Brazil where it is presently quite uniform, in populations which, being fairly well differentiated from those farther to the north, may merit a name.

On the basis of careful analysis of chromosome numbers, de Lesse (1970) separated populations formerly united under *Melinaea mneme* in (French) Guyane into two species. One, with $N = 16-17$, corresponded to the true *M. mneme* of Linné. The other, with $N = 22$, was identified by de Lesse with the name *mediatrix* Weymer, through designation of an appropriate lectotype from the type-series of this taxon. Specimens of *mediatrix* can be identified superficially by inspection of the ventral hindwing (de Lesse, 1970), which bears a broad orange median band with no yellow scaling at the anal margin (Fig. 35); in *mneme*, the orange median band narrows and becomes yellow at the anal margin (Fig. 33). *Mediatrrix* and its minor aberration *anina* Haensch (Fig. 36) are treated below under *M. maenius*; they have been found in Venezuela, the three Guianas, and Pará and Amapá in northern Brazil, always flying together with *M. mneme*.

Fox (1960: 126) mentioned that 'the British Museum (Natural History) has an aberrational specimen (of *mneme*) from the Rio Madeira in which the postmedian fascia and subapical spots of the forewing are tawny rather than yellow.' As *M. m. mauensis* is common in many parts of the Rio Madeira area, such an aberration would not be unlikely to appear; the specimen in the BM(NH) bears a note handwritten by Fox in which he affirms that it is but an individual variant. The specimen, however, was separated by Mr N. D. Riley into a drawer of *mediatrix* after the publication of de Lesse's paper. Careful inspection of the ventral hindwing (Fig. 37) indicates that this may have been a correct judgment. As the specimen lacks all yellow pigment on the wings, however, and as the area is inhabited by another subspecies of *maenius* (*juruensis*), it may indeed be a simple mutant of *mneme*.

A further unusual melanic *Melinaea* from

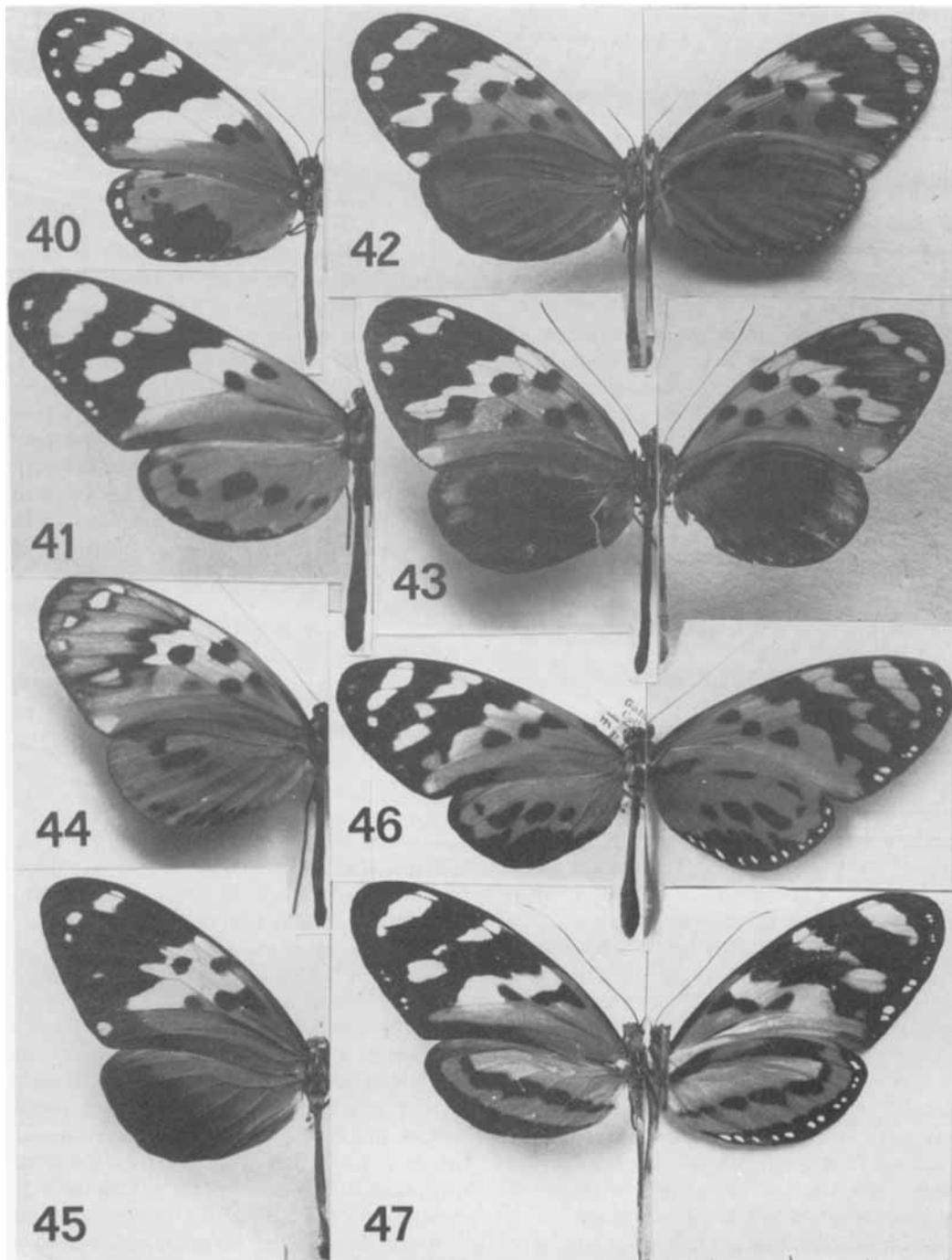
Óbidos, Pará, in the Museu Nacional (Rio de Janeiro) (Fig. 38), is regarded as an aberration of *mneme* which has lost essentially all yellow markings through invasion of black pigment in the apical areas. A similarly apicomelanic specimen of *M. menophilus menophilus* was captured by the author in Jaru, Rondônia, in southwestern Brazil, in August 1975 (Fig. 39).

(4) *Melinaea ludovica* (Cramer) (= *egina* Cramer, 1777) (including *M. satevis* (Double-day) and *M. idae* (Felder & Felder)).

The name *Papilio egina* Cramer, 1777 is an invalid junior homonym of *P. regina* Cramer, 1775, and the later name *ludovica* of the same author must be applied to the common species with a markedly proximal yellow band on the forewing (Ebert, 1965: 76). The very widespread *l. ludovica* (Fig. 40) is common from the base of the Colombian, Ecuadorian and north Peruvian Andes through all of northern Brazil to southern Venezuela and the Guianas, forming everywhere an effective mimetic association with the 'silvana' morphs of *Heliconius numata* (see Brown & Benson, 1974). It is replaced in eastern coastal Brazil, from Paraíba to São Paulo, by the isolated subspecies *M. l. paraiya* Reakirt which forms a mimetic association with *Heliconius numata ethra* Hübner and *robigus* Weymer. A further little-known race, *M. l. manuelito* Tessmann, occurs together with the local mimetic *H. numata illustris* Weymer in central Peru (Ucayali refuge area); this subspecies (Fig. 41) is phenotypically quite similar to *paraiya*.

The mahogany-coloured, clean-hindwing *satevis* from Bolivia (Fig. 42) and the orange-coloured, black- or orange-suffused-hindwing *crameri* Godman and Salvin (Fig. 43) and *aurantia* Forbes (Fig. 44) from western Guyana and Venezuela possess many pattern elements in common. Fox treated these as a single species, but they are separated by 2000 km of the Amazon Basin in which it is difficult to find reasonable candidates for linking them. It seems highly unlikely that they should be so separate and still be regarded as races of a single species, which in the extensive tropical

Berlin). (37) *M. m. ca. mauensis* aberration?, male, dorsal (left) and ventral (right), 'Marmore, Rio Madeira' (BM-London). (38) *M. mneme*, aberration?, male, dorsal, Óbidos, Pará (MN-Rio, no. 13/785). (39) *M. menophilus menophilus*, apicomelanic aberration, male, dorsal (left) and ventral (right), Jaru, Rondônia, 2.viii.75 (KB).



FIGS. 40-47. *Melinaea ludovica*. All life size, black, yellow, and orange to brown. (40) *M.l.ludovica* (Cramer), male, dorsal, Belém, Pará (KB). (41) *M.l.manuelito* Tessmann, male, dorsal, Rio Monzón, Tingo María, Peru (JP-Lima). (42) *M.l.satevis* (Doubleday), male, dorsal (left) and ventral (right), Caranavi, La Paz, Bolivia, 6.x.74 (KB). (43) *M.l.crameri* Godman & Salvin, male, dorsal (left) and ventral (right), Curiapo, Delta Amacuro, Venezuela, 13.iv.69 (KB, K. Negishi leg.). (44) *M.l.aurantia* Forbes, male, dorsal, Caripito, Monagas, Venezuela, 17.ix.69 (KB, K. Negishi leg.). (45) *M.l.idae*

forests of the present time are virtually always nearly contiguous or else even extensively mixed along the edges of their respective ranges. While widely disjunct distributions are not rare in subtropical, temperate, or highly habitat-specialized organisms in Central and South America, they are practically unknown in tropical forest species. *M.ludovica* occupies essentially the entire area between *satevis* and *crameri*, and shares with them an unusual shape of the forewing midcell and discocellular spots, and lack of the forewing hindmarginal bar. These characters are present also in the closely related northwestern *M.idae* complex (Fig. 45), which is allopatric to both *satevis* and *ludovica*-related subspecies. Union of the three into a single widespread and polytypic species is strongly suggested.

A number of arguments could be advanced against the union of these species but none is definitive. Although the subspecies may differ in chromosome number (de Lesse, 1970; de Lesse & Brown, 1972; Brown, Emmel & Suomalainen, in preparation), similar differences have been found between subspecies and even within local populations of mimetic heliconians and ithomiines (de Lesse, 1967; Wesley & Emmel, 1975). The races of *satevis* possess a yellow spot in the anal angle of the forewing (a character regarded as fundamental and differentiative by Fox), and this is also present in *idae* but absent in *ludovica*. However, this is clearly a variable character in *M.mnemias* and *M.ethra* subspecies, and probably in *M.maenius* as well (see below). They also have the yellow band of the forewing in a more apical position than in any known forms of *idae* or *ludovica* (but see Fig. 44). However, the position of this band has been shown to be controlled by a single gene in the mimetic *Heliconius numata* (Brown & Benson, 1974), and a similar mechanism could operate in this ithomiine species. The disposition of the paired white submarginal spots on the ventral surface of *ludovica* (Fig. 40) is different from that in *idae* or *crameri* (Fig. 43) (though more similar to that in *satevis*, Fig. 42), each pair

being closely disposed rather than widely separated; but this is not necessarily a 'good' character in *Melinaea*, being quite variable in other species. *Satevis* and *crameri* have more rounded forewings than *idae* or *ludovica*, but this character is variable in *M.ethra* and *M.menophilus*. Finally, both *l.ludovica* and *crameri* have been reliably recorded from western Guyana, and near Km 85 of the El Dorado-Santa Elena road in southeastern Venezuela (not in the same locality nor on the same date), indicating possibly imperfect allopatry of these entities. However, in the only locality known in which both have been reliably taken on the same day (Potaro Road; Kaye, 1907), they are both rather infrequent (9% and 5%, respectively, of *M.mneme*), *ludovica* is almost absent for half the year, and 'no less than 63% of the *ludovica* show some slight development towards the pattern of *crameri* on the underside' (Kaye, 1907: 415), in the form of an expanded black patch on the hindwing. Additionally, a few *crameri* show a divided black patch on the hindwing (form 'incisa' Kaye), further suggesting intergradation with *ludovica*. In general, *crameri* seems confined to eastern Venezuela and western Guyana, from Delta Amacuro and Berbice to Roraima and commoner coastally. It does not occur into the interior, in southeastern Guyana or southwestern Venezuela, or in Surinam, Guyane, or northern Brazil (Amapá, Pará and Amazonas), where its co-mimics *mneme*, *mediatrix* and *Mechanitis mazaeus pannifera*, in addition to many heliconians and other butterflies with the same pattern, are common. Indeed, it seems most unusual that *crameri* has not invaded the vast majority of the enormous region where its co-mimics occur; the presence of a different but conspecific race (*ludovica*) in these areas could help to explain the unexpected absence of *crameri*.

Thus, we have at present a number of justifications for the union of *crameri*, *ludovica* and *satevis*, and as yet no compelling reason for their separation; certainly, they appear to

(Felder & Felder), male, dorsal, Cerro Campana, Panamá, 17.viii.64 (KB, G. Small leg.). (46) *M. (ludovica ludovica X mneme mauensis)* (holotype of *agricola* Hall), probably an interspecific hybrid, male, dorsal (left) and ventral (right), Tefé, Amazonas, Brazil (BM-London). (47) *M. (ludovica paraiya X ethra ethra)*, interspecific hybrid, male, dorsal (left) and ventral (right), Baixo Guandú, Espírito Santo, Brazil (KB, P. C. Elias leg.).

be of common phyletic stock, and essentially allopatric.

