

A review of the genus *Manerebia* Staudinger (Lepidoptera: Nymphalidae: Satyrinae) in the northern Andes

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Abstract: The taxonomic limits of the neotropical montane satyrine genus *Manerebia* Staudinger are defined, with the names *Penrosada* Brown and *Posteuptychia* Forster treated as junior subjective synonyms. The taxonomic history of the genus is discussed and the current knowledge on the distribution, ecology and behavior of all north Andean species is summarised. A species-level taxonomic review of north Andean *Manerebia* is presented that includes 23 species and 37 taxa. Of these, 10 new species and 13 new subspecies are described here: *M. germaniae* n. sp., *M. golondrina* n. sp., *M. magnifica* n. sp., *M. mammothus* n. sp., *M. pervaga* n. sp., *M. pluviosa* n. sp., *M. prattorum* n. sp., *M. rufanalis* n. sp., *M. seducta* n. sp., *M. undulata* n. sp., *M. franciscae rodriguezi* n. ssp., *M. germaniae vitalei* n. ssp., *M. inderena antioquiensis* n. ssp., *M. inderena clara* n. ssp., *M. inderena fina* n. ssp., *M. inderena leaeniva* n. ssp., *M. inderena mirena* n. ssp., *M. inderena similis* n. ssp., *M. leaena gonzalezi* n. ssp., *M. rufanalis fernandina* n. ssp., *M. satura lamasi* n. ssp., *M. satura pauperata* n. ssp., *M. undulata milaena* n. ssp. A lectotype is designated for *M. leaena* to stabilise future nomenclature and *Penrosada lanassa* f. *neglecta* is placed as a subspecies of *Manerebia ignilineata* n. stat. Accounts are presented for each species, discussing identification, taxonomy and ecology, and listing known geographic and elevational range data. Adult specimens, drawings of male genitalia and distribution maps are figured for all taxa where possible and the location of type material is given.

Key Words: cloud forest, Colombia, ecotone, Ecuador, elevational range, elfin forest, identification, *M. franciscae rodriguezi* n. ssp., *M. germaniae* n. sp., *M. germaniae vitalei* n. ssp., *M. golondrina* n. sp., *M. inderena antioquiensis* n. ssp., *M. inderena clara* n. ssp., *M. inderena fina* n. ssp., *M. inderena leaeniva* n. ssp., *M. inderena mirena* n. ssp., *M. inderena similis* n. ssp., *M. seducta* n. sp., *M. leaena gonzalezi* n. ssp., *M. magnifica* n. sp., *M. mammothus* n. sp., *M. pervaga* n. sp., *M. pluviosa* n. sp., *M. prattorum* n. sp., *M. rufanalis* n. sp., *M. rufanalis fernandina* n. ssp., *M. satura lamasi* n. ssp., *M. satura pauperata* n. ssp., *M. undulata* n. sp., *M. undulata milaena* n. ssp., páramo, *Penrosada*, Peru, *Posteuptychia*, systematics, taxonomy, tree-line, Venezuela.

INTRODUCTION AND METHODS

The taxonomy of the neotropical Satyrinae remains the most poorly understood of any nymphalid butterfly group. The high levels of endemism and diversity in the tropical Andes make understanding the systematics of its fauna particularly challenging,

and this is certainly true of the speciose genus *Manerebia* Staudinger. A notable feature of the genus is the external similarity of many species, which can only be identified with certainty through dissection, and this fact has led to much confusion in the literature and resulted in a significant underestimation of the true taxonomic diversity of the genus. In this paper we review the *Manerebia* fauna of the north Andean region, where the highest number of undescribed and taxonomically confusing taxa occur. The genus is

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remarkable for only 13 of the 23 known north Andean species, and 14 of the 37 known north Andean taxa, having been described to date, clearly illustrating the importance of continuing collection activity in this region. We aim to establish the identity of all historical names applying to taxa from this region and describe all unnamed taxa known to us, hopefully creating a firm foundation for future taxonomic revision of the entire genus.

The authors have been involved in studying the diversity and taxonomy of the Andean satyrine butterflies of Venezuela, Colombia and Ecuador for more than a decade (e.g. Pycz *et al.*, 1999; Pycz & Vilorio, 2004; Vilorio, 2001). The region between southern Ecuador and northern Peru forms a prominent biogeographic divide for many montane butterfly taxa (Willmott, Hall, Pycz, unpublished data), and the majority of north Andean *Manerebia* species do not occur further to the south. We therefore define, for the purpose of this paper, the north Andes as the area north of the Río Chamaya - Marañón valley in northern Peru, also known as the Huancabamba deflection (Dillon, 1994).

Original descriptions were consulted for all published *Manerebia* names and attempts made to locate type material. *Manerebia* specimens were examined in collections in Europe, North and South America, as listed below. One problem faced by earlier authors was a lack of reliably labelled material in collections. However, extensive fieldwork throughout the region by ourselves and others has provided a large amount of new information on habitat preferences, geographic and elevational distribution and phenotypic variation. This information has been extensively used in proposing new relationships between allopatric taxa, but we have nevertheless had to make a number of arbitrary assignments of taxonomic rank, based on incomplete information. In general, where there are no apparent differences in either genitalic characters, or wing pattern characters that do not vary intraspecifically elsewhere in the genus, and closely allopatric taxa have similar elevational ranges and occur in similar habitats, we have regarded them as conspecific.

Dissections were made of males only, due to the rarity of females in collections, and where necessary, type specimens were dissected to confirm their identity. Abdomens were soaked in hot 10% KOH solution for 15 min and subsequently stored in glycerol for study under binocular microscope. Morphological terms for genitalia largely follow Klotz (1956) and for venation follow Comstock & Needham (1918). The following collection codens are used in the text:

AFEN: Collection of Andrew F. E. Neild, London, UK

AME: Allyn Museum of Entomology, Sarasota, USA (now at

McGuire Center for Lepidoptera and Biodiversity, Gainesville, USA)

BMNH: The Natural History Museum, London, UK (T=Type coll., R=Rothschild coll., A&B=Adams & Bernard coll.)

GR: Collection of Gabriel Rodríguez, Medellín, Colombia

IMLT: Fundación e Instituto Miguel Lillo, Tucumán, Argentina

JFLC: Collection of Jean-François Le Crom, Bogotá, Colombia

KWJH: Collection of Keith Willmott and Jason Hall, Gainesville, USA

MALUZ: Museo de Artrópodos de la Universidad del Zulia, Maracaibo, Venezuela

MBLI: Collection of Maurizio Bollino, Lecce, Italy

MECN: Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador

MHNUN: Museo de Historia Natural de la Universidad Nacional, Bogotá, Colombia

MHNUP: Museo de Historia Natural de la Universidad Pedagógica, Bogotá, Colombia

MIZA: Museo de Entomología de la Universidad Central, Maracay, Venezuela

MZPAN: Muzeum i Instytut Zoologii Polskiej Akademii Nauk, Warsaw, Poland

MUSM: Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru

MZUJ: Muzeum Zoologiczne Uniwersytetu Jagiellońskiego, Kraków, Poland

PB: Collection of Pierre Boyer, Le Puy Sainte Réparate, France

PUCE: Museo de Entomología, Pontificia Universidad Católica del Ecuador, Quito

PUJ: Departamento de Biología, Pontificia Universidad Javeriana, Bogotá, Colombia

SMTD: Staatliche Museum für Tierkunde, Dresden, Germany

TWP: Collection of Tomasz Wilhelm Pycz, Warsaw, Poland

USNM: United States National Museum - Smithsonian Institution, Washington, USA

ZMHU: Museum für Naturkunde der Humboldt Universität, Berlin, Germany

DHW, VHW, DFW, VFW: dorsal hindwing, ventral hindwing, dorsal forewing, ventral forewing

Systematic overview

The name *Manerebia* was initially proposed by Staudinger (1897) for five new, closely related Bolivian and Peruvian species (*M. cyclopina*, *M. cyclopella*, *M. cyclops*, *M. typhlops* and *M. thyphlopsella*). Subsequent taxa described in the genus were also typically from the southern tropical Andes (Schaus, 1902; Hayward, 1949; Forster, 1964), with the exception of the Colombian *M. nevadensis* Krüger (Krüger, 1925) and Ecuadorian *M. keradialeuka* Hayward (Hayward, 1968). Brown (1944) introduced the generic name *Penrosada* for a cluster of mainly north Andean species formerly often placed in *Lymanopoda* Westwood, 1851, including *P. leaena* (Hewitson), *P. apiculata* (C. & R. Felder), *P. lanassa* (C. & R. Felder), *P. lisa* (Weymer, 1911), *P. satura* (Weymer), *P. cillutinarca* (Weymer, 1912, a synonym of *M. zoippus* (H. Druce, 1876)), and *P. keithi* (Dyar, 1913, a synonym of *M. satura*). Adams & Bernard (1979, 1981) and Adams (1986) described a further four species of *Penrosada* from Colombia and Venezuela, and historically authors have continued

to regard both *Manerebia* and *Penrosada* as distinct genera, without further discussion of the taxonomic relationships of their members (e.g., Forster, 1964; Miller, 1968; Adams & Bernard, 1977, 1979, 1981; Adams, 1985, 1986; D'Abrera, 1988; Racheli & Racheli, 2001).

Having examined the head, thorax, wing venation and pattern, and male genitalia of all species formerly placed in *Penrosada* Brown and *Manerebia* we have found no synapomorphies that distinguish the two genera, and we therefore follow Lamas & Vilorio (2004) in considering the former as a subjective junior synonym of the latter. Brown's (1944) original description of *Penrosada* made no reference to *Manerebia*, and his morphological diagnosis of the genus applies fully to the species originally treated in *Manerebia* by Staudinger (1897), namely, the hindwing vein M1-M2 is characteristically short (shorter than in *Lymanopoda* Westwood) and gently curved, the root of vein M3 is much closer to vein Cu1 than M2, the hindwing is slightly incised near the anal angle, the ocellus in cell 1A-Cu2 of the forewing and hindwing is usually fully developed, and the walking legs are yellowish. The conspicuous oblique, straight yellow or whitish band on the hindwing underside present in most *Penrosada* of Brown and absent in the five original *Manerebia* of Staudinger almost certainly does not define a monophyletic group, being highly variable between and even within populations. Some species of *Manerebia*, as defined here, such as *M. ignilineata*, *M. interrupta* and *M. apiculata*, are polymorphic, with the band shortened, discontinuous or even entirely absent. Other typical features of the genus *Manerebia* include male genitalia characterised by a long, arched uncus, fully developed subuncus, and slender valvae with a strongly dentate dorsal edge.

We also consider the genus *Posteuptychia* Forster a subjective junior synonym of *Manerebia*, where it was placed by Lamas & Vilorio (2004). Forster (1964) erected the monotypic *Posteuptychia* for *Pronophila mycalesoides* C. & R. Felder on the strength of its slightly unusual male genitalic morphology, but did not notice that species he treated in *Manerebia* were also similar in this respect, and shared similar wing color pattern and venation. Indeed, *M. mycalesoides* is perhaps genitally most similar to *M. nevadensis*, one of the few north Andean species actually originally described in *Manerebia*.

Miller (1968) placed *Manerebia* in the tribe Pronophilini Reuter, a neotropical section of the Satyrinae. Adams & Bernard (1977, 1979, 1981), Adams (1986) and Pyrcz (1999) did not question this decision, but Vilorio (2001) suggested that *Manerebia* does not belong in the Pronophilina, but in the pre-

dominantly Holarctic Erebiina (following Harvey's (1991) arrangement, downranking former tribes to subtribes of the Satyrini). Vilorio (2001) listed three putative synapomorphies of the Pronophilina absent in *Manerebia*: setose eyes, hindwing cross vein M1-M2 curved basad into the discal cell and hindwing discal cell equal or shorter than the maximum length of the hindwing. The absence of setae on the eyes also occurs in the Erebiina, where the genus is currently placed (Lamas & Vilorio, 2004), as well as in the Palearctic Satyrina. We believe the character evidence in support of this subtribal position is currently weak, and a thorough cladistic analysis of the tribe Satyrini is clearly needed, hopefully including additional characters, especially those from the early stages (e.g., Harvey, 1991) and molecular sequence data. Pyrcz (1995) and Vilorio (2001) suggest *Tamania* Pyrcz or *Idioneurula* Strand as possible sister genera of *Manerebia*.

The species-level systematics of *Manerebia* are very complex and have not been rendered easier by multiple errors made by earlier workers (see Appendix 1). Three publications are especially significant for the description of new taxa: Brown (1944), Forster (1964) and Adams (1986). In addition to describing the generic synonym *Penrosada*, Brown (1944) also attempted to treat all Ecuadorian species, though he seemed unaware of two species already described at that time from the country, *M. trimaculata* and *M. ignilineata*, redescribing the latter as forms of "*Penrosada lanassa*". He also mistakenly applied the names *leana*, *lanassa* and *apiculata* to various species and described several infrasubspecific forms differing in the expression of the hindwing band as new taxa. In the absence of any figures of specimens, identification of the taxa that Brown was really treating must be based largely on the imprecise genitalic illustrations. Forster (1964) clarified, to some extent, the classification of the Bolivian species and illustrated the most poorly known taxa described by Staudinger (1897). Unfortunately, he did not examine the genitalia of any species, and hence he also did not notice that *Penrosada* and *Posteuptychia* were morphologically similar to other *Manerebia*. Finally, Adams (1986) treated most of the species of *Manerebia* (under the name *Penrosada*) occurring in Colombia and Venezuela, providing valuable distributional data and describing a number of new taxa, but also made some errors in identification similar to earlier authors. Lamas & Vilorio (2004) provided a synonymic checklist for the entire genus, thus correcting previous taxonomic errors.