The orange-washed, variable *aurantia* flies only in the Sucre area of northeastern Venezuela, although a stray has been captured in Trinidad (Barcant, 1970: 275, as '*Melinaea melus madeira*'); the Orinoco delta is occupied by typical *crameri*, which probably arose in the Imataca region.

The northwestern races carry pattern elements present in the *crameri* forewing (form of discocellular spots), the *ludovica* forewing (proximal yellow band), and the *satevis* hindwing (absence of the median bar), and seem to fit satisfactorily into the species also, though reproductive compatibility has not been tested. The more northerly *idae* (Fig. 45) forms a close mimetic association with *Helioconius ismenius boulleti* Neustetter and *H. hecale melicerta* Bates in Panamá and Colombia, while the west Ecuadorian race *vespertina* Fox has a narrower black hindwing border like the sympatric *H. ismenius metaphorus* Weymer and the rare and recently discovered *H. hecale australis* (see Brown, 1976a).

There remains in this complex *Melinaea agricola* Hall, an unusual form known only from the type, captured in Tefé, Brazil (Fig. 46). It differs from the nominate subspecies, also known from Tefé, by the presence of a cubital spot, the reduction of yellow in the median band, and the complete series of yellow postmedian spots forming a near-continuous band, on the forewing; there is orange in the submarginal part of cell Cu₂, and between the median and distal bands of the hindwing, and a trace of a yellow anal spot on the forewing.

A rather similar and equally puzzling specimen (Fig. 47) was captured recently by Paulo César Elias in Baixo Guandú, Espírito Santo, near the east coast of Brazil. This specimen, which will be fully discussed in a general paper on Ithomiinae hybrids now in preparation, is clearly an interspecific hybrid between *M.e.ethra* and *M.ludovica paraiva*. It seems probable that the unique type of *agricola*, representing a pattern never again collected, is also an interspecific hybrid. One of the parents would be *M.ludovica ludovica*, while the other is probably the only closely related sympatric species, *M.mneme mauensis*; the pattern of *agricola* suggests exactly this mixture.

In Rio de Janeiro, *M.ludovica paraiva* oviposits on *Markea viridiflora*, a Solanaceous tree; the mature larva has not been observed yet, however.

(5) *Melinaea marsaeus* (Hewitson) (including *M.egesta* Godman and Salvin (sensu Fox, part), *M.maenius* (Hewitson) (sensu Fox, part), and *M.mothone* (Hewitson)).

The intergrading specimens of *Melinaea* from the Amazon Basin in the collections of the British Museum (Natural History) and the Museu Nacional (Rio de Janeiro) suggest that only two rather than three species are present in Fox's *marsaeus-egesta-maenius* complex, for which he himself offered a supplementary revision (1965). No more than two entities in this complex (discounting obvious intergrades) are found in any given area, and intermediate specimens link most of these with corresponding pairs in adjacent regions. The species *marsaeus*, whose nominate subspecies occurs near Tefé with the much darker nominate subspecies of *maenius*, can often be separated from the latter species by the more hooked (less squared) comma-mark, the tendency of the forewing discocellular spots to fuse into a broad bar, and the different (often more proximal) position of the last distal undulation in the forewing postmedian fascia, but all of these characters are variable within and between populations. *Marsaeus* appears to include the following additional subspecies:

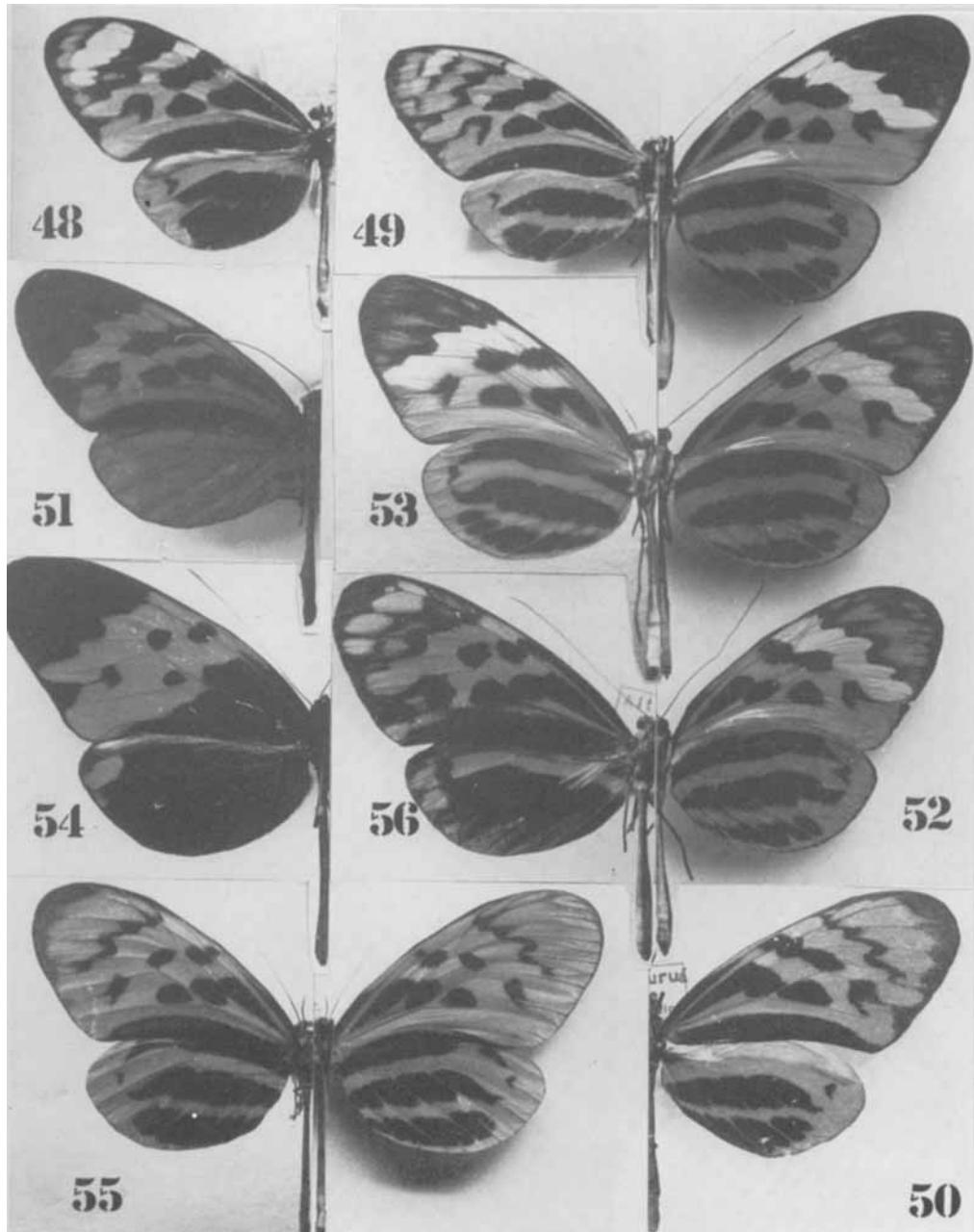
m.rileyi Fox (mostly western Brazil and northeastern Peru, Loreto refuge; transitions to *m.marsaeus* and the following two subspecies are well known (Fig. 48), including 'acreana' d'Almeida (Fig. 49); 'manga' Haensch represents a transition to *m.marsaeus*);

m.macaria Godman and Salvin (mostly southern Colombia, Putumayo refuge; many specimens farther east show influence of *rileyi* genes);

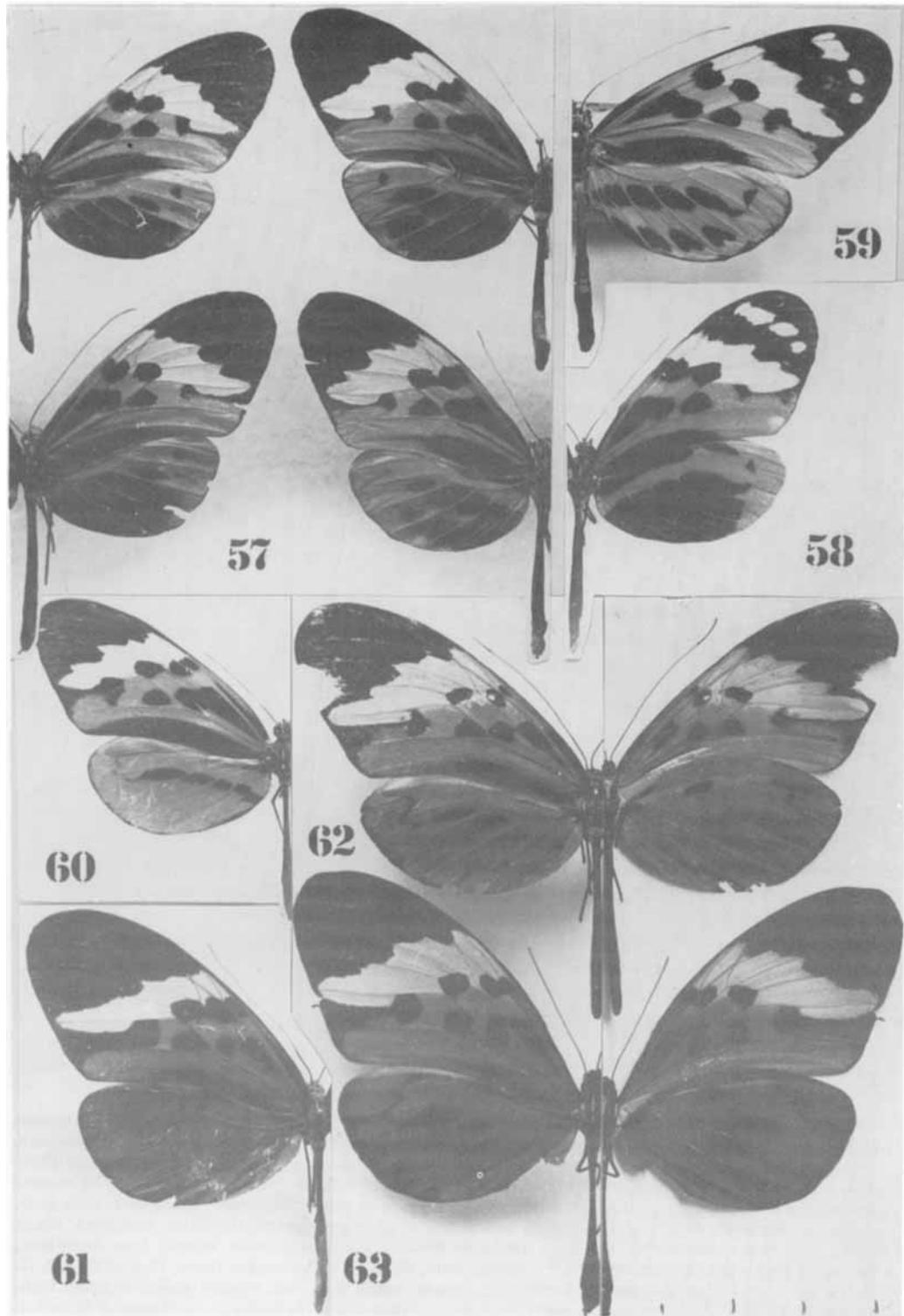
m.phasiana Butler (Fig. 50) (central Peru to southwestern Brazil, Ucayali refuge; many transitions to all three adjacent subspecies are known from western Acre);

m.clara Rosenberg and Talbot (Fig. 51) (a typical mimetic form of southern Peru and southeastern Acre, probably derived in the Inambari refuge); and

m.pothete d'Almeida (a variable subspecies from Rondônia whose populations often include individuals tending towards *phasiana*



FIGS. 48–56. *Melinaea marsaeus*. All life size, black, yellow, and/or orange. (48) *M.m. (marsaeus* (Hewitson) *X rileyi* Fox), male, dorsal, Benjamin Constant, Amazonas (MN-Rio). (49) *M.m. (marsaeus X rileyi X phasiana* Butler) (paratype of *M.acreana* d'Almeida), male, dorsal, Alto Rio Juruá, Acre (MN-Rio, no. 13/775). (50) *M.m.phasiana*, male, dorsal, Alto Rio Juruá, Acre (MN-Rio). (51) *M.m.clara* Rosenberg & Talbot, male, dorsal, Xapuri, Acre, Brazil (DZ-Paraná, d'Almeida collection). (52) *M.m. pothete* d'Almeida, three males including transitions to *phasiana*, ventral, Riozinho, Rondônia, Brazil (KB). (53) *M.m.pothete* with markings similar to those of *ethra* races, male, ventral, Jaru, Rondônia, 28.vii.75 (KB). (54) *M.m.mothone* (Hewitson), male, dorsal, Chanchamayo, Junin, Peru (KB, L. & G. Harris leg.). (55) *M.m. (phasiana X mothone?)*, female, dorsal (left) and ventral (right), Shapaja, Peru, 12.xii.75 (KB). (56) *M. (marsaeus rileyi X mneme or ethra cydon?)* (holotype of *M.mayi* d'Almeida), male, dorsal, Alto Rio Juruá, Acre (MN-Rio, no. 13/768).