Morphology

The wing patterns of all *Manerebia* species are very

simple (Figs. 1-9). Both dorsal and ventral surfaces are generally uniformly brown (though *M. lisa* and two new species described here have a coloured dorsal band), and the most visible character, the ventral hindwing postdiscal band, is also one of the most variable. In addition to simple local and geographic variation in width, orientation and color, the band may be absent altogether, split into spots, or reduced to small sections, all within a single population. The evolutionary basis for the polymorphism within this hindwing band remains unknown, but it occurs in several species that are apparently not a monophyletic group. The only other apparent pattern elements are fine, darker postdiscal and submarginal lines, and occasional submarginal ocelli in cells Cu1-Cu2 on the forewing and cells Cu1-Cu2 and 1A-Cu2 on the hindwing, and these subtle characters prove to be some of the most useful for distinguishing species.

The male genitalia (Figs. 10-14) are also taxonomically extremely useful, for although also simple in structure they may differ significantly between species that are externally almost indistinguishable. In the north Andean fauna, taxa frequently fall into one of two principal morphological groups (that may or may not be monophyletic); one in which the uncus is strongly arched, the subunci relatively long, the 'teeth' at the distal tip of the valva often extending anteriorly along the dorsal edge, and the dorsal base of the valva armed with a projection with numerous small 'teeth' (*M. leaena*, *M. germaniae*, *M. phiviosa* n. sp., *M. apiculata*, *M. navarrae*, *M. franciscae*, *M. mam-muthus* n. sp., *M. satura*), and one in which the uncus is slightly curving or straight, the subunci relatively short, the 'teeth' confined to the distal tip of the valva, and the dorsal base of the valva armed with a simple projection only (*M. inderena*, *M. golondrina* n. sp., *M. prattorum* n. sp., *M. trimaculata*, *M. undulata* n. sp., *M. interrupta*). Within these two groups, more subtle characters in the shape of the uncus, subunci and valvae are often consistent within and between populations, and provide clues to the relationships of allopatric taxa.

Diversity, distribution, ecology and behavior

Lamas & Vilorio (2004) recognise a total of 45 *Manerebia* species, including both described and undescribed species. The genus is exclusively Andean, including the peripheral ranges of Sierra Nevada de Santa Marta and the Venezuelan Cordillera de la Costa (Figs. 15-20), and local faunas in the central and northern Andes comprise three to eight species (Appendices 2, 3). Some species of *Manerebia* occur in premontane forests as low as 800 m (*M. mycalesoides*, *M.*

magnifica n. sp. and some Bolivian species). The genus is, however, most diverse in middle and upper elevation cloud forest and elfin forests from 2300-3000m. A few species occur in the páramo grassland above the tree line up to 4000m (*M. levana*, *M. ignilineata*, *M. seducta* n. sp.).

Most north Andean *Manerebia* occur in low population densities. This is particularly true for species in Venezuela and northern Colombia, where they are among the rarest cloud forest butterflies. *Manerebia mycalesoides*, the sole representative of the genus in the Venezuelan Cordillera de la Costa, remained unknown there until 1999, despite this being probably the best sampled mountainous area in South America. In Colombia and Ecuador *Manerebia* species abundance remains relatively low in comparison to that of other sympatric cloud forest satyrine genera, such as *Pedaliodes* Butler, 1867, *Pronophila* Doubleday, [1849], or *Lymanopoda*. Aggregations at water seepages of more than a couple of individuals are a rare sight, but, surprisingly, towards the southern tropical Andes the reverse may be true. In the cloud forests of Bolivia certain species of *Manerebia* are occasionally extremely abundant, and literally hundreds of individuals can be frequently observed along roadsides and forest trails (Pyrz, pers. obs.). Seasonal fluctuations in abundance have also been noted (Adams & Bernard, 1981) for some north Andean species, especially those occurring in the páramo. Adults of some species are observed almost exclusively during the wet season (*M. franciscae*, *M. interrupta*), whereas others seem to be much more abundant during the dry season (*M. undulata* n. sp., *M. inderena*).

Several *Manerebia* species are confined to very narrow ecological zones, such as the forest-páramo ecotone (*M. interrupta*), while other north Andean *Manerebia*, although wider ranging, are inconspicuous butterflies of dense cloud forests, usually overlooked by lepidopterists. These facts have resulted in their poor representation in major collections. Fortunately, however, all of the cloud forest species of *Manerebia* are readily attracted to decomposing organic matter, especially dung and carrion, and the use of baited traps provides a rapid and reliable method of sampling. Páramo species also come to bait, but less readily, and sampling for species above the tree-line must also be done with hand-nets.

Some species of *Manerebia* demonstrate notable wing pattern similarities to unrelated, microsympatric pronophiline satyrines. Adams & Bernard (1979) remarked on the similarity of two Colombian species, *M. quinterae* and *M. navarrae*, to two respectively sympatric *Eretris* species, and stated that there was "little doubt" that mimicry was occurring. A further, even

more striking example concerns *M. pluviosa* n. sp., which has a very unusual wing pattern for the genus, a wide postdiscal orange band on both wings. This species is microsympatric with a similarly patterned *Pedaliodes* species (Pyrz & Vilorio, in press). To date there is no evidence for unpalatability in any of these species, and it remains to be demonstrated that these similarities result from mimicry.

Very little is known about the early stages of *Manerebia*. Adams & Bernard (1981) recorded the montane bamboo *Chusquea* (Poaceae) as the food plant for *Manerebia franciscae*. Greeney (Greeney & Pyrcz, in prep.) observed second to fourth instar larvae of *M. inderena clara* n. sp. in Yanayacu (Ecuador, Napo) also on a species of *Chusquea*. This food plant is also that of most Neotropical cloud-forest satyrines and will probably apply to the entire genus.

SPECIES ACCOUNTS

Manerebia Staudinger, 1897

Manerebia Staudinger, 1897: 139. Type-species *Manerebia cyclopi-na* Staudinger, by subsequent designation (Hemming, 1943: 24).

= *Penrosada* Brown, 1944: 255. Type-species *Lymanopoda leaena* Hewitson, by original designation.

= *Posteuptychia* Forster, 1964: 137. Type-species *Pronophila mycalesoides* C. & R. Felder, by monotypy.

[NOTE: only north Andean taxa are included here, with the exception of *M. satura satura*; - indicates a subspecies, — indicates a synonym]

leaena (Hewitson, 1861)

-*lanassa* (C. & R. Felder, 1867)

-*gonzalezi* Pyrcz & Vilorio, n. ssp.

-*germaniae* Pyrcz & Hall, n. sp.

-*vitalei* Pyrcz & Willmott, n. ssp.

-*pluviosa* Pyrcz & Vilorio, n. sp.

-*apiculata* (C. & R. Felder, 1867)

—*curvilinea* Weymer, 1912

-*franciscae* (Adams & Bernard, 1981)

-*rodriguezi* Pyrcz & Willmott, n. ssp.

-*mammuthus* Pyrcz & Willmott, n. sp.

-*satura* (Weymer, 1911)

-*pauperata* Pyrcz & Willmott, n. ssp.

-*lamasi* Pyrcz & Willmott, n. ssp.

-*navarrae* (Adams & Bernard, 1979)

-*quinterae* (Adams & Bernard, 1979)

-*inderena* (Adams, 1986)

-*antioquiensis* Pyrcz & Willmott, n. ssp.

-*fini* Pyrcz & Willmott, n. ssp.

-*similis* Pyrcz & Willmott, n. ssp.

-*clara* Pyrcz & Willmott, n. ssp.

-*leavenia* Pyrcz & Willmott, n. ssp.

-*mirena* Pyrcz & Willmott, n. ssp.

-*golondrina* Pyrcz & Willmott, n. sp.

-*prattorum* Pyrcz & Willmott, n. sp.

-*trimaculata* (Hewitson, 1870)

-*undulata* Pyrcz & Hall, n. sp.

-*milaena* Pyrcz & Willmott, n. ssp.

-*interrupta* (Brown, 1944)

—*keradialeuka* (Hayward, 1968)

-*rufanalis* Pyrcz & Hall, n. sp.

-*fernandina* Pyrcz & Willmott, n. ssp.

-*ignilinata* (Dognin, 1896)

-*neglecta* (Brown, 1944) n. stat.

—*discontinua* (Brown, 1944)

-*seducta* Pyrcz & Willmott, n. sp.

-*mycalesoides* (C. & R. Felder, 1867)

—*lethe* (Butler, 1867)

-*magnifica* Pyrcz & Willmott, n. sp.

-*nevadensis* Krüger, 1925

-*levana* (Godman, 1905)

-*pervaga* Pyrcz & Vilorio, n. sp.

Manerebia leaena (Hewitson, 1861)

The identity of *leaena*, the oldest available name in *Manerebia*, is crucial for establishing a stable nomenclature for this genus in the northern Andes. The original description is concise ("Upperside dark brown from the base to the middle, rufous-brown [beyond. Underside as above, except that the posterior wing is crossed transversely beyond the middle, from margin to margin, by a regular, nearly straight band of pale yellow. Exp. 19/20 inch") and accompanied by a black and white figure of the ventral surface (Hewitson, 1861). Hewitson did not give any type locality, sex or number of specimens examined, which makes the correct identification of *leaena* difficult. However, several other pronophiline satyrines were described in the same paper (e.g., *Lymanopoda lactea*, *Lymanopoda labda*, *Lymanopoda albocincta*), all of which were from Colombia.

Kirby (1879), in his catalogue of butterflies in the collection of Hewitson in the BMNH, mentions seven specimens of *leaena* from Ecuador. Four Hewitson specimens labelled as *leaena* were located at the BMNH, including two labelled Ecuador and two without any locality. Since these specimens actually represent two different species, *M. leaena* and *M. undulata* n. sp., a lectotype designation is necessary. The specimen selected as the lectotype of *leaena* very closely matches the original figure, in particular in the precise shape of the pale hindwing ventral surface band, which is slightly notched along the basal edge at the base of vein M3 and tapers at the tornus, and in its uniform ground colour and lack of ocelli. Given the accuracy of Hewitson figures, we believe it is probably the specimen on which the illustration was based. The specimen has a typed label, which would have been added subsequent to the specimen's accession to the BMNH, which has "?Ecuador" written on it, with "Quito" written over the top. Presumably the original specimen lacked locality data and a guess was made as to its origin based on other similar Hewitson specimens. However, a very careful comparison of *leaena*-like specimens from all sampled localities in Ecuador

(specified in this paper) and Colombia reveals that the wing shape and colour pattern of the lectotype matches perfectly only those found in the Colombian Cordillera Oriental east of Bogotá. Adams (1986) collected a series of specimens of *M. leaena* recently in that area. The genitalia of the lectotype confirm this, being typical of Colombian *leaena* as treated here. It is not the only case when a pronophiline butterfly described by Hewitson bears incorrect "Ecuador" locality data. *Eretris phyllalia* (Hewitson), whose syntype specimen shares the same type of label as the lectotype of *leaena*, is a synonym of *Eretris apuleja apuleja* (C. & R. Felder, 1867) found in the vicinity of Bogotá.

Having no access to the British type material, Brown (1944) misidentified *M. leaena* and applied the name to an uncertain number of Ecuadorian species. Adams (1986) correctly recognised that *M. leaena* is found in the Bogotá region, but implied that it was sympatric with *M. l. lanassa*, which he considered a separate species. He treated *M. leaena* as a species occurring throughout the eastern Andes from Colombia to Peru, and figured the genitalia of a Peruvian specimen of *Manerebia haywardi* (Pyrz, 2004) that is similar externally but actually has very distinct genitalia. Hence, the genitalia illustrations of *M. leaena* and most other taxa in Brown (1944) and Adams (1986) are incorrect. Further misidentifications are found in D'Abrera (1988), whose treatment was based on the arrangement of the main collections in the BMNH, and corrections to names of figured specimens are provided here (Appendix 1). In fact, *M. leaena*, although externally similar to many other species, has distinctive male genitalia, which have a toothed projection near the base of the ampulla and a strongly arched uncus, similar to *M. germaniae* n. sp., *M. pluviosa* n. sp., *M. apiculata*, *M. navarrae*, *M. satura*, *M. franciscae* and *M. mammothus* n. sp. Within this group, the short, squat valvae, with numerous spines at the tip and pronounced spines on the ampulla, closely resemble only those of *M. germaniae* n. sp. However, *M. leaena* consistently differs from *M. germaniae* in having fewer spines on the dorsal edge of the valva near the base. In addition, the thin dark brown submarginal lines on the ventral surface are undulate in *M. leaena*, but almost straight in *M. germaniae*. Although these two taxa are not known to be sympatric to date, the wing pattern and genitalic characters that distinguish them are consistent throughout their respective ranges (with the exception of a single specimen of *M. leaena leaena* discussed under that taxon). In addition, *M. germaniae* may actually prove to be the sister taxon of *M. pluviosa* (see under that species), which also has straight ventral submarginal lines, and which occurs sympatrically with *M. leaena*

gonzalezi n. ssp. in the Venezuelan Sierra de El Tamá. There is slight subspecific genitalic variation in *M. leaena*, in the number and distribution of spines along the dorsal edge of the valva.