(Fig. 52), as mentioned in the original description (d'Almeida, 1945), and even specimens with *ethra*-like markings (Fig. 53).

The melanic race *mothone* (Fig. 54) is apparently nowhere microsympatric with *marsaeus* subspecies, and may be regarded (along with its northern differentiate *messenina* Felder & Felder) as a premontane isolate of this species. Transitional specimens have been reported by Haensch (1903) and illustrated by Fox (1960: Fig. 54). An apparent *phasiana*/*mothone* transition (Fig. 55) was caught by the author in December 1975 near Shapaja, 20 km SE of Tarapoto, Peru, where the parent populations are known to meet (Fox, 1960).

Melinaea mayi d'Almeida, a very strange and unique specimen from the Alto Juruá (Fig. 56), is very probably an interspecific hybrid between *marsaeus* and *mneme* or *ethra cydon*; its very aberrant colour-pattern could be approximated, however, by a rather selective mixture of elements occurring irregularly in *marsaeus rileyi*, *phasiana*, *clara* and *macaria*. It surely is not a normal *ethra* race, as placed by Fox (note the discocellular spots), nor can its relationships be analysed simply.

(6) *Melinaea maenius* (Hewitson) (including *M.egesta* (sensu Fox, part), *M.isocomma* Forbes, and *M.mediatrix* Weymer).

The elements of *M.maenius* fit together somewhat less comfortably than those of *marsaeus*, as fewer transitions are known and large variations in pattern are evident. However, a long series in the author's hands from Limoncocha in eastern Ecuador (Fig. 57) shows a part of the expected intergradation between typical and resident *cocana* (whose type locality is very nearby) and occasional immigrant *flavosignata* Staudinger (see below) and *hicetas* Godman & Salvin. A further intergrade from southern Colombia, closer to *flavosignata*, is illustrated in Fig. 58 (mislabelled by

Brown & Benson, 1974, as *M.marsaeus macaria*, with which it flies and which it very strongly resembles).

Fox (1960: 149) mentions a characteristic, vestigial and unringed yellow anal spot present on the forewing of *m.egesta*. This spot is unquestionably present in the holotype of *flavosignata* Staudinger (Fig. 59), selected by Fox but later placed by him in *M.menophilus*; this name must thereby take precedence over *egesta* for the yellow-striped subspecies of *maenius* with the broken hindwing bands.

Furthermore, the recently separated *mediatrix* Weymer, resident in the Guianas and northern Brazil (see above, and Fig. 35), shows many pattern elements in common with *maenius* subspecies, including that by which it is separated from sympatric *mneme* (the broad, fully orange anal end of the supramedian orange stripe on the ventral hindwing). Tentatively, *mediatrix* is regarded as a northeastern isolate of the widespread species *maenius*, differing from all other subspecies by the retention of a strong yellow spot in the anal angle of the forewing (indicated above to be variable in *mnemias*, *ethra* and *ludovica* subspecies as well). The extensive range of *maenius* in eastern South America has recently been confirmed by the capture of *m.maenius*-like specimens in south-central Pará, east of the middle Rio Xingú (reported by David Gifford, Brasília).

The southern race *juruensis* d'Almeida (Fig. 60) seems to fit here also.

The melanic pair *isocomma* (Colombia) and *simulator* Fox (Ecuador and Peru) probably belong with *maenius*, just as their mimics *messenina* and *mothone* seem to be close to *marsaeus*. d'Almeida (1951) pointed out the great resemblance between *isocomma* and dark *m.maenius*, strengthening the impression of conspecificity.

FIGS. 57–63. *Melinaea maenius* and *M.menophilus*. All life size, black, yellow, and orange to orange-brown. (57) *M.maenius cocana* Haensch, and varieties, four males, dorsal, Limoncocha, east Ecuador, 31.i.71 (KB). (58) *M.maenius* (*cocana* × *flavosignata*), female, dorsal, Vista Hermosa, La Macarena, Meta, Colombia, 25.i.72 (KB). (59) *M.maenius flavosignata* Staudinger (= *egesta auctorum*), holotype male, dorsal, Jurimaguas, Peru (ZM-Berlin). (60) *M.maenius juruaensis* d'Almeida, male, dorsal, Riozinho, Rondônia (KB). (61) *M.menophilus zaneka* Butler, female, dorsal, Km 25 of the Puyo–Napo road, east Ecuador, 10.xii.71 (KB). (62) *M.menophilus ernestoi* nov., holotype male, dorsal (left) and ventral (right), 40 km above Florencia, Caquetá, Colombia, 22.iii.67 (MN-Rio, E. W. Schmidt-Mumm leg.). (63) *M.menophilus ernestoi*, paratype female, dorsal (left) and ventral (right), 40 km above Florencia, 22.iii.67 (KB, E. W. Schmidt-Mumm leg.).

(7) *Melinaea menophilus* (Hewitson).

Fox's analysis of this species requires little modification. It is worthy of note that typical *m. menophilus* occurs southeast of as well as northwest of populations of *m. orestes* Salvin, and that these two subspecies may be found in mixed populations over much of central Peru and southwestern Brazil, as far as Rondônia. Colombian populations of *m. menophilus* have wider yellow postmedian bands on the forewing than southern representatives.

The unusual race *zaneka* Butler (Fig. 61) is known through eastern Ecuador to northern Peru; at its eastern (and lower) limits it may meet *menophilus*, with which intergradation is suspected in such forms as 'maculosa' Haensch and 'discurrentis' Haensch. *Menophilus* and *zaneka* differ in important details of size, colour-pattern (including the comma-mark and the postmedian band on the forewing), and behaviour, and probably represent the same sort of lowland/premontane pair as *marsaeus/mothone* and *maenius/isocomma*; like these, they are regarded as conspecific for the time being.

A new subspecies, close to *m. zaneka*, can be found at moderate elevations in southern Colombia, above Florencia:

Melinaea menophilus ernestoi subsp.n.

Male (Fig. 62)

FW 46 mm. Very similar to *M.m.zaneka*, with, however, a wider yellow postmedian band on the forewing, and appreciable black markings on the hindwing, heavier apically.

Female (Fig. 63)

FW 50 mm. Similar to male, without scent-patch on hindwing.

Holotype ♂, COLOMBIA: Caqueta, 40 km above Florencia, 1000 m ($1^{\circ} 42' N$, $75^{\circ} 38' W$), 22.iii.67 (E. W. Schmidt-Mumm), donated to the Museu Nacional, Rio de Janeiro.

Paratypes: two ♂♂ (one strongly transitional to *m. menophilus*) and one ♀, same data as holotype, in the collection of E. W. Schmidt-Mumm, Bogotá; one ♀, same data, in the collection of the author.

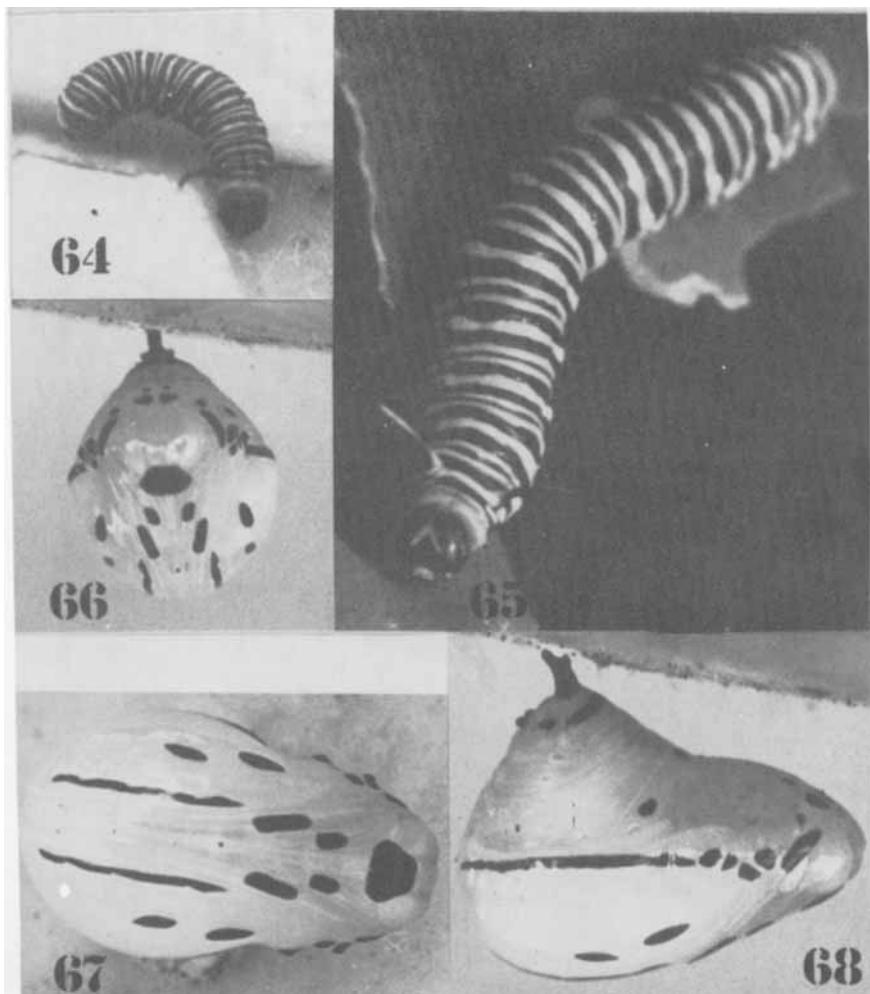
A female from somewhat farther southwest, in Huila (road from Pitalito to Mocoa,

1650 m ($1^{\circ} 38' N$, $76^{\circ} 11' W$)), is close to *m. zaneka*, suggesting that *ernestoi* may have a highly restricted peripheral range to *zaneka* phenotypes. It may be possible that *ernestoi* only represents a transitional population between *zaneka* and the wide-yellow-banded Colombian *menophilus*, though the parent phenotypes are not represented in the type-series.

The subspecies is dedicated to its collector, Dr Ernesto W. Schmidt-Mumm of Bogotá, who has greatly helped the author in the understanding of the complex biogeography of Colombian Lepidoptera.

The larva of *M. menophilus* (Figs. 64 and 65), like those of *Tithorea* and *Aeria* (Guppy, 1904; Gilbert & Ehrlich, 1970; Brown, Lamas, Ebert & Dias Filho, in preparation), closely resembles a danaine caterpillar, departing dramatically from the 'usual' ithomiine larval form and pattern (Fox, 1967; Brown & d'Almeida, 1970). The foodplant (in Rondônia) is a still unidentified epiphyte, probably *Forsteronia* sp. (Apocynaceae: Echitoideae). Larvae of sympatric *M. maenius juruaensis* and *M. marsaeus pothete* were essentially identical and fed on the same plant. This larval type would seem to confirm Fox's placement of *Melinaea* as a primitive genus, near the Tithoreini. The pupa (Figs. 66–68) is unlike either Danainae or Ithomiinae models, but closer to the latter, being bowed more than 90° in the first abdominal segments like in species of more advanced ithomiine groups, and marked like the pupa of the primitive genus *Methona* which seems to be precursorial to these more evolved groups (Diricennini, Godyridini).

The coincidence of appearance and food-plant for larvae derived from distinct females identified as *M. menophilus*, *M. maenius* and *M. marsaeus*, strongly implies that the last word on the relationships among the various races of these three species has not yet been written. Series from southern Colombia (Fig. 58), eastern Ecuador (Fig. 57), and southwestern Brazil (Figs. 52, 53 and 60; d'Almeida, 1945: Plate II) suggest mutually contradictory associations of forms, which become even more difficult to interpret when Peruvian and Acre lots are examined. The present text can only be regarded as logical proposal, in accord



FIGS. 64–68. *Melinaea menophilus menophilus*. Jaru, Rondônia, early stages, black and yellow. (64) Third instar larva, 6 X. (65) Mature (fifth instar) larva, 3.5 X. (66) Pupa, dorsofrontal view, 5 X. (67) Pupa, ventral view, 5 X. (68) Pupa, lateral view, 5 X.

with the data now in hand, subject to revision when further biosystematic work becomes possible.

(8) Summary

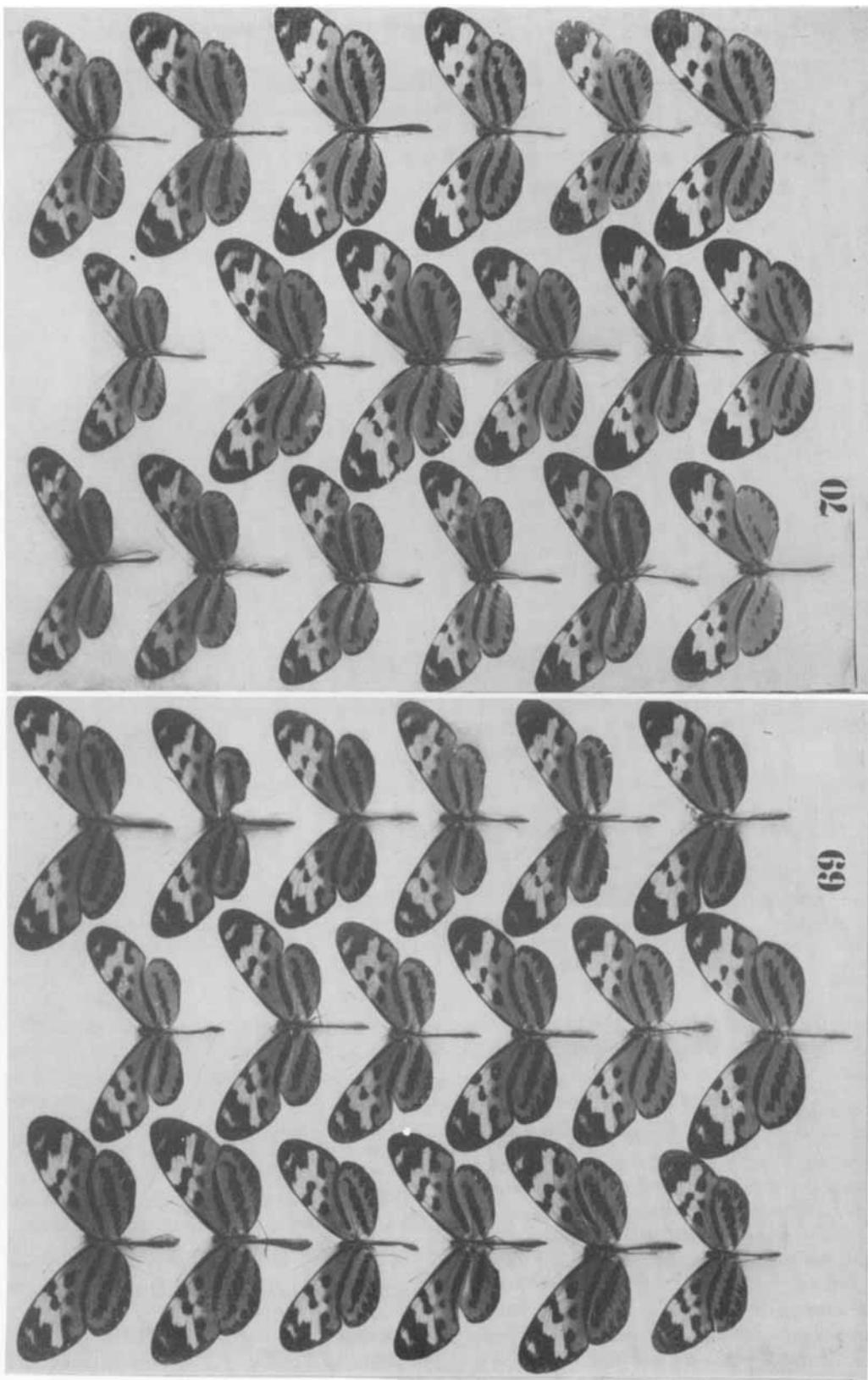
By the present analysis, the genus *Melinaea* is composed of seven species, some perhaps representing species-groups, redivisible when more biological information becomes available. Sixty-three well-differentiated geographic subspecies are recognized, and, in addition, there are three transitional forms of *M. mnasias*, each known from but a single specimen, which may merit subspecific status; also transitional forms of other species which may have

been improperly demoted to infrasubspecific status; and a number of predictable forms which are yet to be discovered. Although the analysis of speciation patterns may require revision, the fundamental patterns of sub- or semi-speciation seem now to be well enough established to permit an evaluation of the effects of Quaternary refuges on the genus, which are fully presented in the Appendix.

Differentiation of the species of *Mechanitis*

The monograph of Fox (1967) requires but one important change. This, however, involves

FIGS. 69 and 70. *Mechanitis polymnia*. Dorsal, 0.6 X, black, yellow and orange. (69) *M.p. (boliviensis Fox × polymnia (Linné))*, series from Boa Vista, Roraima, north Brazil (KB). (70) *M.p. (angustifascia Talbot × eurydice Haensch)*, series from Caranavi, La Paz, Bolivia, x.74 (KB).



the reshuffling and recombination of forms assigned by him to seven of his nine species, forming three very widespread species, one of which is highly polymorphic in most known populations.

(1) *Mechanitis polynnia* (Linné) (including *M. isthmia* Bates).

The most surprising discovery which has come to light in the re-examination of the genus *Mechanitis*, shared by a number of current workers in the group, is that subspecies assigned by Fox to the northern *M. isthmia* clearly intergrade with others assigned to *M. polynnia* in various areas around the periphery of the Amazon Basin. Thus, Fox (1967) named *isthmia bolivarensis* from southern Venezuela, noting that it strongly resembled *polynnia*. The differences between *bolivarensis* and neighbouring (Guyana) *p. polynnia* are appreciable, but become irrelevant when populations occurring in Roraima (extreme northern Brazil) are examined (Fig. 69). These include individuals approximating typical *bolivarensis* and others near typical *polynnia*, and intergrades showing every possible recombination of the different characters. The long type-series of *bolivarensis* in the BM(NH), re-examined in 1974, further confirms this intergradation; many strikingly *polynnia*-like individuals are included, possessing much less yellow on the hindwing than in Fox's illustration. A further obvious intergrade, closer to *bolivarensis*, is represented by Zikan's name 'apicenotata' (illustrated by d'Almeida, 1956: 3), from the upper Rio Negro; in fact, one of the paratypes of *bolivarensis* comes from slightly farther north, on the upper Rio Orinoco.

The intergradation of *polynnia angustifascia* Talbot with 'isthmia' *eurydice* Haensch can also be seen in the other corner of the Amazon Basin (Rondônia, Acre, and northern Bolivia). A long series taken by the author in Caranavi, La Paz, Bolivia (600 m) in October 1974 shows this integration reasonably well (Fig. 70). Further intergradation is evident in the Acre form 'travassosi' d'Almeida (1951: 11, Plate 2, Figs. 1 and 2). However, *angustifascia* itself may be merely a series of transitional populations between southern *p. casabranca* Haensch and Amazonian *p. polynnia*, though the hindwing markings are characteristic of only these southwestern populations.

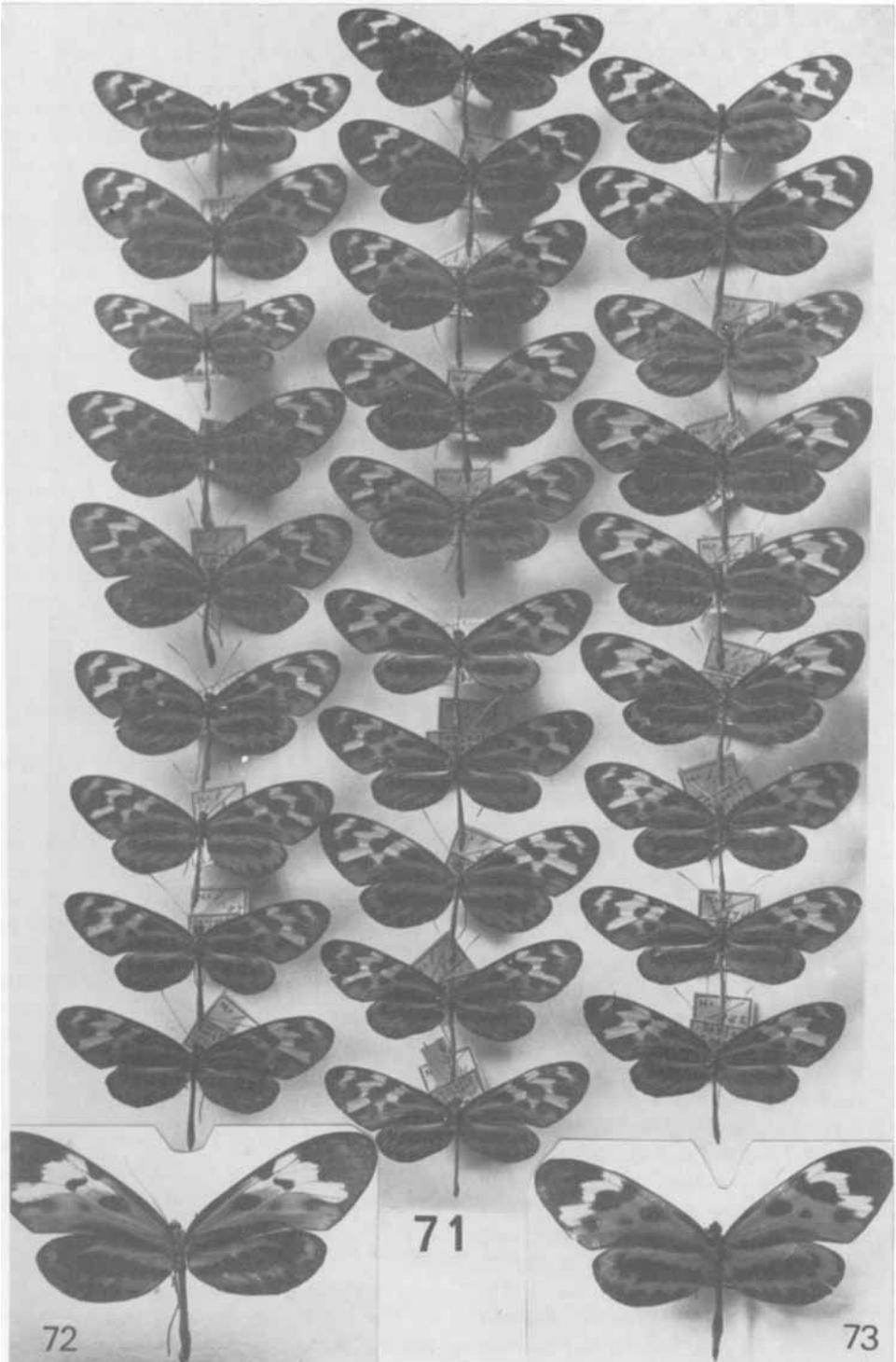
To the north, extensive intergrading series have been captured between *p. polynnia*, not common west of Manaus, and the darker northeastern populations (possibly meriting a name) of the Peruvian *p. dorissides* Staudinger (*doryssides auctorum*), found as far east as Tefé (Fig. 71).

The races associated by Fox with *isthmia* and *polynnia*, often the commonest ithomiines wherever they occur and usually incredibly abundant in some seasons, are essentially allopatric except for the north coastal South American and Central American *doryssus*, *labotas* and *solaria* (placed by Fox with *polynnia*), which overlap with former *isthmia* subspecies (*lycidice* Bates, *isthmia*, *veritabilis* Butler, *kayei* Fox, *caucaensis* Haensch, *chimborazona* Bates, and possibly *wernerii* Hering from the Chocó, which however seems to represent a series of intergrading populations between *caucaensis* and *chimborazona*). Fortunately, *doryssus* has now been shown to intergrade cleanly with *M. lysimnia macrinus* wherever the two occur together (see below), and the three northwestern races of Fox's 'polynnia' are thus transferred to *M. lysimnia*.

Northwestern populations of *p. polynnia* often show a dark hindwing (Fig. 72), and may eventually merit a name; southern Amazon populations have already been designated *mauenensis* by Forbes (Fig. 73), and are often appreciably different phenotypically from usual Amazon forms. However, the great dispersal ability of *M. polynnia* probably has erased much of its past or potential differentiation in continuous tropical forests, retaining races only where a combination of heavy selective pressures and well-defined physiogeographic barriers make this possible, against the pressures of gene-flow and autoselective stabilization (see Brown, 1976a: 210; *Mechanitis polynnia*, like the heliconians mentioned there, is a mass breeder which shows deficient mimetic association in many parts of its range).

(2) *Mechanitis limnaea* Forbes.

This little known and unusual 'splinter species' was treated satisfactorily by Fox. It has been captured in numbers recently in Amapá (Ebert, 1965: 5–6) and near Óbidos. It is sympatric with *M. polynnia* and *M. mazaeus*, but not *M. lysimnia* or *M. menapis*,



FIGS. 71-73. *Mechanitis polymnia*. Dorsal, black, yellow, and orange to red-brown. (71) *M.p. (polymnia) var. dorissides* Staudinger), series from Benjamin Constant, Amazonas, western Brazil (MN-Rio), 0.6 X. (72) *M.p. ca. polymnia*, female, dorsal, St Laurent, French Guyane, 25.viii.70 (W. W. Benson, Campinas), 0.8 X. (73) *M.p. ca. mauensis* Forbes, male, dorsal, Maués, Amazonas (DZ-Paraná, d'Almeida collection), 0.8 X.

but it does not have any obvious relationship to these last two species. It seems best to retain it as a good species though it may eventually be shown to be an Amazonian isolate derived from *M.lysimnia*.

(3) *Mechanitis lysimnia* (Fabricius) (including *M.polymnia* (*sensu* Fox, part)).

Fox's discussion of this species (1967) requires a few additional comments and one important addition.