Manerebia leaena leaena (Hewitson, 1861)

Figs. 1A,B, 10A, 15

Lymanopoda leaena Hewitson (1861: 156, pl. 9, fig. 1). **TL:** [Colombia, Cordillera Oriental]. **LT male** (here designated): "Ecuador, Quito", Hewitson Coll. 79-69. B.M. Type No. Rh. 3935. BMNH(T) [examined].

Penrosada leaena (Hewitson); Brown (1944: 256) (misidentification).

Manerebia leaena (Hewitson); Lamas & Vilorio (2004: 215).

Diagnosis: In the nominate subspecies (Figs. 1A, B) the VHW postdiscal band is approximately twice the width of that in *M. leaena lanassa*, and also broader than in *M. l. gonzalezi* (described below). This taxon is similar in wing pattern to *M. inderena leaeniva* (described below), but the VHW band is slightly contracted basally at the anal margin and a richer yellow than in *M. inderena leaeniva* or *M. inderena clara* (described below). In addition to the characters given in the species account above, *M. germaniae* n. sp. is also generally larger, has narrower VHW postdiscal bands and a characteristic convex FW outer margin, that is straight in *M. leaena*. A single male specimen in the BMNH(A&B) from the Colombian Sierra Nevada del Cocuy has straighter ventral submarginal lines, similar to *M. germaniae*, but the genitalia, size and other wing pattern characters suggest that it is a slightly aberrant specimen of *M. leaena*.

Comments: The nominate subspecies occurs in the Cordillera Oriental in Colombia (Cundinamarca, Boyacá) on the eastern slopes of the Andes, in Gachetá at 2500 m (Adams, 1986) and Cruz Verde, over 2700m (Krüger, 1925). Remaining literature localities must be considered less reliable, with some probably applying to *M. inderena* (Adams, 1986). Pyrcz's (1999) report of a specimen of *M. leaena* collected by Krüger in the Cordillera Central refers to *M. germaniae* n. sp. (described below).

Manerebia leaena lanassa (C. & R. Felder, 1867), **stat. rest.**

Figs. 1C, D, 10B, 15

Pronophila leaena var. *lanassa* C. & R. Felder (1867: 474). **TL:** Colombia, Cundinamarca, Bogotá. **HT male:** Colombia, Cundinamarca, Bogotá, Lindig, Felder coll. BMNH(R) [examined].

Lymanopoda leaena form *lanassa* (C. & R. Felder); Weymer (1911: pl. 52, row f; 1912: 249).

Penrosada lanassa (C. & R. Felder); Brown (1944: 258) (misidentified); Adams (1986: 305).

Manerebia leaena lanassa (C. & R. Felder); Lamas & Vilorio (2004: 215).

Diagnosis: Male genitalic and wing pattern characters show that this taxon is very closely related to *M. leaena leaena*. The male genitalia (Fig. 10B), including that of the holotype, share the characters of other *M. leaena* subspecies, an arched uncus and spines at the dorsal edge of the valva near the base. However, the latter are less prominent, there are no 'teeth' between the shoulder and the apex, the apical 'teeth' are fewer and the valva is more slender. The VHW yellow band is half the width of nominate *M. leaena* and slightly narrower than in *M. l. gonzalezi* n. ssp. Adams (1986) considered *M. leaena* and *lanassa* to be separate species, and stated that the latter taxon occurred on both slopes of the Colombian Cordillera Oriental. However, we have found no evidence to support the latter statement, and a careful examination of Adams material deposited in the BMNH, and material in collections in Bogotá did not reveal any specimen of *lanassa* from the east slopes of the Cordillera. Similarly, in other consulted collections (TWP, JFLC, MHNUP,

PUJ) this taxon is represented only by specimens collected west and northwest of Bogotá. Since *lanassa* therefore seems to be the western slope replacement of *M. leaena leaena*, we consider the two taxa conspecific (Lamas & Vilorio, 2004).

Comments: *Manerebia leaena lanassa* is restricted to the western slope of the Cordillera Oriental in Colombia (Cundinamarca, Boyacá). Adams (1986) reports that it occurs from 2250-2700 m, while TWP has collected it at 2900 m near Facativá.

***Manerebia leaena gonzalezi* Pyrcz & Vilorio, n. ssp.**

Figs. 1E, 10C, 15

Manerebia leaena n. ssp. (Pyrcz & Vilorio); Lamas & Vilorio (2004: 215).

Diagnosis: This taxon differs from the nominate subspecies primarily by having narrower VHW postdiscal bands, that are, however, not as narrow as in *M. leaena lanassa*. The VHW postdiscal band is slightly arched in comparison with the straighter bands of *M. l. lanassa* or the nominate subspecies. The genitalia (Fig. 10C) are also distinct in having additional 'teeth' along the whole dorsal edge of the valva.

Description: MALE (Fig. 1E): **Head, thorax and abdomen:** same as in other subspecies. **Wings:** Forewing (length: 18.5-19 mm, mean: 18.75 mm, n = 4) triangular, tornus obtuse. Hindwing rounded, anal margin very slightly excavated near angle. DFW uniform coffee brown. DHW coffee brown; reddish scales sparsely scattered towards submarginal and marginal areas; basal half of hindwing with dense, long hairs. VFW dark brown; reddish scales scattered along costal margin and distal half of wing, more heavily towards apex and marginal area; submarginal dark chocolate brown zigzag line; vestigial postdiscal white dot in cell Cu1. VHW ground colour chestnut, except for veins which are covered with chocolate brown scales; narrow yellow band (c. 1 mm wide) from apex to anal margin close to tornal angle, crossing just at extremity of discal cell but not entering into it, dark brown submarginal line lightly undulate. **Male genitalia** (Fig. 10C): similar to other subspecies except with additional 'teeth' along dorsal edge of valva.

FEMALE: Unknown.

Etymology: We dedicate this new subspecies to Luis Alfonso González, a forest guard of the Venezuelan Parque Nacional El Tamá, one of the few in the area who knows every detail of its geography and nature, in gratitude for his cooperation and hospitality.

Types: **Holotype male:** VENEZUELA: Táchira, Parque Nacional El Tamá, selva nublada arriba de Betania, 2400-2480 m, 24.VIII.1996, A. Vilorio leg., MALUZ; **Paratypes (3 males):** VENEZUELA: **1 male:** Táchira, Parque Nacional El Tamá, vía La Línea, 2300-2700 m, 17.IV.1996, T. Pyrcz leg., TWP; **1 male:** Táchira, vía Bramón a Delicias, Mata Mula, 1850-2020 m, 18.IX.1997, A. Neild leg., AFEN; COLOMBIA: **1 male:** Norte de Santander, Parque Nacional Natural El Tamá, Herrán, 2500 m, XII.1993, J. F. Le Crom leg., JFLC.

Comments: *Manerebia leaena gonzalezi* is known from a few individuals seen and collected in the cloud forest at elevations between 2300-2700 m. It flies high around bamboos (*Chusquea*) along with *Lymanopoda lebbaea* C. & R. Felder, 1867, ssp. (Pyrcz & Vilorio, in press), *Lymanopoda albocincta* (Hewitson, 1861) and *Eretris porphyria* (C. & R. Felder, 1867) ssp. (Pyrcz & Vilorio, in press), but it is not such a fast flying insect as most of the butterflies found with it.

***Manerebia germaniae* Pyrcz & Hall, n. sp.**

This species is superficially very similar to several sympatric *Manerebia*, especially *M. inderena*. *Manerebia inderena* is best distinguished by the usual presence of submarginal ocelli on the VHW that are most visible in cells Cu2-Cu1 and Cu1-M3, while in *M. germaniae* the pale dots representing the submarginal ocelli

are most visible in the middle of the wing. Also, in most *M. inderena* taxa the thin dark submarginal line is undulate, but straighter in *M. germaniae*. The male genitalia of *M. germaniae*, however, which has a toothed projection near the base of the ampulla and strongly arched uncus, readily helps distinguish *M. germaniae* from all other externally similar species. The genitalia is most similar to that of *M. leaena*, *M. pluviosa* n. sp., *M. apiculata*, *M. navarrae* and *M. satura*. Within this group, the short, squat valvae, with numerous spines at the tip and pronounced spines on the ampulla, are most similar to probable close relatives *M. leaena* and *M. pluviosa*, both of which also occupy similar habitats and occur allopatrically. In comparison with *M. leaena*, *M. germaniae* has more 'teeth' at the dorsal edge of the valva, is larger, and the submarginal lines on the ventral surface are nearly straight (rather than zigzag), running close to the outer margin. The latter character also occurs in *M. pluviosa*, which is easily distinguished by wing pattern and which is sympatric with *M. leaena* in the Venezuelan Sierra de El Tamá.

There is considerable infraspecific variation in *M. germaniae* involving the width of the VHW yellow postdiscal band, but only one geographic population is differentiated enough to deserve subspecific status. However, when additional data become available, more fine-scale patterns in geographic variation in *M. germaniae* may become apparent.

***Manerebia germaniae germaniae* Pyrcz & Hall, (n. sp.)**

Figs. 1F,G, 10D, 15

Manerebia n. sp. (Pyrcz, Willmott & Hall); Lamas & Vilorio (2004: 216, n. 1123).

Diagnosis: The nominate subspecies differs from *M. g. vitalei* in having a narrower yellow postdiscal band on the VHW.

Description: MALE (Fig. 1F): **Head:** frons with a tuft of dark brown hair; eyes blackish-brown, smooth; labial palpi covered with blackish-brown hair; antennae dorsally chestnut, ventrally rufous, with white scales at the base of each segment, club dorsally slightly darker than shaft. **Thorax:** dorsal and ventral surface dark brown; legs paler yellowish-brown. **Abdomen:** dorsal and ventral surface dark brown. **Wings:** forewing (length: 17.5-20.5 mm; mean: 19 mm; n=12) distal margin convex, apex rounded to subacute; hindwing rounded with weakly pronounced notch at tornus. DFW medium brown. DHW medium brown, slightly darker towards base, with pale postdiscal band from apex to tornus indistinctly showing from ventral surface. VFW ground colour medium brown, becoming slightly paler from base to apex; very faint, thin, straight, darker brown postdiscal line, parallel to distal margin, in cells Cu2-Cu1 to M1-R5; a row of faint, pale postdiscal spots in center of cells Cu2-Cu1 to M2-M1 gently curved basally, in some individuals outer spots indistinct; thin, faint, uneven (but not zigzag), darker brown submarginal line from apex to tornus. VHW medium brown, slightly paler towards distal margin; straight, cream-colored postdiscal band from costa to tornus through base of cell Cu1-M3; thin, faint, slightly uneven (but not zigzag), darker brown submarginal line from apex to tornus. **Male genitalia** (Fig. 10D): uncus smoothly arching, subunci relatively long, valvae short and squat with numerous 'teeth' at distal tip, some extending towards base, and

dense cluster of 'teeth' at dorsal edge of valva near base; aedeagus shallowly curving dorsally, with several short, posteriorly directed spines laterally near middle.

FEMALE (Fig. 1G): Similar to male except slightly larger (forewing length 21 mm) and lighter coloured on both wing surfaces.

Types: *Holotype male*: ECUADOR: Cotopaxi, Pilaló, 2750-3000 m, VII.1996, I. Aldas leg., MZUJ; *Allotype female*: same data as the holotype except 1997, TWP; *Paratypes* (76 males and 6 females): ECUADOR: 3 males: Pichincha, San Juan-La Victoria road, 3200 m, 30.I.2002, T. Pyrcz leg., TWP (2), MUSM (1); 1 male: same locality, 2900-2950 m, 01.II.2002, T. Pyrcz leg., TWP; 2 males: same locality, 3350 m, II.2002, I. Aldas leg., TWP; 2 males: Pichincha, Aloag-Tandapi road, km 13, 3000-3050 m, II.2002, I. Aldas leg., TWP; 2 males: Pichincha, Aloag-Tandapi road, Sector Los Alpes, 2700-2750 m, 26.I.2004, T. Pyrcz & R. Garlacz leg., TWP; 1 male: Pichincha, Volcán Pasochoa 2600-2750, 22.VIII.2003, T. Pyrcz leg., TWP; 2 males: Cotopaxi, Pilaló, 2750-3000 m, VII.1996, I. Aldas leg., TWP (1), MECN (1); 1 male: Pichincha, old Quito - Sto. Domingo rd. 2700m, 12.VIII.1993, J. Hall leg., KWJH; 1 male: Pichincha, Yanacocha, Volcán Pichincha, 3500 m, 18.IX.1997, K. Willmott leg., KWJH; 4 males: Tungurahua, Triunfo - Patate, El Tablón, 3000 m, 21.XI.1998, P. Boyer leg., TWP (1), PB (3); 2 males: Tungurahua, Triunfo - Patate, El Tablón, 3000 m, I.1999, I. Aldas leg., TWP; 3 males: Tungurahua, Baños, Runtún, 3000 m, III.1999, I. Aldas leg., TWP; 2 males: Tungurahua, Baños, Pondoá, 3365 m, 19.I.2002, J. Wojtusiak & R. Garlacz leg., TWP; 32 males: Tungurahua, Baños, El Tablón, 3000 m, III.1999, I. Aldas leg., MBLI; 5 males: Tungurahua, Baños, 3000 m, III.1999, I. Aldas leg., MBLI; 1 male: Morona-Santiago, Gualaceo-Limón road, 3100 m, 09.II.2002, T. Pyrcz leg., TWP; 1 male: same locality, 3100 m, 09.III.1998, P. Boyer leg., TWP; 1 male: Carchi, Tulcán-Maldonado, Volcán Chiles, 3000-3050 m, 27.VIII.2004, T. Pyrcz leg., TWP; 1 male: Carchi, near Huaca, 2900-3200 m, III.1999, I. Aldas leg., MBLI; 1 female: Pichincha, San Juan-La Victoria, 3300-3400 m, 30.I.2002, T. Pyrcz leg., TWP; 1 female: Tungurahua, Triunfo-Patate, El Tablón, 3000 m, 21.IX.1998, P. Boyer leg., TWP; 1 female: Tungurahua, Baños, Runtún, 3000m, VIII.1998, I. Aldas leg., TWP; 1 female: Tungurahua, Runtún, 2900-2950 m, 21.I.2002, J. Wojtusiak, leg., TWP; 1 female: Tungurahua, Baños, El Tablón, 3000m, III.1999, I. Aldas leg., MBLI; COLOMBIA: 5 males: Cauca, Volcán Puracé, Termales de San Juan, 3150-3200 m, 28-30.III.1996, T. Pyrcz leg., TWP; 1 male: Caldas, Páramo de Letras, 23.VII.1993, J-F. Le Crom leg., TWP; 2 males: Antioquia, El Retiro, 2300-2800 m, 26-30.VIII.2003, G. Rodríguez leg., TWP; 1 male: Antioquia, El Retiro, Reserva San Sebastián, 2500-2800 m, 12.IX.2003, T. Pyrcz leg., TWP; 1 female: Antioquia, El Retiro, 2300-2800 m, 18-25.VII.2003, G. Rodríguez leg., TWP.

Etymology: This species is named after the Ecuadorian entomologist, Germania Estévez, formerly of the Museo Ecuatoriano de Ciencias Naturales in Quito, in recognition of her help during our research in Ecuador.

Comments: *Manerebia germaniae* occurs at high elevations, near or at the tree-line, and has been recorded in Ecuador from 2700-3500 m. The nominate subspecies is widespread along the central Andean ridge from Colombia (Antioquia) to south-central Ecuador, where it occurs on both Andean slopes (Fig. 15). It is associated with intact cloud forest and remnant scrub. In western Ecuador (Pichincha, Cotopaxi) it generally replaces the local subspecies of *M. inderena* at higher elevations, but there is a narrow elevational band where the two occur in sympatry, generally between 2800-3100 m.

Manerebia germaniae vitalei Pyrcz & Willmott, n. ssp.

Figs. 1H, 10E, 15

Manerebia n. sp., n. ssp. (Pyrcz, Willmott & Hall); Lamas & Viloria (2004: 216, n. 1123b).

Diagnosis: In this taxon the VHW yellow postdiscal band is

approximately 1.5 times the width of that of the nominate subspecies.

Description: MALE (Fig. 1H): *Head, thorax* and *abdomen*: as in the nominate subspecies. *Wings:* Forewing (length: 19.5 mm; mean: 19.5 mm; n=2) distal margin very slightly convex, apex subacute; hindwing rounded with weakly pronounced notch at tornus. DFW surface medium brown. DHW medium brown; pale postdiscal band from apex to tornus indistinctly showing from ventral surface. VFW ground colour medium brown, slightly lighter in submarginal area; very faint, thin, darker brown postdiscal line, straight and parallel to outer margin from vein R5 to Cu2, then curving towards tornus; a row of faint, barely visible pale yellow postdiscal spots in center of cells Cu2-Cu1 to M2-M1; thin, faint, uneven (but not zigzag), darker brown submarginal line from apex to tornus. VHW medium brown, slightly paler towards distal margin; straight, approximately 2mm wide, cream-colored (with an orange shade towards anal margin) postdiscal band from costa to tornus through base of cell Cu1-M3; occasional 3 to 4 minute pale yellow postdiscal spots; faint, slightly uneven (but not zigzag), darker brown submarginal line from apex to tornus. *Male genitalia* (Fig. 10E): similar to that of the nominate subspecies.

FEMALE: Unknown.

Types: *Holotype male*: ECUADOR: Loja, OSId road Loja - Zamora, 2500 m, XI-XII.1999, I. Aldas leg., ex MBLI, MZUJ. *Paratype male*: same data as the holotype, MBLI.

Etymology: This subspecies is dedicated to the Italian lepidopterist Fabio Vitale, from Lecce, who specializes in the Ithomiinae.

Comments: This subspecies consistently differs from the nominate throughout its range in the width of the VHW postdiscal band. It is the southernmost representative of *M. germaniae*, and is known to date only from the eastern slopes of the Ecuadorian Andes in the province of Zamora-Chinipe (Fig. 15), though it may also extend into extreme northern Peru.

Manerebia pluviosa Pyrcz & Viloria, n. sp.

Figs. 2A, 10F, 15

Manerebia n. sp. (Pyrcz & Viloria); Lamas & Viloria (2004: 216, n. 1120).

Diagnosis: This species is easily distinguished from any congener by the wide yellow postdiscal band on both fore- and hindwing dorsal and ventral surface.

Description: MALE (Fig. 2A): *Head:* frons with a tuft of dark brown hair; labial palpi covered with short dark brown hair; eyes dark brown, smooth; antennae dark brown dorsally, chocolate brown ventrally with white scales at base of each segment, club twice as wide as shaft, of same colour. *Thorax:* dorsally dark brown, hairy, ventrally pale brown; legs paler yellowish-brown. *Abdomen:* dorsally dark brown, laterally and ventrally pale brown. *Wings:* Forewing (length: 19 mm, n=2) triangular; tornus slightly obtuse. Hindwing rounded, anal margin slightly excavated near tornus. Dorsal ground colour uniform chocolate brown, except for entire postdiscal yellow band on both wings, more distinct on hindwing; basal half and anal region of hindwing with long thin brown hairs. VFW colour pattern similar to dorsal surface but in general more intense; postdiscal band more distinct and wider, reaching tornus; submarginal and marginal regions lighter brown. VHW similar to dorsal surface but more intense in colour; postdiscal band slightly broadened towards central portion; series of four submarginal white dots in cells M2-M3 to Cu2-1A, respectively, the first one half diameter of others, which are ca. 0.8 mm. *Male genitalia* (Fig. 10F): uncus arched, valva with spiny dorsal process near base, aedeagus short.

FEMALE: Unknown.

Types: *Holotype male*: VENEZUELA: Táchira, Parque Nacional El Tamá, entre Betánia y La Banderola, 2810 m, 23.VIII.1996, A. Viloria leg., MALUZ. *Paratype male*: VENEZUELA: Táchira, Parque Nacional El Tamá, Fundo Piedra Blanca, San Vicente de la Revancha, 2400 m, 9-12.XII.1997, F. Rey leg., TWP.

Etymology: The name is the feminine form of the Latin adjective "pluviosus", meaning rainy. The male holotype was collected while flying very weakly during heavy rain in the upper cloud forest of the Sierra de El Tamá.

Comments: The male genitalia of this species are most similar to those of *M. leaena* and *M. germaniae*, with an arched uncus and spiny process at the dorsal base of the valva. In *M. pluviosa* the narrow dark VHW submarginal line is smoothly curving, not dentate like *M. leaena*, and in this respect resembles that of *M. germaniae*, which may prove to be its sister species. *Manerebia pluviosa* occurs in the Sierra de El Tamá in habitats similar to those of *M. germaniae*, close to the tree-line, and possibly replaces *M. leaena gonzalezi* at higher elevations. The paratype was collected in disturbed habitat in San Vicente de la Revancha at an elevation that is probably beneath that at which the species usually occurs. *Manerebia pluviosa* is extremely similar (though about half the size) to the microsympatric pronophiline *Pedaliodes* sp. Pyrcz & Vilorio (in press), though it is not clear whether this similarity results from mimicry, and if so, what the basis for this mimicry might be. Some 30 years ago *M. pluviosa* was also captured by J. Bechyné, at 3100 m in the páramo of a remote mountain range in the north Colombian department of Norte de Santander (Cerro Oroque), where no other butterflies have since been collected. That specimen shows some distinctive characters and might represent a separate subspecies, so it is therefore excluded from the type series. This species seems to be a rare insect and has only been recorded during the wet season.

Manerebia apiculata (C. & R. Felder, 1867)

Figs. 2B,C, 11A, 15

Pronophila apiculata C. & R. Felder (1867: 474). **TL:** Colombia, Cundinamarca, Bogotá. **ST male:** "apicu-lata Feld/Felder Colln./Rothschild Bequest B.M. 1939-1/4/Bogota Lindig type/Type". BMNH(R) [examined].

= *Lymanopoda apiculata* form *curvilinea* Weymer (1912: 248). **TL:** Colombia, East Cordillera, Cundinamarca, Boquerón de C(h)ipaque. **ST male(s):** ZMHU? [not located].

Lymanopoda apiculata (C. & R. Felder); Weymer (1911: pl. 53, row a (*apiculata* [sic])); 1912: 248).

Penrosada apiculata (C. & R. Felder); Brown (1944: 257, pl. 1, fig. 1622) (male genitalia); Pyrcz (1999: 367).

Manerebia apiculata (C. & R. Felder); Lamas & Vilorio (2004: 215).

Diagnosis: The male genitalia (Fig. 11A) of this species are similar to those of *M. leaena*. The species is easily distinguished externally from all other sympatric *Manerebia* in the Colombian Cordillera Oriental by the acute forewing apex. The expression of the VHW band is variable, exhibiting a similar polymorphism to the Ecuadorian *M. interrupta* (Fig. 6E,F,G) and *M. ignilineata* (Fig. 7D,E,F). The syntype specimen in the BMNH lacks any VHW post-discal band, while the form in which the band is fully developed flies with typical specimens (Adams, 1986) and was named form *curvilinea* by Weymer (1912) (Lamas & Vilorio, 2004). Although we have not located any types of *curvilinea*, the description clearly applies to this form of *M. apiculata*, which cannot be confused with any other *Manerebia* species from the region of the type locality.

Comments: This species inhabits the forest/páramo ecotone on both slopes of the central Cordillera Oriental in Colombia (Cundinamarca: Sibaté, Fusagasugá, Facatativá), from 3150-3300 m, where it occurs with *M. levana* (Adams, 1986).

Manerebia franciscae (Adams & Bernard, 1981)

This species is most closely related to *M. mam-muthus* n. sp., *M. satura* and *M. navarrae*, and all four species are allopatric. The males of all of these species

are unique among north Andean *Manerebia* in having a distinct dark brown patch of androconial scales on the DFW in the posterior third of the discal cell and basal part of cells 1A-Cu2 to M2-M1 (Figs. 2, 3). The male genitalia are also similar, with an arched uncus, relatively long subunci and valva with a spiny dorsal process near the base, similar to *M. leaena* and related species (Figs. 10, 11; see Discussion under that species). *Manerebia franciscae* differs from the two neighbouring species *M. navarrae* and *M. mam-muthus* in having an almost smooth aedeagus, with only a few spines on the left side. Other differences are discussed under those two species. It differs from *M. satura* in the narrower, distal process of the valva being relatively longer, with the mid-ventral edge of the valva more indented.

There is geographic variation in the presence or absence of the pale VHW postdiscal band, as in *M. satura*, and two subspecies are recognised.

Manerebia franciscae franciscae (Adams & Bernard, 1981)

Figs. 2D, E, 11B, 16

Penrosada franciscae Adams & Bernard (1981: 365, figs 11, 25, 26). **TL:** Venezuela, Mérida, above La Montaña, S. of Mérida. **HT male:** BMNH(A&B) [examined].

Manerebia franciscae (Adams & Bernard); Lamas & Vilorio (2004: 215).

Diagnosis: This subspecies is superficially most similar to *M. inderena inderena*, with which it occurs, but the large tornal and apical ocelli on the VHW, with those in the middle of the wing reduced, are diagnostic.

Comments: Contrary to the statement of Adams & Bernard (1981), this taxon is not restricted to the Venezuelan Cordillera de Mérida, but also occurs in the Sierra de El Tamá and on the western slopes of the Cordillera Oriental in Colombia (Pacho, TWP, SMTD) (Fig. 16). Adams & Bernard (1981) report that *M. f. franciscae* flies with a skipping action, usually more than 2 m above the ground, and rests on foliage. Eggs are laid on the brownish petioles of young leaflets, near the nodes of *Chusquea* bamboo canes, from 1-4 m above the ground. The species was seasonally common at the type locality, and Adams & Bernard (1981) collected it from 2300-2600 m. We have also found the species to be seasonal, only observing and collecting it in the Cordillera de Mérida in the rainy season from June to September (Pyrcz, pers. obs.).

Manerebia franciscae rodriguezi Pyrcz & Willmott, n. ssp.

Figs. 2F,G, 11C, 16

Diagnosis: This taxon differs from nominate *M. franciscae* primarily by the absence of VHW yellow postdiscal band. The apical ocelli on the VHW are also reduced, the yellowish rings surrounding the VHW ocelli are indistinct, and the dark, thin submarginal lines on the VFW and VHW are slightly reddish.

Description: MALE (Fig. 2F): **Head, thorax** and **abdomen** same as in the nominate subspecies. **Wings:** Forewing (length: 21.5-22 mm; mean: 21.7; n=3) distal margin straight to slightly convex, apex rounded; hindwing rounded with almost no notch at tornus. DFW chocolate brown; darker brown androconial scales occupying posterior one-third of discal cell, basal half of cells 1A-Cu2, basal third of cell Cu1-M3, and basal quarter of cells M3-M2 and M2-M1.