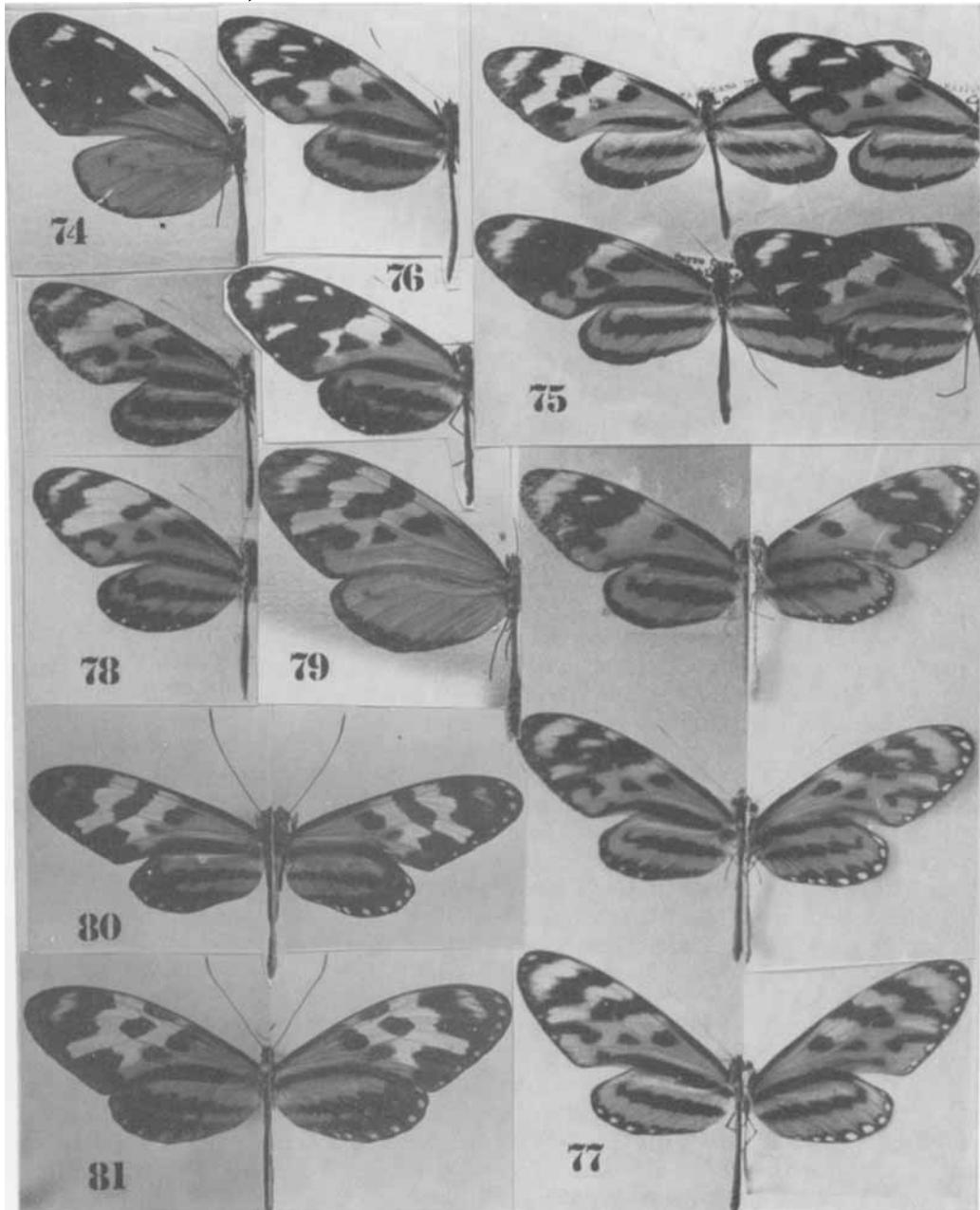
The supposed subspecies 'connectens' Talbot was well named. It is, in fact, but a series of intergrading populations occupying a narrow contact zone between *M.l.lysimnia* (which occurs in pure populations as far west as eastern Mato Grosso, near Alto Garças, and as a minor element in 'connectens' populations as far west as extreme western Mato Grosso) and *M.l.elisa* (Guerin-Méneville) (which is found in nearly pure populations 500 km west of Alto Garças, in the Rio Cabaçal area, and occurs occasionally all the way east to the Serra do Mar in southeastern Brazil). The area in central Mato Grosso contains no recognizable forest refuge, and indeed is mostly scrub and field interspersed with occasional gallery forest and headwater woods where 'connectens' may be found. The polymorphism of 'connectens' populations is evident in the type-series and has been illustrated (Brown, 1970). The topotypic series at hand includes both *M.l.lysimnia* and *M.l.elisa*. The name 'connectens' should thus not continue to be applied in the sense of a geographic subspecies or well-defined race.

As d'Almeida (1951) noted, *M.l.lysimnia* and *M.l.nesaea* Hübner are widely sympatric in eastern Brazil, without extensive intergradation. Both have been recently captured in mixed populations, as far north as Dois Irmãos (Pernambuco) and as far south as Baixo Guandu (Espírito Santo); these points are separated by almost 1200 km of near-continuous humid forest, and in the intermediate localities both phenotypes may be equally common. In this overlap region, the only candidates for intermediate phenotypes are 'albescens' Haensch (resembling *lysimnia* but with additional white postmedian spots on the forewing, where *nesaea* bears yellow spots), which occurs regularly as far south as the limits of *l.lysimnia* in Argentina, and

'sulphurescens' Haensch (resembling *nesaea* but lacking the yellow postmedian spots, or alternatively like *lysimnia* with a yellow subapical spot), which occurs as far north as does *nesaea* in Belém, Pará. In fact, these two represent the expected transitions (presuming a two-gene difference), but they are so infrequent in the overlap zone that it must be assumed that either the white/yellow and postmedian spots present/absent genes are closely linked, producing a 'switch' from one subspecies to the other, or else there are behavioural and/or chromosomal barriers to easy fertilization between *lysimnia* and *nesaea*. The wide overlap is not difficult to accept, as the differences between the two subspecies are not large, and mobility is great in the species; some degree of autoselective stabilization may also exist, as *lysimnia* larvae occur in groups, though not as large as those of *polymnia*. The gene spread to the confines of the species' range is also not hard to acknowledge, since southern Brazil populations of *lysimnia* occasionally include *elisa*-like individuals (whose pure populations are over 1200 km to the west), presumably from similar gene spread. Thus, while *nesaea* and *lysimnia* are accepted as conspecific their overlapping populations seem to merit more intensive biological study.

M.lysimnia acreana d'Almeida, while occurring sparsely in many populations throughout Peru, is essentially monomorphic from the Madre de Dios region as far east as central Rondônia (Fig. 74); in this area it is mimetic of many other endemic butterfly species. It probably can be regarded as a geographic race associated with the Inambari refuge. Further differentiation of *l.elisa* northward into extreme southern Colombia is easily seen. For example, *ocona* Drury, with a more lightly marked forewing, predominates in the Chanchamayo area of central Peru, and is much less frequent than typical *elisa* in Bolivia or other parts of Peru and Ecuador. The discrete patterns are so mixed in most known populations, however, that no simple association of any of the available names other than *ocona* with any past refuge can be effected, with the material presently in hand.

The northwestern subspecies *macrinus* Hewitson, whose conspecificity with *lysimnia* cannot yet be regarded as certain (some



FIGS. 74-81. *Mechanitis lysimnia* and *M. menapis*, life size, black, yellow and orange. (74) *M.I.acreana* d'Almeida, female, dorsal, Jaru, Rondônia, 5.viii.75 (KB). (75) *M.I.(doryssus) Bates X macrinus* Hewitson, four specimens showing transition, dorsal, Cerro Campana, Panamá (G. B. Small). (76) *M.I.(doryssus X macrinus)*, two transitions, dorsal, Rio Dagua (upper) and Cananche (lower), Colombia (BM-London). (77) *M.I.(doryssus X macrinus)*, transitional series, dorsal (left) and ventral (right), El Tucuco, Sierra Perijá, Zulia, Venezuela, iii.68 (upper) and 21-27.v.71 (centre and lower) (FA-Maracay). (78) *M.I.solaria* Fox, transitional to *doryssus* (upper) and typical (lower), male and female, dorsal, Caripe, Monagas, Venezuela, 12.ix.65 and 15.ix.65 (FA-Maracay). (79) *M.I.labotas* Distant, female, dorsal, Rincon, Osa Peninsula, Costa Rica, 26.iv.68 (WB-Campinas). (80) *M.m. dariensis* nov., holotype male, base of Cerro Pirre near El Real, Darién, Panamá, 16.iv.76 (American Museum of Natural History, New York, G. B. Small leg.). (81) *M.m. dariensis*, paratype female, base of Cerro Pirre, 15.iv.76 (AMNH-New York, K. Cook leg.).

important behavioural differences can be noted), produces at all its distribution limits unusual variants apparently intermediate to some other race with a 'normal' postmedian yellow band and well-developed cubital spots. Gordon B. Small of Panamá has suggested that these may be hybrids with *doryssus*, which would thus represent a very atypical subspecies of *lysimnia*; this suggestion is supported by the gross allopatry of *doryssus* and *macrinus* in the northwestern Neotropics. In fact, as mentioned above, the recognition that Central American *isthmia* races are conspecific with Amazonian *polymnia* required transferral of the Mexican to north Colombian and north Venezuelan *doryssus* Bates, the Chiriquí *labotas* Distant, and the Sucre/Trinidad *solaria* Forbes out of the subspecies of *polymnia*, since they are everywhere sympatric with former 'isthmia'-related races. In Panamá, *doryssus* occurs as far east as Veraguas province and Cerro Campana, where it encounters *macrinus* and produces abundant intergrading specimens (Fig. 75), which can also be found as far west as Costa Rica. Only *macrinus* is found in Darién and the central valleys of Colombia, but *doryssus* is known in the Cali area and on the north coast of Colombia, producing similar intergrades where it meets *macrinus* (Fig. 76). In all of Venezuela, a form very near *doryssus* is found, but *macrinus* occasionally occurs in the Sierra Perijá on the northwest frontier (facing the Santa Marta range in Colombia). That the two hybridize is indicated by the number of intermediate specimens which can be captured in this region (Fig. 77). Thus, *doryssus* and *solaria* (which intergrade in eastern Venezuela; Fig. 78) are here placed as subspecies of *lysimnia*; at least, they are conspecific with *macrinus*.

The clean-hindwing race *labotas* (Fig. 79), predominant in the Chiriquí refuge area (along with frequent *doryssus* and accidental *macrinus*) and mimetic of many sympatric species such as *Melinaea ethra scylax* (Fig. 14), *Heliconius ismenius clarescens* Butler and *Ithomia celemia plaginota* Butler & Druce, has spread out genetically to produce similar forms today in populations of the surrounding parts of Central America, where *doryssus* usually predominates. *Labotas*-like phenotypes may also be produced (at least in females) in other areas where *macrinus* genes contaminate

doryssus populations; this would explain their appearance in Venezuela, Colombia, and central Panamá.

(4) *Mechanitis menapis* Hewitson.

The discussion of this northwestern species by Fox (1967) is completely satisfactory. Only the subspecies *m. menapis* in central Colombia presents a problem in its polymorphism, produced in part by infusion of genes from neighbouring *saturata* Godman, *caribensis* Fox and *occasiva* Fox. The last two subspecies intergrade in the upper Rio Anchicayá west of Cali, Colombia; it is possible that the Chocó populations merit a subspecific name separate from *caribensis*, with which they are not identical. Intermediates to the southwesternmost *mantineus* Hewitson have not yet been seen. Gordon Small has also informed me that Central American *m. saturata* show very distinct behaviour and habitat preferences from those of *menapis* in general. Whether this differentiation will also be reflected in reproductive isolation of *saturata* from the rest of *menapis*, can only be ascertained when the relevant biological data are in hand; preferably, crossing should be performed in Panamá with a new subspecies of *menapis*, discovered by Mr Small in the eastern part of the country and described here.

Mechanitis menapis dariensis subsp.n.

Male (Fig. 80)

FW 30 mm. Partakes of pattern characteristics of *m. menapis* and *m. caribensis*, but the over-all appearance is unique in the species and in the genus. Forewing base orange out to a large black midcell spot and small black spot in the inner corner of space Cul-Cu2, then yellow (enclosing a heavy bar-shaped comma-mark filling the marginal three-fifths of space Cul-Cu2 and fused to the black inner angle, and a heavy, barely joined endcell bar) to a strongly sinuate outer border identical with that in other *menapis* subspecies; apex black with a small, diffuse yellow spot. Hindwing orange with a narrow, undulate median band, uniting with the broad black border near vein M3 to produce a very extensive black apical area. Ventrally similar, with a yellow humeral spot on the hindwing, small

single white intervenal spots on both wings, and the subapical yellow streak on the forewing better developed. Patagia orange, abdomen yellow ventrally.

Female (Fig. 81)

Similar to male, but forewing more rounded, endcell black bar broken into two separated spots, and inner angle of forewing may have an orange spot; lacking silvery hair-pencil on hindwing costa.