DHW uniform chocolate brown; occasionally one small black submarginal white oval dot ringed with black in Cu1-Cu2 and two, even smaller, in 1A-Cu2. VFW ground colour medium brown becoming paler and lighter towards distal half; thin, irregular reddish brown submarginal line, parallel to distal margin and very thin, reddish brown marginal line parallel to outer margin, from apex to tornus. VHW uniform medium brown; very faint, darker brown, straight postdistal line from apex to anal margin near tornus; uneven, faint submarginal reddish brown line and reddish brown marginal line; small, white, oval submarginal dots in cell Cu2-Cu1, and two in cell 1A-Cu2, ringed with black. **Male genitalia** (Fig. 11C): uncus long and arched; subunci long and thin; numerous small spines on distal tip of valva extending anteriorly along dorsal edge, dorsal base of valva with a projection with two 'teeth'; aedeagus length of valva, slightly curved.

FEMALE (Fig. 2G): Slightly larger than male (forewing length 23 mm), with more prominent white dots on ventral surface occasionally taking shape of fully developed ocelli, particularly in cell Cu1-M3 on VFW, showing through on dorsal surface, and additionally with minute submarginal white dots present in most cells of fore and hindwing.

Types: Holotype male: COLOMBIA: Antioquia, Guarné, 2600-2650 m, 14.III.1997, G. Rodríguez *leg.*, MZUJ; **Allotype female:** Antioquia, El Retiro, 1800 m, 19.VIII.2002, G. Rodríguez *leg.*, TWP; **Paratypes (4 males and 2 females):** COLOMBIA: **1 male:** Antioquia, no data, G. Rodríguez *leg.*, GR; **1 male:** Antioquia, El Retiro, Río Agudelo, 2400 m, VII.1999, G. Rodríguez *leg.*, GR; **1 male:** Antioquia, El Retiro, 2800 m, 24.VI.2001, G. Rodríguez *leg.*, GR; **1 male:** Antioquia, El Retiro, 2200-2600 m, 20.VIII.2003, G. Rodríguez *leg.*, MZUJ; **1 female:** Antioquia, Envigado, 2600 m, 29.XI.2002, G. Rodríguez *leg.*, GR; Antioquia, Santa Elena, Represa de Piedras Blancas, 2600m, 15.IX.2003, Rodríguez *leg.*, GR.

Etymology: This subspecies is named after its first collector, Gabriel Rodríguez from Medellín.

Comments: This taxon is associated with *M. franciscae* based on similar male genitalia and VHW pattern, with characteristic submarginal white dots in cells Cu2-Cu1 and 1A-Cu2. *Manerebia franciscae rodriguezi* is apparently endemic to the northern Cordillera Central in Colombia, where it occurs in mid-elevation cloud forest, similar to the nominate subspecies.

Manerebia mammuthus Pyrcz & Willmott, n. sp.

Figs. 2H, 11D, 16

Manerebia n. sp. (Pyrcz, Willmott & Hall); Lamas & Viloria (2004: 216, n. 1127).

Diagnosis: This species is distinguished from its closest relatives, *M. franciscae* and *M. satura* (see Discussion under *M. franciscae*), by its large size, the virtual absence of any ventral submarginal ocelli and characters of the male genitalia. The aedeagus has a large patch of dense, tiny spines on both sides, while *M. franciscae* and *M. satura* have at most a single lateral line of spines on each side or are smooth. The narrower distal portion of the valva is relatively shorter than in *M. franciscae*, and the mid-ventral edge of the valva is indented, like *M. franciscae* but not *M. satura*, in which it is flatter.

Description: **MALE** (Fig. 2H): **Head:** frons with a tuft of dark brown hair; eyes blackish-brown, smooth; labial palpi covered with blackish-brown hair; antennae dorsally chestnut, ventrally rufous, with white scales at the base of each segment, club dorsally slightly darker than shaft. **Thorax:** dorsal and ventral surface dark brown; legs paler yellowish-brown. **Abdomen:** dorsal and ventral surface dark brown. **Wings:** forewing (length: 22.5-24 mm, mean: 23.3 mm, n=2) distal margin convex, apex rounded; hindwing rounded with almost no notch at tornus. DFW medium brown; darker brown androconial scales occupying posterior half of discal cell, basal half of cells 1A-Cu1, basal third of cell Cu1-M3, and basal quarter of cell M3-M2. DHW medium brown, slightly darker towards base, with pale postdiscal band from apex to tornus indistinctly show-

ing from ventral surface. VFW ground colour medium brown, becoming slightly paler from base to apex; very faint, thin, straight, darker brown postdiscal line, parallel to distal margin, in cells 1A-R5; three whitish postdiscal dots in centers of cells Cu1-M1; thin, faint, uneven, darker reddish brown submarginal line from apex to tornus; margin thinly lined with darker brown. VHW medium brown; thin, straight, yellowish cream-colored postdiscal band from costa to tornus through base of cell Cu1-M3; thin, faint, zigzag, darker reddish brown submarginal line from apex to tornus; tiny white submarginal dots in centers of cells 1A-M2. **Male genitalia** (Fig. 11D): uncus long and smoothly arching; subunci relatively long; valvae thinning gradually at middle towards posterior tip, dorsally grooved, with 4-6 'teeth' at distal tip and several additional 'teeth' extending basally along inner edge; thin, pointed projection at dorsal edge of valva near base, with numerous tiny spines; aedeagus curving dorsally, with patches of numerous short, posteriorly directed spines laterally near middle, on both sides.

FEMALE: Unknown.

Types: Holotype male: ECUADOR: Sucumbíos, km 9 La Bonita-Tulcán rd., El Higuerón, 2200 m, 10.XI.1997, K. Willmott *leg.*, to be deposited in AME; **Paratypes (3 males):** ECUADOR: **1 male:** same data as the holotype, KWJH; COLOMBIA: **1 male:** same locality as the holotype, 2000-2400 m, X.2001, I. Aldas *leg.*, ex MBLI, TWP; **1 male:** same data as preceding, MBLI.

Etymology: The specific name is a noun in apposition derived from the elephant genus *Mammuthus*, with reference to this species' large size, almost uniform brown coloration and elongate uncus and subunci, resembling the trunk and tusks of these extinct creatures.

Comments: We deliberated as to whether to treat this taxon as a subspecies of either *M. satura* or *M. franciscae*. However, the number of consistent wing pattern and genitalic differences between these three species suggest they should be maintained. In addition, it appears to occur at higher elevations than *M. satura*. This species is known from only four specimens, all collected in far northeastern Ecuador along the valley of the Río Chingual along a trail through secondary growth, with large tracts of undisturbed forest within 50 m distance, from 2000-2400 m. The two males collected by KW were encountered on the same day puddling on wet sand and feeding on horse dung. Despite a number of other visits to the same locality the species has only been seen on two occasions.

Manerebia satura (Weymer, 1911)

Figs. 3A, 11G

Lymanopoda leaenavar. satura Weymer (1911: pl. 52, row f; 1912: 249). **TL:** Peru, Cuzco; Colombia, Tolima, Quindiu Pass. **ST male(s):** ZMHU? [not examined].

Penrosada satura (Weymer); Brown (1944: 258) (status uncertain).

Manerebia satura (Weymer); Lamas & Viloria (2004: 216).

This is a large species, closely related to the allopatric *M. franciscae*, *M. mammuthus* and *M. navarrae*, as discussed under *M. franciscae*. The male genitalia are distinctive, with the distal, narrower portion of the valva being relatively short, and often only bearing a few large spines, rather than numerous smaller spines. Unlike *M. mammuthus*, the aedeagus is smooth or has only a single lateral line of spines. It is the most widespread member of the genus and it is fairly polytypic, occurring along the eastern slopes of the Andes from Bolivia to Ecuador in lower to mid-elevation cloud forests.

Manerebia satura was described based on specimens

from two localities, Cuzco (Peru) and Quindiu Pass (Colombia), representing two distinct species. The specimen figured in the original description represents the species as treated here, while those from Colombia are actually *M. inderena* Adams (see Adams, 1986), which also has a white VHW band but is smaller, with smaller VHW ocelli, and is not closely related to *M. satura*. The syntype specimen(s) should be in the ZMHU (G. Lamas, pers. comm.), but despite some searching we have been unable to locate any. For the present we do not designate either a lectotype or neotype, since the type specimens may yet be found, but our usage of the name preserves nomenclatural stability, as should any future type designation. The nominate subspecies, distinguished by the wide white VHW postdiscal band and large tornal and apical ocelli, particularly in cell Cu2-Cu1 (Fig. 3A), occurs in southern Peru only (Cuzco, Puno, perhaps to northern Bolivia). An undescribed subspecies of *M. satura*, characterised by a yellow VHW band, occurs from central Peru (Junín, Pasco) to northern Peru (San Martín, Amazonas) (Pyrz, in prep.). In extreme northeastern Peru in the Cordillera del Cóndor, and in eastern Ecuador, occur two distinct subspecies, described below.

***Manerebia satura lamasi* Pyrcz & Willmott, n. ssp.**

Figs. 3B, 11F, 16

Diagnosis: This subspecies is larger than the similar and neighbouring *M. s. pauperata* (described below), darker brown on both wing surfaces, with smaller ocelli on the VHW and a small ocellus in cell M1-M2 on the VFW. There is no slightly paler brown postdiscal line and the narrow, dark submarginal lines are less marked.

Description: MALE (Fig. 3B): **Head**, **thorax** and **abdomen** as in *M. satura pauperata*. **Wings:** forewing (length: 22.5-23.5 mm; mean: 23 mm; n=3) distal margin straight, apex rounded; hindwing rounded with very weakly pronounced notch at tornus. DFW dark brown; androconial scales occupying posterior half of discal cell, basal half of cells 1A-Cu1, basal third of cell Cu1-M3, and basal quarter of cell M3-M2. DHW uniform dark brown, with two small submarginal black ocelli thinly ringed with yellow in cells 1A-Cu2 and Cu2-Cu1; a barely visible submarginal blackish line. VFW ground colour dark brown, slightly lighter along outer margins; tiny black submarginal ocelli with white pupils in cells M2-M1, Cu2-Cu1 (and in M1-R5 in one individual); faint, black submarginal line from tornus to apex; two thin, straight, dark brown marginal lines. VHW uniform dark brown; barely visible straight, thin, blackish postdiscal line from tornus to apex, joining with a better marked, blackish submarginal line that is smoothly curving and parallel to distal margin; black submarginal ocelli, ringed with dark yellow, with white pupils, as follows: two small in cell 1A-Cu2, one larger in cell Cu2-Cu1 (half width of cell), one in cell M2-M1, one small in cell M1-Rs, and tiny white dots in cells Cu2-M3; thin, blackish marginal line close to and parallel with distal margin. **Male genitalia** (Fig. 11F): uncus long and arched; subunci relatively long; valva thinning gradually throughout from base to posterior tip, dorsally grooved, with 6 'teeth' at distal tip; wide, toothed projection at dorsal edge of valva near base; saccus shallow; aedeagus short, slightly curved dorsally and smooth.

FEMALE: Unknown.

Types: *Holotype male*: PERU: Amazonas, Cordillera del Cóndor,

2-3 km N PV3 (Alfonso Ugarte), 0345/7826, 1600-1750 m, 22.VII.1994, G. Lamas leg., MUSM; **Paratypes:** 2 males: same data as the holotype, MUSM.

Etymology: This subspecies is named for Gerardo Lamas, the collector of the type series, in gratitude for all his help and correspondence over many years.

Comments: *Manerebia satura lamasi* appears to be endemic to the Cordillera del Cóndor. Other pronophilines that are also apparently endemic to this mountain range include *Manerebia magnifica* n. sp. (described below), which occurs in the same area but at lower elevations, and an undescribed species of *Panyapedaliodes* Forster, 1964 (Viloria & Lamas, in prep.).

***Manerebia satura pauperata* Pyrcz & Willmott, n. ssp.**

Figs. 3C,D, 11E, 16

Euptychia jovita (C. & R. Felder); D'Abrera (1988: 778) (misidentification).

Penrosada sp.; D'Abrera (1988: 824) (misidentification).

Manerebia satura n. ssp. (Pyrz, Willmott & Hall); Lamas & Viloria (2004: 216).

Diagnosis: Males of this subspecies are distinguished from all other *M. satura* subspecies, except *M. s. lamasi*, by the absence of the pale VHW postdiscal band. In females the band is well-developed and chalky white, but specimens may easily be identified by the large ocellus in cell Cu2-Cu1 that is visible on the dorsal surface of both wings. The characters that distinguish this subspecies from *M. s. lamasi* are discussed under that taxon.

Description: MALE (Fig. 3C): **Head:** frons with a tuft of dark brown hair; eyes blackish-brown, smooth; labial palpi covered with blackish-brown hair; antennae dorsally chestnut, ventrally rufous, with white scales at the base of each segment, club dorsally slightly darker than shaft. **Thorax:** dorsal and ventral surface dark brown; legs paler yellowish-brown. **Abdomen:** dorsal and ventral surface dark brown. **Wings:** forewing (length: 19.5-22 mm; mean: 20.7 mm, n=10) distal margin straight, apex rounded; hindwing rounded with very weakly pronounced notch at tornus. DFW medium brown; darker brown androconial scales occupying posterior half of discal cell, basal half of cells 1A-Cu1, basal third of cell Cu1-M3, and basal quarter of cell M3-M2. DHW medium brown, slightly darker towards base, with two submarginal black ocelli ringed with yellow in cells 1A-Cu2 and Cu2-Cu1. VFW ground colour medium brown, becoming slightly paler from base to distal margin; thin, straight, darker brown postdiscal line, parallel to distal margin, in cells 1A-R5; a tiny black submarginal spot ringed with yellow in cell Cu2-Cu1; distinct, uneven, darker brown submarginal line from tornus to apex, becoming more undulate towards apex; two thin, straight, dark brown marginal lines. VHW medium brown, darker in basal half; distinct, thin, darker brown postdiscal line from tornus to apex, joining with a distinct, darker brown submarginal line that is smoothly curving and parallel to distal margin; black submarginal ocelli, ringed with dark yellow, with white pupils, as follows: two small in cell 1A-Cu2, one large in cell Cu2-Cu1 (almost width of cell), one medium in cell M2-M1, one small in cell M1-Rs, and tiny white dots in cells Cu2-M3; thin, dark brown marginal line close to and parallel with distal margin. **Male genitalia** (Fig. 11E): uncus long and smoothly arching; subunci relatively long; valva thinning gradually throughout from base to posterior tip, dorsally grooved, with 4-6 'teeth' at distal tip; thin, rounded projection at dorsal edge of valva near base; aedeagus curving dorsally, with a row of several short, posteriorly directed spines laterally near middle, on each side.

FEMALE (Fig. 3D): Differs from male as follows: larger (slightly length: 22-23 mm; mean: 22.5 mm, n=2) paler brown throughout. DFW lacking androconial scales, with large submarginal black, yellow-ringed ocellus with white pupil in cell Cu2-Cu1. DHW with ventral ocelli visible in cells 1A-Cu2, Cu2-Cu1, Cu1-M3, and M2-M1. VFW with similar large ocellus in cell Cu2-Cu1, with yellow

ring extending into cells anterior and posterior, and tiny white submarginal dots in cells Cu1-M1. VHW with broad, chalky white postdiscal band posterior to dark brown postdiscal line, broadest in cells 1A-Cu2 and Cu2-Cu1, ocellus in cell M1-Rs larger.

Types: *Holotype male*: ECUADOR: Zamora-Chinchipe, Loja - Zamora km 40, 1500 m, 31.VIII.1990, P. Gros & S. Attal, MZUJ; *Allotype female*: same data as the holotype, MZUJ; *Paratypes (10 males and 2 females)*: ECUADOR: **1 male and 1 female**: Zamora-Chinchipe, Loja-Zamora rd., nr. Sabanillas, Quebrada San Ramón, 1700 m, 27-29.X.1997, K. Willmott *leg.*, KWJH; **2 males**: Zamora-Chinchipe, Zamora-Loja rd., 1800 m, 9.XI.1996, K. Willmott *leg.*, KWJH (1), MECN (1); **1 female**: Zamora-Chinchipe, Loja - Zamora km 40, 1500 m, 01.IX.1990, P. Gros & S. Attal, TWP; **3 males**: same data as the holotype, TWP; **1 male**: same data but 03.IX.1990, TWP; **1 male**: same data but 08.XI.1996, TWP; **1 male**, Zamora-Chinchipe, West of Valladolid, 1800 m, 22.IV.1997, A. Jasiński *leg.*, TWP; **1 male**: Zamora-Chinchipe, Valladolid, 25.VII.1992, G. Estévez, MECN; **1 male**: Tungurahua, Machay, 17.X.1994, I. Aldas *leg.*, TWP.

Etymology: The name is the feminine form of the Latin adjective "pauperatus", meaning impoverished, with reference to the absence of the pale ventral hindwing postdiscal band in males, in comparison with the nominate subspecies.

Comments: This taxon was illustrated twice by D'Abrera (1988) as *Penrosada* sp. (p. 824) and as *Euptychia jovita* (p. 778). It apparently occurs from northeastern (Napo - one male in coll. TWP from Cordillera de Huacamayos, no date, A. Jasiński *leg.*, Tungurahua) to southeastern (Zamora-Chinchipe) Ecuador (Fig. 16), although it is more common in the south, and has been collected in cloud forest habitats in a narrow elevational band from 1500-1800 m. The specimen from Cordillera de los Huacamayos is excluded from the type series since it shows slight differences to southern specimens. We have found males puddling along forested streams, and a single female flying low to the ground in a small field at the forest edge.

Manerebia navarrae (Adams & Bernard, 1979)

Figs. 3E, 11H, 16

Penrosada navarrae Adams & Bernard (1979: 114, figs 11, 32).

TL: Colombia, César, Serranía de Valledupar, 2300 m. **HT male:** BMNH(A&B) [examined].

Manerebia navarrae (Adams & Bernard); Lamas & Viloria (2004: 215).

Diagnosis: This species superficially resembles several other *Manerebia* that lack the pale VHW postdiscal band, but may be distinguished by the orange wedge extending basally from the VHW postdiscal line at the tornus, and by the ocellus in cell Cu2-Cu1, which is absent in the superficially similar *M. quinterae*. The male genitalia (Fig. 11H) are distinctive in the dorsal process at the base of the valva being more elongate than in other species, while the thickened, strongly curved aedeagus with a dense patch of spines on the right side only is unique.

Comments: This species appears to be most closely related to *M. satura*, *M. mammothus* and *M. franciscae*, as discussed under the last of these species. It is known only from the type locality in the Serranía de Valledupar in the Sierra de Perijá range on the Colombia/Venezuela border, at 2300 m. Adams & Bernard (1979) state that the entire type series was caught before 10:00 hrs, flying around a single patch of bamboo.

Manerebia quinterae (Adams & Bernard, 1979)

Figs. 3F, 11I, 16

Penrosada quinterae Adams & Bernard (1979: 115, figs 12, 33, 34). **TL:** Venezuela, Zulia, Serranía de Valledupar, 3050 m. **HT male:** BMNH(A&B) [examined].

Manerebia quinterae (Adams & Bernard); Lamas & Viloria (2004: 215).

Diagnosis: The ventral surface of *M. quinterae* (Fig. 3F) somewhat resembles that of *M. navarrae*, but *M. quinterae* may be easily distinguished by the irregular dark postdiscal line, lack of any well developed submarginal ocelli, and instead a submarginal line of whitish spots in cells Cu2-M1. The male genitalia (Fig. 11I) are distinctive in lacking a spiny dorsal process at the base of the valva, unlike all preceding species, but notably have an arched uncus, like many of the preceding species. The affinities of this species are therefore unclear. The small, lateral patches of spines on both sides of the aedeagus near its posterior tip are distinctive.

Comments: Adams & Bernard (1979) reported that this species occurred from 2750-3050 m in the Serranía de Valledupar, where it could be locally and seasonally common. It is known to date only from the type locality.

Manerebia inderena (Adams, 1986)

The male genitalia of this species do not differ from those of *M. golondrina* n. sp., which can be immediately recognised by the lack of a VHW postdiscal yellow or white band, and are also similar to *M. prattorum* n. sp. These three species can be distinguished from other species by the simple valva (lacking a prominent spiny process at the dorsal edge near the base), the uncus which is strongly "bent" near the base (almost straight in *M. undulata* n. sp., *M. trimaculata* and *M. interrupta*), then approximately straight (smoothly curving in *M. rufanalis*), and in usually having several tiny 'teeth' on the lefthand side of the aedeagus. The VHW narrow dark submarginal line is irregularly zigzag, but never as undulate as in *M. undulata* or parallel to the distal margin as in *M. germaniae*.

This is a widespread and polytypic species. The various taxa are grouped together on the basis of similar genitalia, habitat and elevation, and close range allopatry. Reasons for considering *M. golondrina* a distinct species are discussed under that species.

Manerebia inderena inderena (Adams, 1986)

Figs. 3G,H, 12A, 17

Penrosada inderena Adams (1986: 305). **TL:** Colombia, Tolima, south above Cajamarca. **HT male:** BMNH(A&B) [examined].

Manerebia inderena (Adams); Lamas & Viloria (2004: 215).

Diagnosis: The nominate subspecies (Fig. 3G,H) is characterized by medium wide, whitish VHW postdiscal band, that is yellow and usually thinner in *M. i. antioquiensis*, white and much thinner in *M. i. fina*, whitish and wider in *M. i. clara*, wider and yellow in *M. i. mirena*, *M. i. leaeniva* and *M. i. similis*. The nominate subspecies and *M. i. antioquiensis* may also be distinguished from other similar species (*M. germaniae*, *M. leaena*, *M. franciscae*) by the three marked submarginal ocelli in cells 1A-Cu2 and Cu2-Cu1 only. Male genitalia as illustrated (Fig. 12A).

Comments: Adams (1986) stated that this taxon could be found skipping around clumps of bamboo, resting on the foliage, and occasionally descending to feed on excrement on the ground. In Colombia it has been found in the Cordillera Central in Tolima and Cauca (Volcán Puracé) where it occurs from 2450-3100 m (Pyrz, 1999) (Fig. 17). It is locally sympatric with *M. germaniae* n. sp. (described below) at the highest reach of its altitudinal range. Specimens of *M. inderena* from extreme northern Ecuador on the eastern slopes of the Andes (Sucumbíos, Carchi) are considered

for the present as representing the nominate subspecies, although in general they are slightly larger, with a slightly broader pale VHW band, and generally reduced VHW ocelli, in some specimens approaching *M. i. fina*.

***Manerebia inderena antioquiensis* Pyrcz & Willmott n. ssp.**

Figs. 4A,B, 12B, 17

Manerebia inderena n. ssp. (Pyrcz, Willmott & Hall); Lamas & Viloria (2004: 215).

Diagnosis: This subspecies has yellow VHW bands, instead of white as in the nominate subspecies, and is typically smaller than the latter.

Description: MALE (Fig. 4A): **Head:** eyes, labial palpi and antennae same as in the nominate subspecies. **Thorax:** dorsal and ventral surface dark brown; legs paler brown. **Abdomen:** dorsal and ventral surface dark brown. **Wings:** forewing (length: 16.5-18.1 mm, mean: 17.3 mm, n=4) distal margin straight, apex rounded; hindwing rounded with very weakly pronounced notch at tornus. DFW medium brown; darker brown in discal area. DHW medium brown, slightly darker towards base, with two submarginal black ocelli ringed with dark orange in cells 1A-Cu2 and Cu2-Cu1. VFW ground colour medium brown, becoming slightly paler from base to apex; thin, straight, darker brown postdiscal line, parallel to distal margin, in cells 1A-R5; a tiny black submarginal spot ringed with dark orange in cell Cu2-Cu1; distinct, zigzag, darker brown submarginal line from tornus to apex; thin, straight, dark brown marginal line. VHW medium brown; pale yellowish postdiscal band from apex to tornus, passing through base of cell Cu1-M3; distinct, darker brown, strongly zigzag submarginal line; two small black submarginal ocelli, ringed with dark orange-brown, with white pupils, in cells 1A-Cu2 and Cu2-Cu1; thin, very faint, dark brown marginal line close to and parallel with distal margin. **Male genitalia** (Fig. 12B): similar to nominate subspecies.

FEMALE (Fig. 4B): Similar to male, except VHW postdiscal band whitish, instead of yellow, and ventral ocelli better marked.

Types: **Holotype male:** COLOMBIA: 1 male: Antioquia, San Felix, Las Antenas, 2700-3050 m, 13.IX.2003, T. Pyrcz leg., MZUJ; **Allotype female:** COLOMBIA: Antioquia, Medellín, El Retiro, Reserva San Sebastián, 2500-2800 m, 12.IX.2003, T. Pyrcz leg., TWP; **Paratypes (14 males):** COLOMBIA: 1 male: Antioquia, Medellín, El Retiro, Reserva San Sebastián, 2500-2800 m, 12.IX.2003, T. Pyrcz leg., TWP; 1 male: same locality, 2600m, 09.XI.2002, G. Rodríguez leg., TWP; 1 male: same locality, 2300-2800 m, 18-25.VII.2003, G. Rodríguez leg., TWP; 2 males: same locality, 2600-2800 m, 20.XII.2002, G. Rodríguez leg., (1 TWP, 1 BMNH); 1 male: same locality, 2600-2800 m, 26-30.VIII.2003, G. Rodríguez leg., TWP; 1 male: same locality, 2200-2600 m, 20.VIII.2003, G. Rodríguez leg., TWP; 2 males: Antioquia, Medellín, El Retiro, 2700m, 01.VIII.1993, J-F. Le Crom leg., TWP; 1 male: Antioquia, Polmifor, 24.VII.2001, G. Rodríguez leg., TWP; 1 male: Antioquia, Envigado, 2600-2800 m, 06.VI.2004, G. Rodríguez leg., TWP; 1 male: Antioquia, Los Llanos, vía a San Andrés km 10-14, 2600-2750 m, 14.XI.2003, T. Pyrcz leg., TWP; 2 males, Antioquia, El Retiro, 2600-2700 m, 18.XII.2001, G. Rodríguez leg., MBLL.

Etymology: This taxon is named after the Colombian department of Antioquia, where the type locality is situated.

Comments: To date this taxon is known only from the northern part of the Colombian Cordillera Central, from 2500-2800 m, where it appears to be locally not uncommon.

***Manerebia inderena fina* Pyrcz & Willmott, n. ssp.**

Figs. 4C,D, 12C, 17

Manerebia n. sp., n. ssp. (Pyrcz, Willmott & Hall); Lamas & Viloria (2004: 216, n. 1124b).