Holotype ♂, PANAMÁ: Darién, near El Real, base of Cerro Pirre ($8^{\circ} 04' N$, $77^{\circ} 44' W$), near sea level, 16.iv.76 (G. Small), donated to the American Museum of Natural History, New York.

Paratypes: One ♀, same locality as holotype, 15.iv.76 (Kerry Cook), donated to the AMNH; one ♀, Darién, Rio Tuquesa ($8^{\circ} 27' N$, $77^{\circ} 43' W$), 100 m, 11.vii.75, in the collection of G. B. Small, Balboa, Canal Zone; one ♀, Panamá province, Rio Bayano at mouth of Rio Majé, near high bridge of Pan-American Highway ($9^{\circ} 08' N$, $78^{\circ} 46' W$), 20.x.74, in the G. B. Small collection.

Mechanitis menapis seems in some ways very close to *M. mazaeus*, and the two are presently sympatric only in extreme northeastern Venezuela (*menapis caribensis/mazaeus beebei*); they probably differentiated from a single widespread stock, but do not seem to be conspecific today.

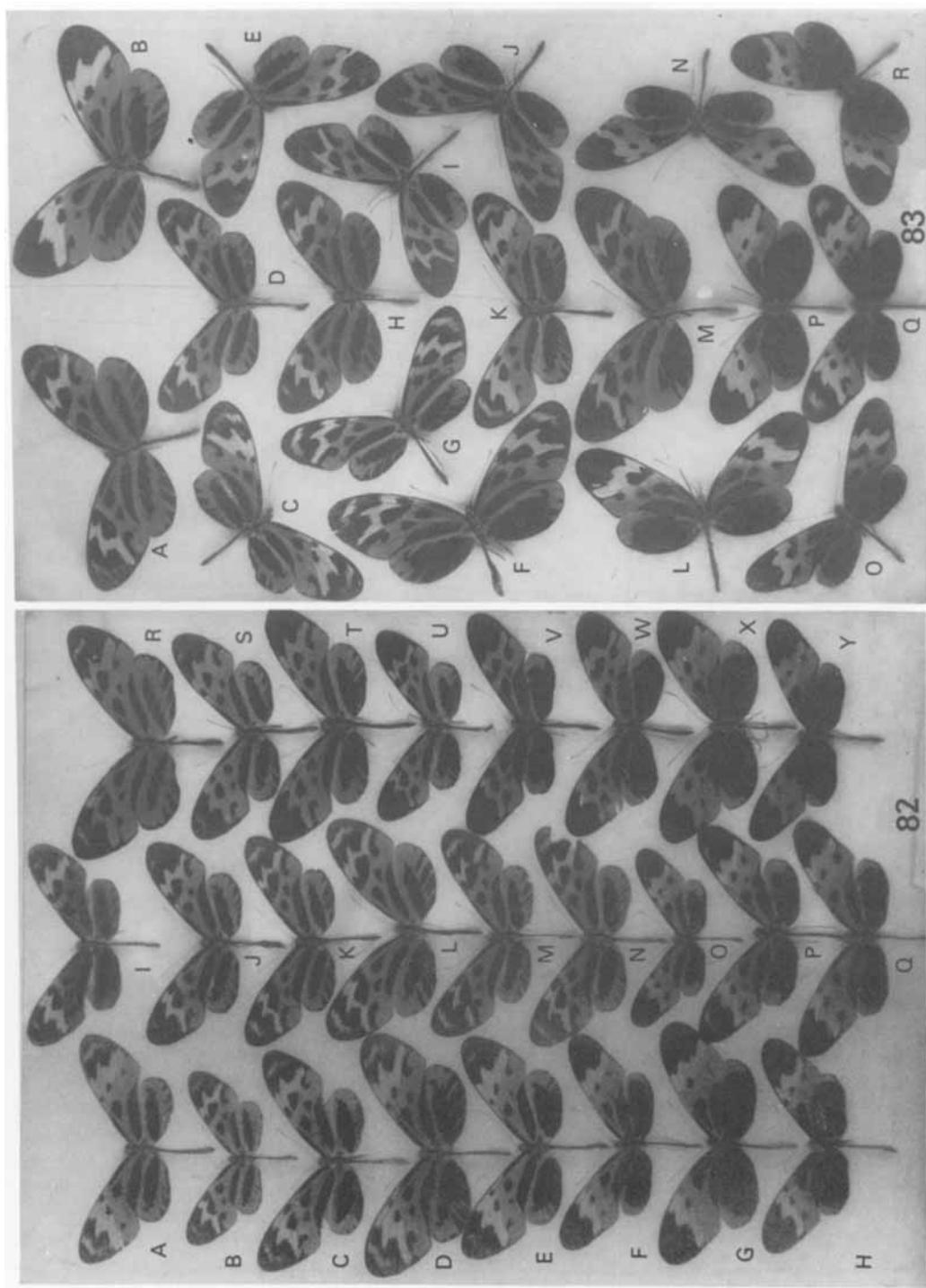
(5) *Mechanitis mazaeus* Hewitson (including *M. lanei* Fox, *M. messenoides* Felder & Felder, *M. egaensis* Bates, and *M. polymnia* (sensu Fox, part)).

The confusion surrounding this polymorphic species was well discussed, if not resolved, by d'Almeida (1951), who divided it into six species, and Fox (1967), who separated it into five; Forbes (1948) seemed to have a more mature grasp of the complex unity of the species. Both of the former authors based their analyses on the extensive sympatry of related entities at a number of given collecting points. Said Fox, 'only by separating them (*mazaeus*, *egaensis*, and *messenoides*) can the geographic confusion... be resolved.' Similarly, after examining abundant material in the Museu Nacional (Rio de Janeiro), d'Almeida remarked (in translation) 'as can be

verified by the above list, all or almost all of the supposed subspecies of *Mechanitis mazaeus* fly together with the typical subspecies, *mazaeus mazaeus*, except for *elevatus* and *pannifera*'.

Having verified from field work and museum collections that *mazaeus*-related phenotypes occur in highly polymorphic populations from the middle Amazon up to the base of the Andes, without however finding any clear support for either d'Almeida's or Fox's separation of Forbes' *mazaeus* into several species, I resolved to try to discover a new basis for possible separation of these taxa into valid biological species. This came through the application of the refuge model, developed initially from analysis of the more cleanly differentiated Heliconiini and Ithomiinae. In several heliconian species analysed, it became apparent that races originally generated by mimetic pressure in isolated refuges had, because of appreciable mobility and the possibility of intersystem crossovers for mimetic association, spread out to appear together with other phenotypes in polymorphic populations. This was especially evident in ithomiine mimics such as *Eueides isabella* and *Heliconius hecale* and *numata* (Brown & Benson, 1974; Brown, 1976b); morphs of the last species had been placed in three different species by the principal recent reviser of *Heliconius* (Emsley, 1965) and in two species by myself (Brown & Mielke, 1972), based on the sympatry of these entities over large areas.

Once a reasonable map of the probable refugia had been drawn by analysis of the Heliconiini and the better-known and less polymorphic Ithomiinae (including *Melinaeae*), and once local polymorphic populations were accepted as possible in Müllerian mimics, it was an easy step to determine if any taxon in the *Mechanitis mazaeus* complex could not be clearly assigned to a well-defined refuge (through association with a principal mimetic complex apparently derived therein), or else obviously considered as a recombinant of such principal phenotypes. As indeed no such taxon could be found, and, more importantly, as no single refuge produced more than one principal and mimetic phenotype in the *mazaeus* complex (even in the cases where this refuge evidently produced a number of distinct mimicry rings), it seemed probable that



FIGS. 82 and 83. *Mechanitis mazaeus*. Dorsal, 0.6×, black, yellow, and/or orange to brown. (82) *M.m.(visenda* Butler \times *fallax* Butler \times *elevata* Riley \times *mazaeus* Hewitson \times *nigropictalis* Haensch \times *deceptor* Butler \times *mesenoides* Felder & Felder), dorsal, series from Limoncocha, east Ecuador, 29.i to 2.ii.71 (KB). (83) *M.m.(visenda* \times *fallax* \times *mazaeus* \times *mesenoides*), dorsal, series from Vista Hermosa, La Macarena, Meta, Colombia, 25-29.i.72 (KB).

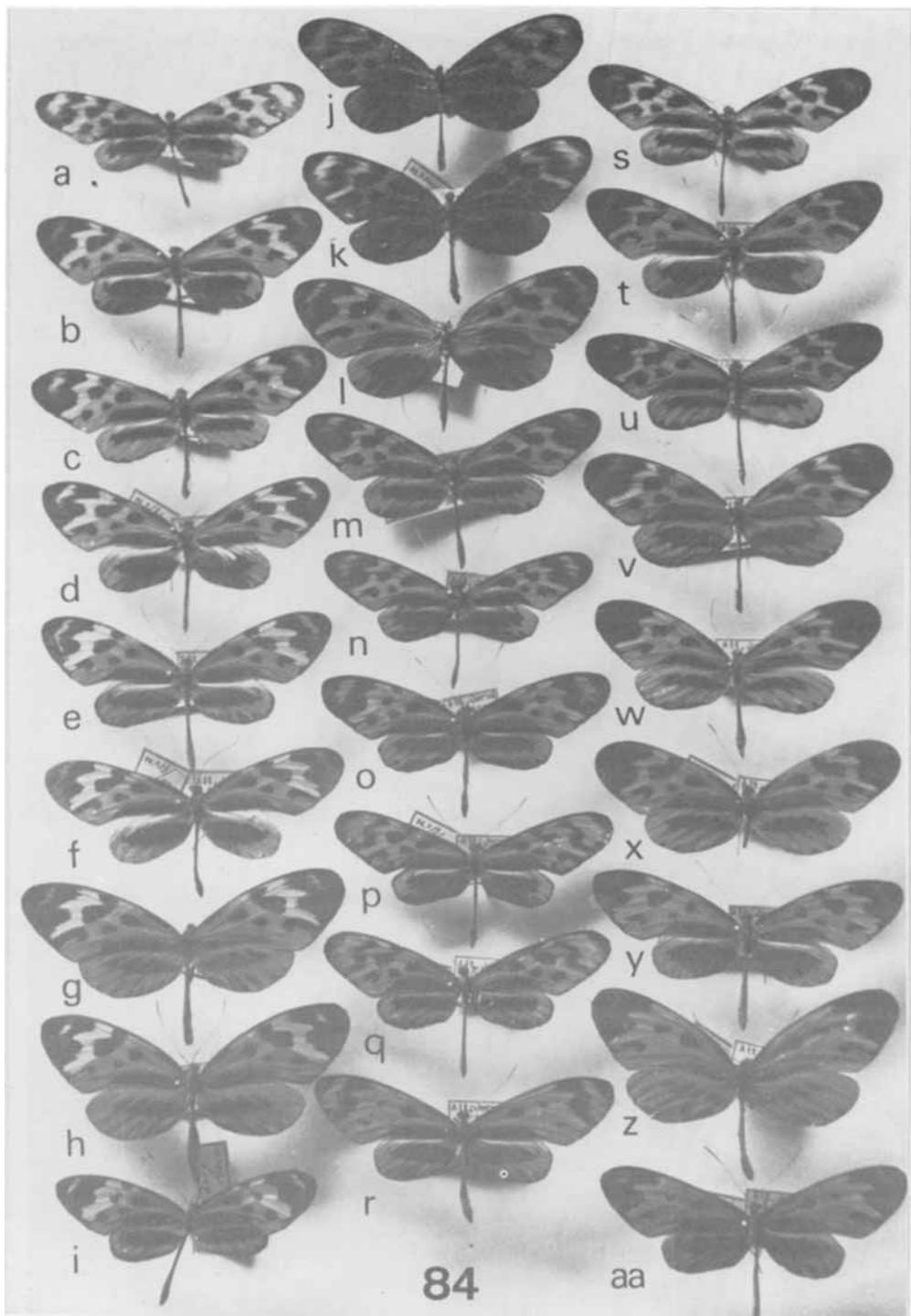


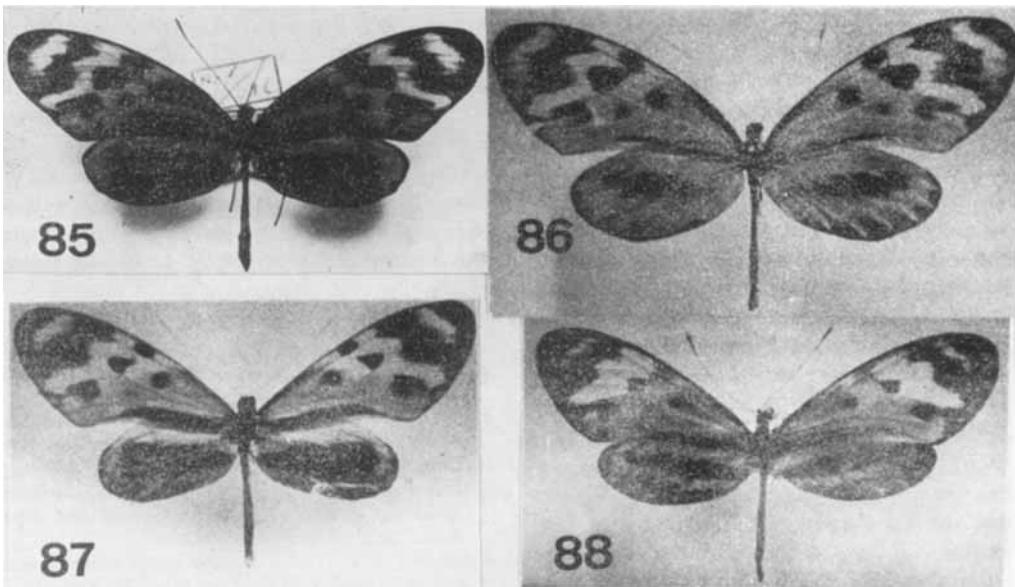
FIG. 84. *Mechanitis mazaeus* (*visenda* × *fallax* × *pothetoides* d'Almeida × *egaensis* Bates × *mazaeus* × *nigroapicalis* × *lucifera* Haensch), dorsal, series from Alto Rio Juruá, Acre, southwestern Brazil (MN-Rio), 0.6 X, black, yellow, and/or orange to brown.

all the taxa belonged to a single polytypic, polymorphic, and interbreeding species, *mazaeus*.

This conclusion was strongly supported by the complete and stepwise intergradations seen between phenotypes assigned by Fox to *mazaeus*, *egaensis* and *messenoides*, or by d'Almeida to *mazaeus*, *fallax* and *messenoides*, in populations occurring in low-elevation areas near the Andes of Ecuador (Fig. 82, Limoncocha) and Colombia (Fig. 83, La Macarena). Further series in the Museu Nacional (Rio de Janeiro) from the middle and upper Amazon (Fig. 84, Alto Rio Juruá) confirmed the complete mixing of characters between these taxa, and also showed intergradation to phenotypes regarded by d'Almeida as *pannifera*, *egaensis*, *foxi*, and 'dorissides' (not Staudinger). Those who would wish to pursue a study of this unusual polymorphic species can find in the Appendix a summary of the probable refugial origins of the better-defined mimetic morphs of *mazaeus*, and in the following paragraph a list of the known taxa in the Amazon/Orinoco area; the numbers and letters in parentheses refer to specimens illustrated in Figs. 82–84.

The named phenotypes of *mazaeus* include: *beebei* Forbes (Fig. 86); *bipuncta* Forbes (Fig. 88; associated with *mazaeus* by ventral HW pattern, though may be a race of *lysimnia* or, more likely, of *limnaea*); *pannifera* Butler (Fig. 87); *visenda* Butler (82AB, 83CD, 84CFI; occurs phenotypically in three isolated regions, in the northeast, south, and northwest of the species' range); *fallax* Butler (82E, 83IM, 84B); *mazaeus* (82RS, 84MNO) and its minor variety 'phasianita' Haensch (84PQ); *nigro-apicalis* Haensch (82TU, 83J, 84STUVW); *lucifera* Haensch (Fig. 85); 'williamsi' Fox (82CDM, 83A, 84E) = *visenda* (Napo form) × *mazaeus*; *pothetoides* d'Almeida (84GH); 'foxi' d'Almeida (84R) = *pothetoides* × *mazaeus*; *egaensis* (84K); 'obscura' Butler ≈ *egaensis*; *elevata* Riley (82IJN); 'contracta' Riley = *egaensis* × *elevata*; 'obumbrata' d'Almeida (82J) = *egaensis* × *mazaeus*; *messenoides* (82GH, 83NPR); *deceptus* Butler (82XY) ≈ 'simplex' Bryk; 'holmgreni' Bryk = *deceptus* × *ballucatus*; *ballucatus* Fox (82Q) which is also produced by *visenda* (Napo) × *deceptus*.

The recently named *lanei* Fox is sympatric with *M. polynnia* and *M. lysimnia* in the region



FIGS. 85–88. *Mechanitis mazaeus*, dorsal, 0.75 X, black, yellow and orange. (85) *M.m.lucifera*, female, Benjamin Constant, western Brazil (MN-Rio). (86) *M.m.beebei* Forbes, female, Caripito, Monagas, Venezuela (FA-Maracay). (87) *M.m.pannifera* Butler, male, road from El Dorado to Santa Elena, Bolívar, Venezuela (FA-Maracay). (88) *M.m.bipuncta*, paratype (?) male, Surukum Basin, alto Caroni, Venezuela (FA-Maracay).

of Belém, Pará and southeastward. Although it is quite rare, a number of recent specimens are known. As *mazaeus* has not been captured in the same region, it seems very likely that the very *elevata*-like *lanei* should be the easternmost (Belém-refuge-derived) race of this highly variable species.

(6) Summary

Thus, by the present analysis, the number of species in *Mechanitis* is reduced from nine to five, with a total of fifty-two recognized differentiated subspecies apparently associated with past refuges (Appendix). While the joining of these forms into polytypic species may yet be modified through further field and insectary experiments, the basic patterns of differentiation seem to be sufficiently clear at this time to permit an evaluation of the evolutionary forces at work in the genus during past climatic cycles; this is indicated in the Appendix.

Acknowledgments

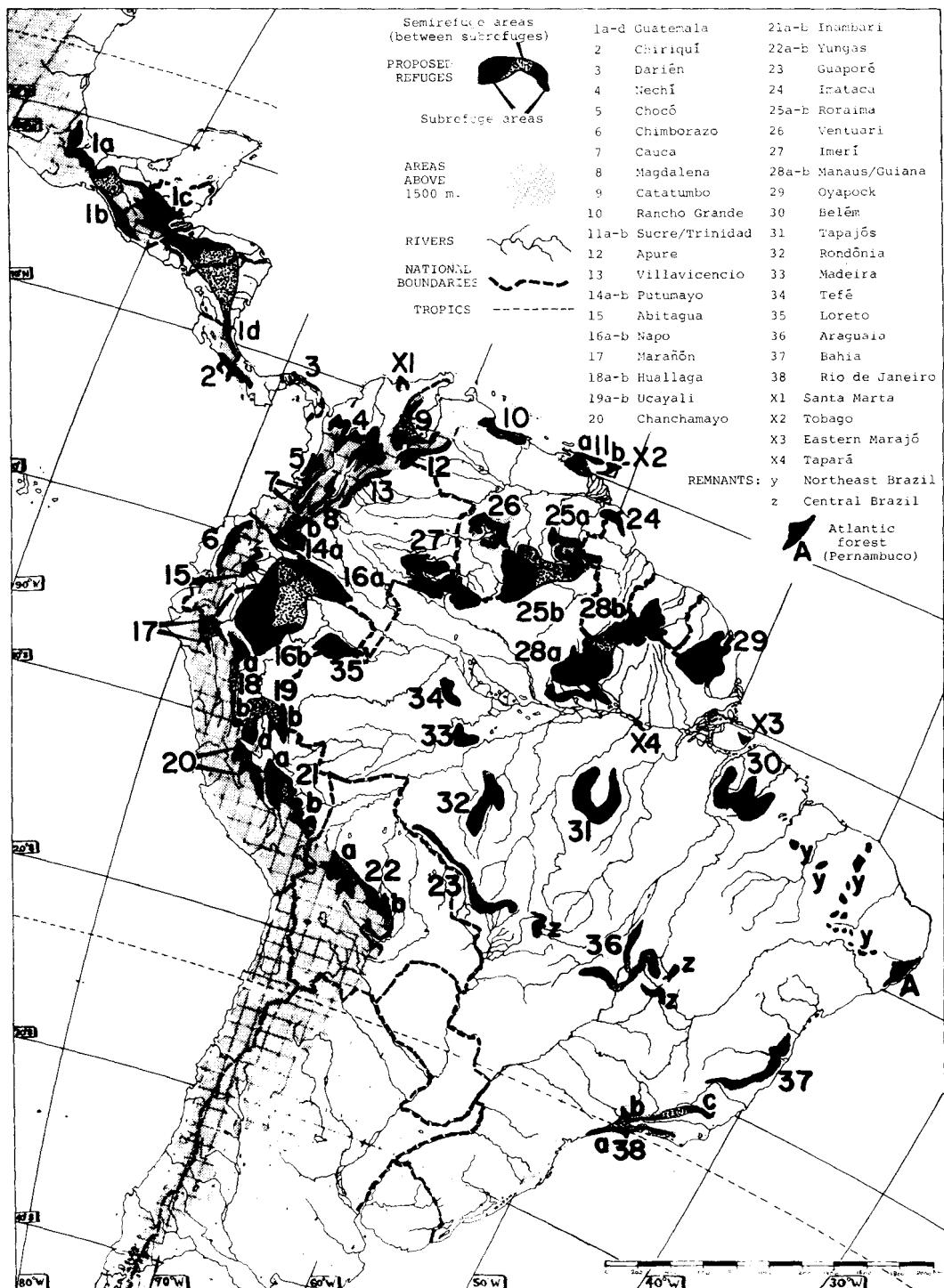
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Appendix

Assignment of *Melinaea* and *Mechanitis* to postulated refuges

As most *Melinaea* and *Mechanitis* are common where found, and as they are almost always taken by entomologists, abundant material is available in collections to permit evaluation of areas of monomorphism, polymorphism, and secondary hybridization. Some species are poorly differentiated, but the vast majority of taxa are clearly assignable to single refuges; often, this assignment is supported by mimetic resemblance with predominant complexes presently endemic to the refuge areas.

In certain cases where post-refugial dispersal has apparently led to the blurring of subspecific boundaries and to polymorphism over wide areas, and the entities have been assigned primarily on the basis of membership in refuge-associated mimicry rings, an asterisk is placed after the butterfly's name in the following list. Non-asterisked names are judged to be valid geographic subspecies.

Uncertain assignment of a race to a refuge

is indicated by a question mark after the refuge name.

Species within each genus are placed in a hypothetical evolutionary order, which differs from that of Fox (1960, 1967) only in details, except that *Melinaea mnasias* is judged to be a relict species, the most primitive of its genus, and *Mechanitis lysimnia* is regarded as more primitive than the polymorphic *M. mazaeus*. The differentiated taxa are placed in order of refuges as described in Brown (1976a).

Full and up-to-date distribution maps for these species will be presented in a future publication along with a more complete discussion of centres of evolution and probable refuges in the Neotropics. A map of proposed refuges, as presently understood, is included here, to help clarify the following analysis.

With each subspecies recognized in the present analysis is included the position given to this taxon by Fox (1960, 1965, 1967) with the page(s) on which it was mentioned and analysed and on which a distribution map for the taxon was presented by that author; also the Figure number for the taxon in Fox (1960, 1967) or in other places where it is illustrated, including in this work ('here').

<i>Melinaea</i> species	Subspecies or form	Fox (1960, 1965)			Presumed refuge
		In species (pages)	Map (page)	Plate (Fig.) or where figured	
<i>mnasias</i>	<i>abitagua nov.</i>	—	—	here	Abitagua
	<i>lutzi</i>	<i>lucifer</i> (165)	(160)	V(74)	Ucayali(?)
	<i>comma</i>	<i>comma</i> (163; 81)	(160)	V(70), here	Chanchamayo
	<i>romualdo</i>	<i>comma</i> (—; 80)	—	—	Inambari
	<i>eryx</i>	<i>lucifer</i> (166)	(160)	d'Alm. 1951; here	(W Acre, Brazil)
	<i>tecta</i>	<i>mnasias</i> (—; 82)	—	Haensch 1909, 33d; Kaye 1907	Roraima
	<i>eratosthenes</i>	<i>thera</i> (164) <i>mnasias</i> (82)	(160)	V(72), here	Manaus/Guina, Ventuari
	<i>neblinae nov.</i>	—	—	here	Imerí
	<i>mnasias</i>	<i>mnasias</i> (—; 81)	—	here	Belém
	new subsp. ?	—	—	here	Tapajós
	<i>rondonia nov.</i>	—	—	here	Rondônia
	new subsp. ?	—	—	here	Tefé
	<i>lucifer</i>	<i>lucifer</i> (165)	(160)	V(73), here	Loreto
	<i>thera</i>	<i>thera</i> (164) <i>mnasias</i> (82)	(160)	V(71), here	Rio de Janeiro
<i>ethra</i>	<i>flavicans</i>	<i>lilis</i> (128)	(134)	here	(E-C México)
	<i>imitata</i>	<i>lilis</i> (129)	(134)	II(31), here	Guatemala
	<i>scylax</i>	<i>scylax</i> (135)	(134)	II(38), here	Chiriquí
	<i>parallelis</i>	<i>lilis</i> (130)	(134)	II(32), here	Darién