Diagnosis: This subspecies differs from other Ecuadorian sub-

species by having a narrower VHW postdiscal band. Along with *M. i. similis*, it may also be distinguished from all other subspecies by the dark, thin submarginal line on the VHW being more smoothly curving, rather than dentate as in other taxa. The nominate subspecies and *M. i. antioquiensis* also differ in having marked VHW submarginal ocelli, especially in 1A-Cu2 and Cu2-Cu1, that are usually absent or much reduced in *M. i. fina*. The width of the band in *M. i. fina* is about the same as in *M. germaniae germaniae*, which is locally sympatric, though generally occurring at higher elevations. The latter is distinguished externally with difficulty, by several subtle characters (see under *M. germaniae*). Another similar (though not sympatric) taxon is the Colombian *M. leaena lanassa*. Both *M. leaena* and *M. germaniae* are most reliably distinguished by the male genitalia, which have a curving uncus, relatively long subunci and 'teeth' at the dorsal edge of the valva near the base.

Description: MALE (Fig. 4C): **Head:** frons with a tuft of dark brown hair; eyes blackish-brown, smooth; labial palpi covered with blackish-brown hair; antennae dorsally chestnut, ventrally rufous, with white scales at the base of each segment, club dorsally slightly darker than shaft. **Thorax:** dorsal and ventral surface dark brown; legs paler yellowish-brown. **Abdomen:** dorsal and ventral surface dark brown. **Wings:** forewing (length: 18.5 mm, mean: 18.5 mm, n=2) distal margin almost straight, apex rounded; hindwing with distal margin rounded, with tornal notch almost absent. DFW medium brown, darker brown towards base. DHW medium brown. VFW ground colour medium brown, basal half slightly darker, bordered distally by very thin, indistinct, darker brown postdiscal line, that is slightly inclined towards apex, and curves slightly distally on approaching costa; faint, slightly wavy, darker brown submarginal line from tornus to apex; very thin, straight, dark brown marginal line. VHW medium brown; thin (c. 1.5 mm) very pale yellowish (almost white) postdiscal band from apex to tornus, very slightly concave, passing through base of cell Cu1-M3; faint darker brown submarginal line, smoothly curving from tornus to cell Cu1-M3, then slightly undulate to apex; white submarginal dots in cells Cu2-Cu1 and Cu1-M3; thin, dark brown marginal line close to and parallel with distal margin. **Male genitalia** (Fig. 12C): uncus curving slightly ventrally near middle, and bent more sharply near base, subunci of medium length; valvae thinning sharply at middle and tapering posteriorly, dorsally grooved, with 5-7 'teeth' at distal tip; aedeagus curving dorsally, with a couple of tiny 'teeth' on left hand side near middle.

FEMALE (Fig. 4D): Differs from male as follows: slightly larger (forewing length: 19 mm, n=1). Both wing surfaces paler brown. VHW postdiscal band wider.

Types: **Holotype male:** ECUADOR: Pichincha, Aloag-Tandapi rd., km 18, Sector Los Alpes, 2700-2750 m, 26.I.2004, T. Pyrcz & R. Garlacz leg., MZUJ; **Allotype female:** Pichincha, Volcán Pasochoa, nr. Amaguaña, 3500 m, 7.X.1997, K. Willmott leg., KWJH; **Paratypes (23 males):** ECUADOR: 4 males: Pichincha, Reserva Geobotánica Pululahua, 2300-2600 m, 11-12.II.2002, T. Pyrcz leg., TWP; 1 male: Pichincha, Chillo Gallo, San Juan-La Victoria, 3300-3400 m (unreliable), 30.I.2002, T. Pyrcz leg., TWP; 1 male: Pichincha, Volcán Pichincha, 3000-3050, X.2002, I. Aldas leg., TWP; 2 males: Pichincha, Aloag-Tandapi rd., 2800 m, II.2002, I. Aldas leg., TWP; 1 male: Pichincha, Nono - Nanegalito km 15/20, 2100 m, P. Boyer leg., MZUJ; 1 male: Pichincha, Volcán Pasochoa, 3000-3200 m, 07.X.1997, A. Neild leg., TWP; 1 male: Pichincha, Volcán Pasochoa, 2600-2700 m, 28.I.2002, T. Pyrcz leg., TWP; 5 males: Pichincha, Aloag-Tandapi rd., km 18, Sector Los Alpes, 2700-2750 m, 26.I.2004, T. Pyrcz & R. Garlacz leg., TWP; 1 male, same data, PB; 1 male: Pichincha, Nono-Nanegalito, 2700-3000 m, 10.V.1999, P. Boyer leg., PB; 1 male: Pichincha, environs de Nono, 2600m, 15.III.1998, P. Boyer leg., PB; 1 male: Pichincha, Nanegalito, 1800 m, IX.1996, P. Boyer leg., PB; 1 male: Pichincha, km 26 Nanegalito-Quito rd., Quebrada Molino, 2400 m, 16.X.1996, K. Willmott leg., KWJH; 1 male: Pichincha, km 7 Aloag-Tandapi rd., 2500 m, 13.VI.1994, J.

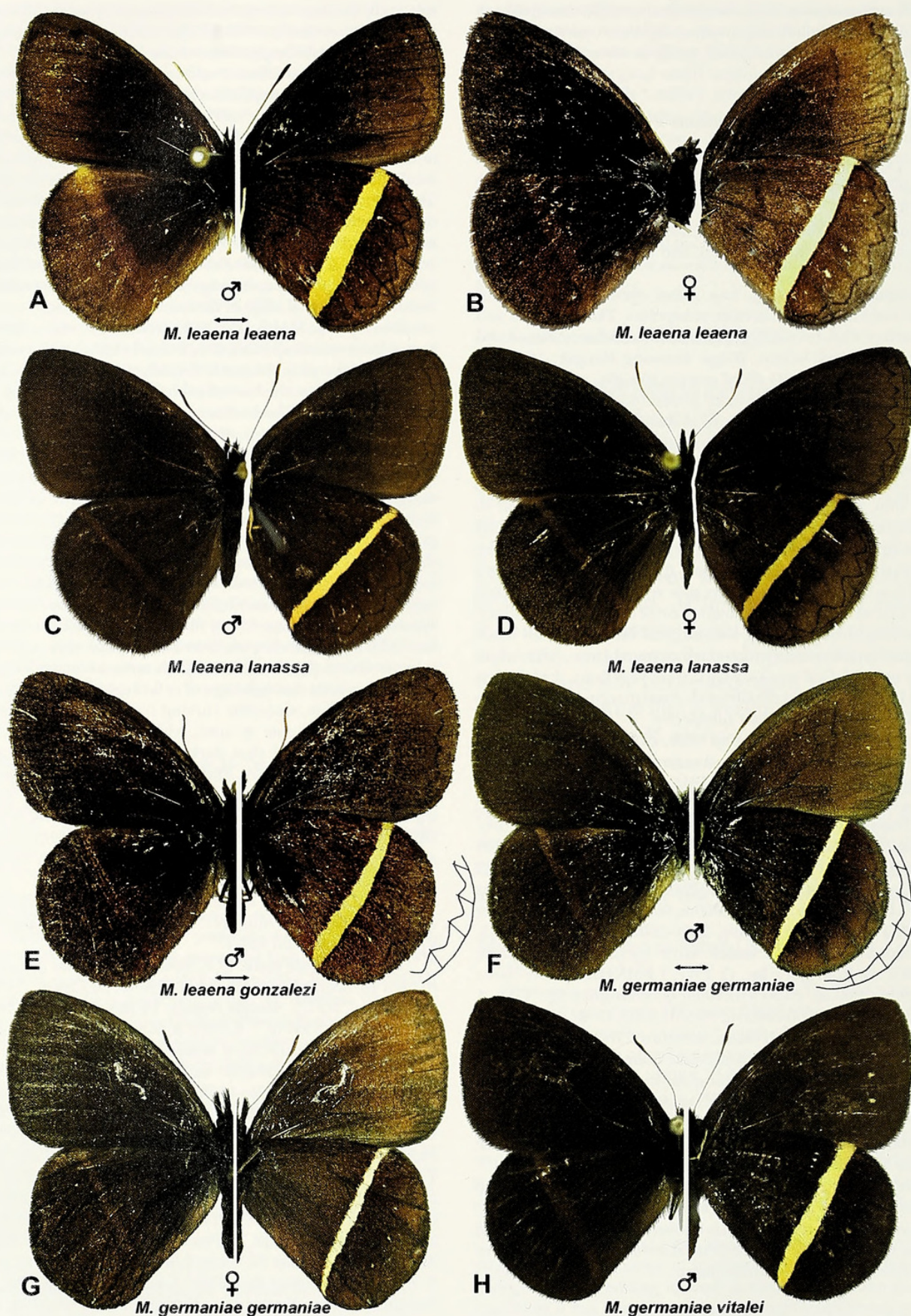


Fig. 1. Adult *Manerebia*, left dorsal view, right ventral view. Double arrows above names indicate image is reflected in vertical plane, so figured wings are righthand pair. A, *M. leaena leaena* male; B, *M. leaena leaena* female; C, *M. leaena lanassa* male; D, *M. leaena lanassa* female; E, *M. leaena gonzalezi* n. ssp. male; F, *M. germaniae germaniae* n. sp. male; G, *M. germaniae germaniae* n. sp. female; H, *M. germaniae vitalei* n. ssp. male. See Appendix 4 for specimen data.

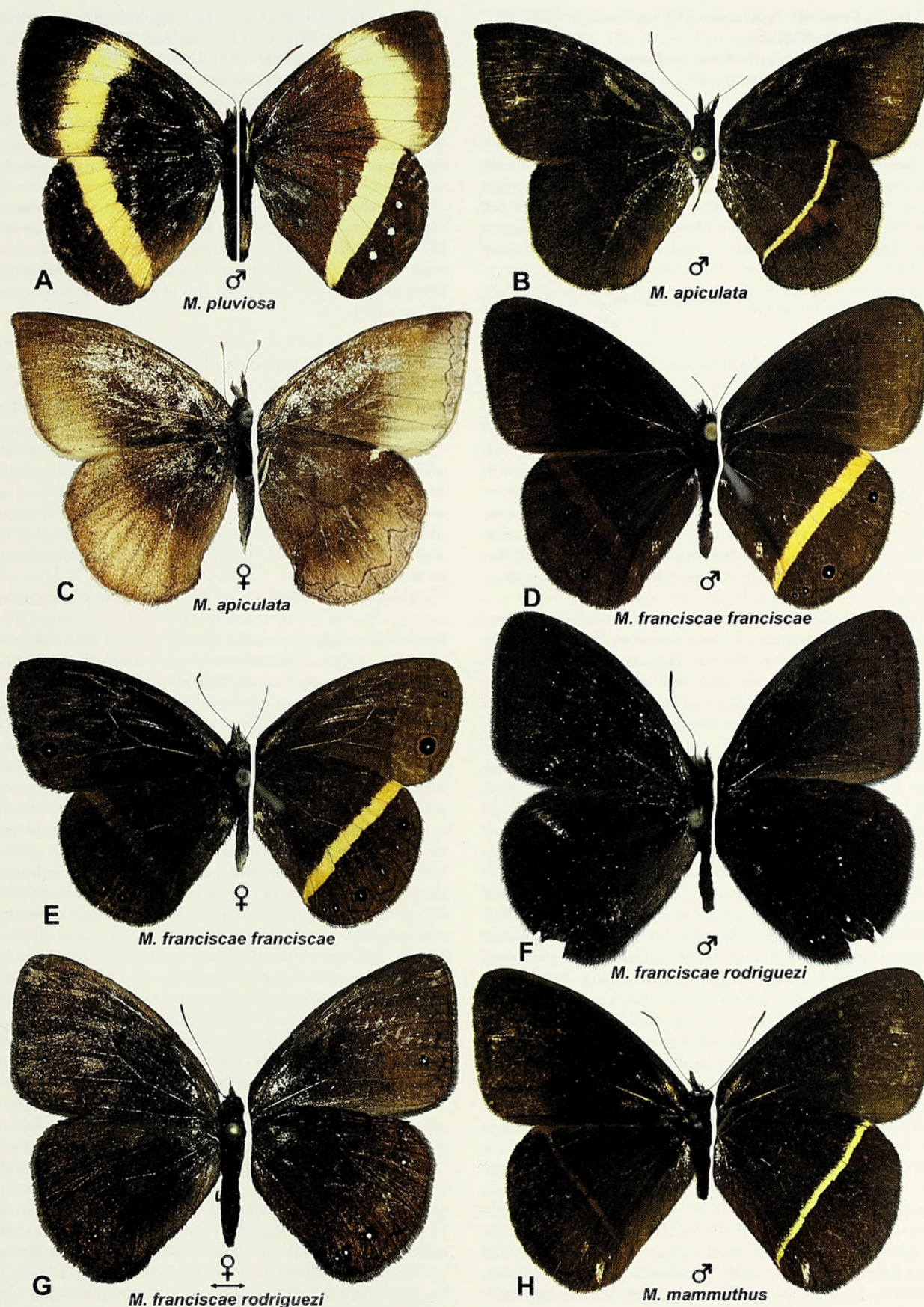


Fig. 2. Adult *Manerebia*, left dorsal view, right ventral view. Double arrows above names indicate image is reflected in vertical plane, so figured wings are righthand pair. A, *M. pluviosa* n. sp. male; B, *M. apiculata* male; C, *M. apiculata* female; D, *M. franciscae franciscae* male; E, *M. franciscae franciscae* female; F, *M. franciscae rodriguezi* n. ssp. male; G, *M. franciscae rodriguezi* n. ssp. female; H, *M. mammothus* n. sp. male. See Appendix 4 for specimen data.

Hall *leg.*, MECN; **1 male**: Pichincha, km 5 Aloag-Tandapi rd., 2700m, 13.VI.1994, J. Hall *leg.*, KWJH;

Etymology: The name is the feminine form of the Latin adjective "finus", meaning narrow, with reference to the thin postdiscal band on the VHW.