Melinaea species	Subspecies or form	Fox (1960, 1965)			Presumed refuge
		In species (pages)	Map (page)	Plate (Fig.) or where figured	
<i>ethra</i>	<i>messatis</i>	<i>lilis</i> (132)	(134)	II(36), here	Nechí
	<i>dodona</i>	<i>lilis</i> (133)	—	here	Chocó
	<i>ezra</i>	<i>lilis</i> (130)	(134)	II(33), here	(Santa Marta)
	<i>lateapicalis</i>	<i>lilis sola</i> (131)	(134)	here	Catatumbo
	<i>lilis</i>	<i>lilis</i> (131)	(134)	II(34)	Rancho Grande
	<i>sola</i>	<i>lilis</i> (131)	(134)	II(35), here	Sucre/Trinidad
	<i>zamora</i>	<i>maeonis borealis</i> (146)	(148)	Br/Ben 1974; here	Apure
	<i>maeonis</i>	<i>maeonis</i> (146)	(148)	III(51), d'Alm. 1951	Napo
	<i>tarapotensis</i>	<i>maenius</i> (154)	(148)	IV(60), here	Huallaga
	<i>cyclon</i>	<i>maelus</i> (144)	(148)	III(49), Br/Ben 1974	Ucayali
	<i>lamasi</i> nov.	—	—	here	Inambari
	<i>mнемопсис</i>	<i>mнемопсис</i> (142)	(148)	III(45), here	Yungas
	<i>kayei</i> nov.	—	—	here	Manaus/Guyana
	<i>flavomacula</i>	<i>maelus madeira</i> (143)	(148)	III(46), here	Madeira
	<i>maelus</i>	<i>maelus</i> (145)	(148)	III(50), Br/Ben 1974	Tefé
	<i>ethra</i>	<i>ethra</i> (133)	(134)	II(37), here	Bahia
<i>mneme</i>	<i>mneme</i>	<i>mneme</i> (124)	(134)	II(29), here	Manaus/Guiana
	<i>mauensis</i>	<i>mneme mneme</i> (125)	(134)	II(30), Br/Ben 1974	Tapajós
	<i>mauensis</i> var.	<i>mneme mneme</i> (125)	(134)	here	Rondônia
<i>ludovica</i>	<i>idae</i>	<i>idae</i> (138)	(134)	III(41), here	Nechí
	<i>vespertina</i>	<i>idae</i> (139)	(134)	III(42)	Chimborazo
	<i>aurantia</i>	<i>satevis</i> (138)	(134)	Forbes 1948, here	Sucre/Trinidad
	<i>manuelito</i>	<i>egina</i> (141)	(148)	here	Ucayali
	<i>satevis</i>	<i>satevis</i> (136)	(134)	II(39), here	Yungas
	<i>crameri</i>	<i>satevis</i> (137)	(134)	II(40), here	Imataca
	<i>ludovica</i>	<i>egina</i> (140)	(148)	III(43), here	Belém
<i>marsaeus</i>	<i>paraiya</i>	<i>egina</i> (141)	(148)	III(44), Br/Ben 1974	Rio de Janeiro
	<i>messenina</i>	<i>mothone</i> (159)	(160)	V(66), Br/Ben 1974	Villavicencio
	<i>macaria</i>	<i>marsaeus</i> (150) <i>egesta</i> (80)	(160)	IV(53)	Putumayo
	<i>mothone</i>	<i>mothone</i> (159)	(160)	V(67), here	(General Andean)
	<i>phasiana</i>	<i>phasiana</i> (152) <i>marsaeus</i> (80)	(148)	IV(56), here	Ucayali
	<i>clara</i>	<i>marsaeus</i> (151) <i>egesta</i> (80)	(160)	IV(55), here	Inambari
	<i>pothete</i>	<i>maenius</i> (154)	(148)	d'Alm. 1945, here	Rondônia
	<i>marsaeus</i>	<i>marsaeus</i> (149; 80)	(160)	Hew. II, Mech. II: 10	Tefé
	<i>rileyi</i>	<i>marsaeus</i> (150) <i>egesta</i> (80)	(160)	III(52), Br/Ben 1974	Loreto
	<i>maenius</i>	<i>isocomma</i> (162) <i>isocomma</i> (81)	(160)	V(68)	Villavicencio
<i>maenius</i>	<i>cocana</i>	<i>maenius</i> (154)	(148)	IV(59), here	Putumayo
	<i>flavosignata</i>	<i>mars.egesta</i> (149) <i>egesta egesta</i> (80)	(160)	IV(62), here	Napo
	<i>simulator</i>	<i>comma</i> (162) <i>isocomma</i> (81)	(160)	V(69)	(General Andean)
	<i>hicetas</i>	<i>maenius</i> (153)	(148)	IV(58)	Ucayali
	<i>mediatrix</i>	<i>mneme mneme</i> (125)	—	deLesse 1970, here	Manaus/Guiana
	<i>juraicensis</i>	<i>maenius</i> (154)	(148)	d'Alm. 1943; here	Rondônia
	<i>maenius</i>	<i>maenius</i> (153)	(148)	IV(57), Br/Ben 1974	Tefé
	<i>menophilus</i>	—	—	here	
<i>menophilus</i>	<i>ernestoi</i> nov.	—	—	here	Putumayo
	<i>zaneka</i>	<i>menophilus</i> (156)	(160)	IV(63), here	Abitagua
	<i>menophilus</i>	<i>menophilus</i> (155)	(160)	IV(61), Br/Ben 1974	Napo
	<i>orestes</i>	<i>menophilus</i> (158)	(160)	V(64), Br/Ben 1974	Ucayali

<i>Mechanitis</i> species	Subspecies or form	Fox (1967)			Presumed refuge
		In species (page)	Map (page)	Figure (page) or where figured	
<i>polymnia</i>	<i>lycidice</i>	<i>i.isthmia</i> (71)	(70)	72A(75)	Guatemala
	<i>isthmia</i>	<i>isthmia</i> (71)	(70)	72B(75)	Chiriquí
	<i>chimborazona</i>	<i>isthmia</i> (80)	(70)	77(75)	Chimborazo
	<i>caucaensis</i>	<i>isthmia</i> (78)	(70)	76(75)	Cauca
	<i>veritabilis</i>	<i>isthmia</i> (74)	(70)	73(75)	Rancho Grande
	<i>kayei</i>	<i>isthmia</i> (78)	(70)	75(75)	Sucre/Trinidad
	<i>ca. veritabilis</i>	<i>isthmia</i> (74)	(70)	—	Apure, Villavicencio
	<i>dorissides</i>	<i>isthmia</i> (80)	(70)	78B(75)	Napo
	<i>eurydice</i> var.	<i>isthmia</i> (82)	(70)	—	Marañón
	<i>eurydice</i>	<i>isthmia</i> (82)	(70)	79(75), here	Chanchamayo(?)
	<i>angustifascia</i>	<i>polymnia</i> (95)	(89)	87(93), here	Yungas
	<i>bolivarensis</i>	<i>isthmia</i> (77)	(70)	74(75), here	Roraima
	<i>polymnia</i> var.	<i>p.polymnia</i> (92)	(89)	here	Manaus/Guiana
	<i>polymnia</i>	<i>polymnia</i> (91)	(89)	86(93), here	Belém
	<i>mauenensis</i>	<i>p.polymnia</i> (92)	(89)	here, Forbes 1948	Tapajós
	<i>ca. dorissides</i>	<i>isthmia</i> (80)	(70)	78A(75), here	Loreto
	<i>casabranca</i>	<i>polymnia</i> (96)	(89)	88(93)	Rio de Janeiro
<i>limnaea</i>	—	<i>limnaea</i> (86)	(70)	81(84), Ebert 1965	Manaus/Guiana
<i>lysimnia</i>	<i>doryssus</i>	<i>polymnia</i> (87)	(89)	84(93), here	Guatemala
	<i>labotas</i>	<i>pol.doryssus</i> (90)	(89)	here	Chiriquí
	<i>macrinus</i>	<i>lysimnia</i> (120)	(119)	111(121), here	Darién, Nechí, Chimborazo
	<i>doryssus</i> var.	<i>pol.doryssus</i> (87)	(89)	here	Rancho Grande
	<i>solaria</i>	<i>polymnia</i> (91)	(89)	85(93), here	Sucre/Trinidad
	<i>ocona</i>	<i>lys.elisa</i> (123)	(119)	112B(121)	Chanchamyo
	<i>acreana</i>	<i>lys.elisa</i> (123)	(119)	d'Alm. 1950, here	Inambari
	<i>elisa</i>	<i>lysimnia</i> (123)	(119)	112A(121)	Yungas
<i>menapis</i>	<i>nesaea</i>	<i>lysimnia</i> (125)	(119)	114(121), Br/Ben 1974	Bahia
	<i>lysimnia</i>	<i>lysimnia</i> (127)	(119)	115(121), Br/Ben 1974	Rio de Janeiro
	<i>saturata</i>	<i>menapis</i> (112)	(112)	105(114)	Guatemala
	<i>dariensis</i> nov.	—	—	here	Darién
	<i>menapis</i>	<i>menapis</i> (116)	(112)	107(114)	Nechí
	<i>ca. caribensis</i>	<i>men.saturata</i> (112)	(112)	—	Chocó
<i>mazaeus</i>	<i>mantineus</i>	<i>menapis</i> (118)	(112)	109(114)	Chimborazo
	<i>occasiva</i>	<i>menapis</i> (117)	(112)	108(114)	Cauca
	<i>caribensis</i>	<i>menapis</i> (114)	(112)	106(114)	Rancho Grande
	<i>messenoides</i>	<i>messenoides</i> (107)	(108)	100(109), here	Villavicencio
	<i>fallax</i> *	<i>m.mazaeus</i> (99)	(97)	here	Putumayo
	<i>visenda</i> var.	<i>m.mazaeus</i> (99)	(97)	92(100), here	Napo
	<i>deceptus</i>	<i>messenoides</i> (109)	(108)	101(109), here	(General Andean)
	<i>mazaeus</i> *	<i>mazaeus</i> (99), <i>eg.phasianita</i>	(97, 104)	96(105), here	Ucayali
	<i>nigroapicalis</i> *	<i>mazaeus</i> (99)	(97)	93(100), here	Inambari
	<i>ballucatus</i>	<i>messenoides</i> (110)	(108)	102(109)	Yungas
	<i>beebei</i>	<i>mazaeus</i> (97)	(97)	90(100), here	Imataca
	<i>bipuncta</i>	<i>pol.polymnia</i> (92)	—	here, Forbes 1948	Roraima
	<i>pannifera</i>	<i>mazaeus</i> (98)	(97)	91(100), here	Manaus/Guiana, Ventuari
	<i>visenda</i> var.	<i>maz.pannifera</i> (98)	(97)	Forbes 1948	Oyapock
	<i>lanei</i>	<i>lanei</i> (84)	(70)	80(84)	Belém
	<i>visenda</i> *	<i>maz.pannifera</i> (98)	(97)	here	Tapajós
	<i>pothetoides</i>	<i>mazaeus</i> (103)	(97)	d'Alm. 1951, here	Rondônia
	<i>elevata</i>	<i>mazaeus</i> (102)	(97)	94(100), here	Madeira
	<i>egaensis</i>	<i>egaensis</i> (105)	(104)	95(105), here	Tefé
	<i>lucifera</i>	<i>m.mazaeus</i> (89)	(97)	here	Loreto

Book notices

THE SPHECIDAE (HYMENOPTERA) OF FENNOSCANDIA AND DENMARK. By O. Lomholdt. Pp. 452. Scandinavian Science Press Ltd, Klampenborg, Denmark: 1975–76 D Kr. 158. (*Fauna Entomologica Scandinavica*, vol. 4, parts 1 and 2).

The *Fauna Entomologica Scandinavica* series is conceived to give comprehensive coverage in the English language of the Insect Fauna of Scandinavia, with keys to genera and to species together with descriptions, many figures and summaries of distributional and biological information. The distributions both in Great Britain and in northern Germany of the species treated are also included, enhancing both the value and the market of the series.

Volume 4, issued in two parts, is the first treating a group of Hymenoptera. The Sphecid fauna of Scandinavia lacks scarcely any of the 114 species present in Great Britain, and includes others which may subsequently be discovered here; the work is thus of direct value to British entomologists who may wish to identify specimens. Introductory material includes sections on morphology and generalizations on the biology, distribution and evolution of the group. The taxonomic treatment is consistent with a recent reclassification of the genera of Sphecidae and in relation to our own species list, there are few nomenclatural disparities at the species level. Good keys are augmented by many figures and detailed descriptions. Of particular interest and value is

a key at generic level to the known larvae. A substantial bibliography, distributional tables and an index complete the work.

THE ORTHOPTERA OF EUROPE, Vol. III. By Kurt Harz and Alfred Kaltenback. Pp. 434. Dr W. Junk, The Hague, 1976. Dutch Guilders 140.00. (Series *Entomologica* Vol. 12.)

This is the third and final volume of a comprehensive work on the Orthoptera of Europe. It is the product of many years spent by the authors studying and checking both the literature and numerous large collections of Orthoptera to register the variability of specific characters and to elaborate keys. The first volume dealt with the Ensifera and the second with the suborder Caelifera. This volume, which is written in both English and German, is concerned with the orders Cheleutoptera, Dermaptera, Mantodea, Blattoptera and Isoptera. Following a key to the orders, each order is treated systematically with keys to the superfamilies, families and subfamilies, genera and species. There are detailed descriptions of the included species and for each species the synonymy, detailed diagnoses and brief distribution details are given. Line drawings are provided of all the important specific characters. An impressive list of references and an index completes the work.