Comments: This subspecies occurs on the western slopes of the Andes in northern Ecuador (Pichincha, Imbabura) and possibly also in southern Colombia (Nariño). It has been recorded from 2100-3200 m, and once at 3500 m (Volcán Pasochoa), though it is most common between 2200-2600 m. It is generally replaced at higher elevations by *M. germaniae*. Males are often encountered puddling along roads or streams, and are also attracted to rotting fish. We have also found males hilltopping on Loma La Palmira, flying low over the stunted bushes growing on the summit during bright sunlight, after 09:30 hrs.

***Manerebia inderena similis* Pyrcz & Willmott n. ssp.**

Figs. 4E,F, 12D, 17

Manerebia n. sp., n. ssp. (Pyrcz, Willmott & Hall); Lamas & Voloria (2004: 216, n. 1124c).

Diagnosis: This subspecies differs from the neighbouring *M. i. fina* to the north by the broader, pale VHW postdiscal band which is more strongly yellow especially towards anal margin. It is very similar to the east Andean *M. i. leaeniva*, but both west Andean subspecies (*M. i. similis* and *M. i. fina*) are distinguished from it and all others by the thin, dark submarginal line on the VHW being in most examined individuals more smoothly curving, rather than dentate.

Description: MALE (Fig. 4E): **Head**: eyes, labial palpi and antennae as in nominate subspecies. **Thorax**: dorsal and ventral surface dark brown; legs paler brown. **Abdomen**: dorsal and ventral surface dark brown. **Wings**: forewing (length: 19-20 mm; mean: 19.3 mm; n=3) distal margin almost straight, apex rounded; hindwing with distal margin rounded, with tornal notch almost absent. DFW medium brown, darker brown towards base. DHW medium brown. VFW ground colour medium brown, basal half slightly darker, bordered distally by very thin, indistinct, darker brown postdiscal line, that is slightly inclined towards apex and curves slightly distally on approaching costa; faint, slightly wavy, darker brown submarginal line from tornus to apex; very thin, straight, dark brown marginal line. VHW medium brown; broad (c. 2.5 mm) yellowish (more intense towards tornus) postdiscal band from apex to tornus, straight and of even width except tapering slightly at tornus, passing through base of cell Cu1-M3; faint, uneven darker brown submarginal line, more undulate in cells Cu2-Cu1 to M3-M2; white submarginal dots in cell Cu1-M3; tiny black submarginal ocellus, ringed with dark orange, with white pupil, in cell Cu2-Cu1, a black spot in anterior half of cell 1A-Cu2; thin, dark brown marginal line close to and parallel with distal margin. **Male genitalia** (Fig. 12D): uncus curving slightly ventrally near middle, and bent more sharply near base, subunci of medium length; valvae thinning sharply at middle and tapering posteriorly, dorsally grooved, with 5-7 'teeth' at distal tip; aedeagus curving dorsally, with a couple of tiny 'teeth' on left hand side near middle.

FEMALE (Fig. 4F): Similar to male but slightly paler brown ventrally.

Types: **Holotype male**: ECUADOR: Bolívar, Balzapamba, arriba de Santa Lucía, 2200-2250 m, 03.IX.2003, T. Pyrcz *leg.*, MZUJ; **Allotype female**: same data as the holotype, TWP; **Paratypes** (34 males and 3 females): ECUADOR: **3 males**: Bolívar, Balzapamba, arriba de Santa Lucía, 2600-2650 m, 03.IX.2003, T. Pyrcz *leg.*, TWP; **12 males**: Bolívar, Balzapamba, arriba de Santa Lucía, 2200-2250 m, 03.IX.2003, T. Pyrcz *leg.*, TWP (11), BMNH (2); **5 males and 1 female**: Bolívar, Balzapamba, arriba de Santa Lucía, 2200-2250 m, 05.IX.2004, T. Pyrcz *leg.*, TWP; **1 male**: same locality and date, 2400-2450 m, T. Pyrcz *leg.*, TWP; **1 male**: same locality and date, 2500-2550 m, T. Pyrcz *leg.*, TWP; **2 males**: Bolívar, Balzapamba, Río

Alcacer, 2700m, 04.XI.1996, S. Attal *leg.*, MZUJ; **1 male**: Bolívar, old Guaranda road, VIII.1997, I. Aldas *leg.*, TWP; **3 males**: Cotopaxi, above Pilaló, 3000-3050 m, 03.IX.2004, T. Pyrcz *leg.*, TWP; **6 males and 2 females**: Azuay, Cuenca - Naranjal road, Molleturo, 2600-2650 m, 01.IX.2003, T. Pyrcz *leg.*, TWP.

Etymology: The name is derived from the Latin "similis", meaning similar, with reference to this taxon's resemblance to the subspecies *M. i. leaeniva*, which occurs on the east slopes in central Ecuador.

Comments: This subspecies occurs in central western to southwestern Ecuador, where it has been recorded above Pilaló (Cotopaxi), Santa Lucía (Bolívar) and on the western slopes of the Cajas massif near Molleturo (Azuay) from 2200-3000 m. In all these localities *M. i. similis* is the upper parapatric replacement of *M. undulata* n. sp.

***Manerebia inderena clara* Pyrcz & Willmott, n. ssp.**

Figs. 4G,H, 12E, 17

Manerebia n. sp., n. ssp. (Pyrcz, Willmott & Hall); Lamas & Voloria (2004: 216, n. 1124d).

Diagnosis: This subspecies differs from all others by the broad, pure whitish VHW postdiscal band, which is yellow in neighboring *M. i. leaeniva* to the south and yellowish posteriorly and tapering anteriorly in the similar *M. i. similis* from western Ecuador. The thin, dark submarginal line on the VHW is noticeably dentate, slightly more so than in *M. i. leaeniva* and noticeably more so than in *M. i. mirena*.

Description: MALE (Fig. 4G): **Head**: as in the nominate subspecies. **Thorax**: dorsal and ventral surface dark brown; legs paler brown. **Abdomen**: dorsal and ventral surface dark brown. **Wings**: forewing (length: 17.5-19 mm; mean: 18.2 mm; n=19) distal margin slightly convex, apex rounded; hindwing with distal margin slightly angled at vein M3, with tornal notch almost absent. DFW medium brown; darker brown in discal area. DHW medium brown, slightly darker towards base, with small black submarginal ocellus ringed with dark orange in cell Cu2-Cu1. VFW ground colour medium brown; thin, very indistinct, slightly curved, darker brown postdiscal line, in cells Cu2-M2; a minute white submarginal dot in cells Cu1-M3; indistinct, zigzag, darker brown submarginal line from tornus to apex; distal margin lined indistinctly with dark brown. VHW medium brown; whitish postdiscal band from apex to tornus, passing through base of cell Cu1-M3, straight and of even width, except tapering slightly in cell 1A-Cu2; faint, darker brown, strongly zigzag submarginal line; a small black submarginal ocellus, with a white pupil, faintly lined with dark orange, in cell Cu2-Cu1, with minute white submarginal dots in cells Cu1-M3 and M3-M2; distal margin lined indistinctly with dark brown. **Male genitalia** (Fig. 12E): uncus bent near base then flat, subunci of medium length; valvae thinning sharply at middle and tapering posteriorly, dorsally grooved, with 4-6 'teeth' at distal tip; aedeagus curving dorsally, with a couple of tiny 'teeth' on left hand side near middle.

FEMALE (Fig. 4H): Differs from male as follows: larger (forewing length 20.5 mm); ventral surface paler brown, with dark submarginal lines more distinct; a large ocellus in cell Cu2-Cu1 on VFW.

Types: **Holotype male**: ECUADOR: Napo, Baeza, Río Horituyacu [Oritoyacu], 1800 m, 08.VI.1999, T. Pyrcz & J. Wojtusiak *leg.*, MZUJ; **Allotype female**: ECUADOR: Napo, Hda. San Isidro, 2000 m, 18.XII.1996, P. Boyer *leg.*, PB; **Paratypes** (31 males): ECUADOR: **2 males**: same data as the holotype, TWP; **1 male**: Napo, Quito-Baeza rd., east of pass, 2300 m, 17.VI.1994, J. Hall *leg.*, KWJH; **1 male**: Napo, Baeza - Papallacta, 2100 m, 07.IV.1998, A. Neild *leg.*, TWP; **1 male**: Napo, SE of Cosanga, Río Chonta, 2000 m, 18.X.1996, K. Willmott *leg.*, KWJH; **1 male**: Napo, Baeza - Papallacta, 2100 m, 07.IV.1998, A. Neild *leg.*, TWP; **5 males**: Napo, Baeza area, 2050-2200 m, 02.X.1995, A. Neild *leg.*, TWP (4), MECN (1); **2 males**: Napo, Baeza, 2000-2200 m, 19.X.1996, A. Neild *leg.*, TWP; **7 males**: Napo, Baeza, 1800 m, IX.1996, P. Boyer *leg.*, TWP (5), BMNH (1), MZUJ

(1); **1 male**: Napo, Baeza, 1800 m, 10.XII.1996, P. Boyer *leg.*, TWP; **1 male**: Napo, San Isidro, 2000 m, 08.XII.1996, P. Boyer *leg.*, TWP; **1 male**: same data but 18.XII.1996, TWP; **1 male**: Napo, Cosanga, 1600 m, 06.XI.1996, P. Boyer *leg.*, PB; **1 male**: Napo, Baeza - Tena km 19, 2100 m, 04.XII.1997, P. Boyer *leg.*, TWP; **3 males**: Napo, Reserva Yanayacu, 2100-2150 m, 06-07.IX.2003, T. Pyrcz *leg.*, TWP; **3 males**: same locality, no date, H. Greeney *leg.*, MBLI.

Etymology: The name is derived from the Latin "clarus", meaning pale, with reference to the pale VHW postdiscal band.

Comments: *Manerebia inderena clara* has been recorded only in the Baeza area, in the valleys of the Ríos Papallacta and Cosanga, south to the Cordillera de los Huacamayos, from 1700-2400 m. It is not uncommon, and males can be found puddling along mountain streams in cloud forest, or feeding on horse dung or rotting fish.

Manerebia inderena leaeniva Pyrcz & Willmott, n. ssp.

Figs. 5C, 12F, 17

Manerebia n. sp., n. ssp. (Pyrcz, Willmott & Hall); Lamas & Viloria (2004: 216, n. 1124a).

Diagnosis: The yellow VHW band is twice as wide in this subspecies as in the nominate, and the VHW submarginal ocelli are reduced, similar to *M. i. fina*, *M. i. similis* and *M. i. clara*. In *M. i. clara* the VHW postdiscal band is as wide as in *M. i. leaeniva*, but white, while in *M. i. similis* from the west Andes it is as wide but a more intense yellow, and the VHW submarginal line is smoothly undulating rather than dentate. The southern subspecies *M. i. mirena* has a VFW ocellus in cell Cu2-Cu1, two to three ocelli in cells 1A-Cu2, Cu2-Cu1 on the VHW and an ocellus in cell Cu2-Cu1 on the DHW.

Description: MALE (Fig. 5C): **Head**: frons with a tuft of dark-brown hair; eyes blackish-brown; labial palpi covered with dark-brown hair; antennae dorsally pale brown, ventrally light beige, club laterally rufous, white scales at base of each segment. **Thorax**: dorsal and ventral surface dark brown; legs paler brown. **Abdomen**: dorsal and ventral surface dark brown. **Wings**: forewing (length: 17-20.5 mm; mean: 19 mm, n=11) distal margin slightly convex, apex rounded; hindwing with distal margin slightly angled at vein M3, with tornal notch almost absent. DFW medium brown; darker brown in discal area; androconial scales not apparent. DHW medium brown, slightly darker towards base, with two minute white submarginal dots in cells Cu2-Cu1 and Cu1-M3. VFW ground colour medium brown, becoming slightly paler from base to apex; thin, indistinct, slightly curved, darker brown postdiscal line, in cells Cu2-M2; a row of minute white submarginal dots in cells Cu2-Cu1 to M2-M1; indistinct, zigzag, darker brown submarginal line from tornus to apex; very thin, straight, dark brown marginal line. VHW medium brown; pale yellowish postdiscal band from apex to tornus, passing through base of cell Cu1-M3, straight and of even width; distinct, darker brown, strongly zigzag submarginal line; a small black submarginal ocellus, with a white pupil, in cell Cu2-Cu1; tiny white submarginal dots in cells Cu1-M1; thin, very faint, dark brown marginal line close to and parallel with distal margin. **Male genitalia** (Fig. 12F): uncus flat and bent near base, subunci of medium length; valvae thinning sharply at middle and tapering posteriorly, dorsally grooved, with 4-6 'teeth' at distal tip; aedeagus curving dorsally, with a couple of tiny 'teeth' on left hand side near middle.

FEMALE: Unknown.

Types: **Holotype male**: ECUADOR: Tungurahua, Chinchin, 2000 m, 06.II.2004, T. Pyrcz *leg.*, MZUJ; **Paratypes (15 males)**: ECUADOR: **2 males**: Tungurahua, Río Verde Chico, 2100 m, 08.X.1995, A. Neild *leg.*, TWP; **2 males**: same data as preceding but 24.IX.1995, TWP; **2 males**: Tungurahua, Baños, Runtún, A. Jasiński *leg.*, TWP; **2 males**: Tungurahua, Viscaya, 2100 m, 17.XI.1996, P. Boyer *leg.*, TWP; **5 males**: Tungurahua, Triunfo - Patate, El Tablón, 3000m, P. Boyer *leg.*, TWP (2), PB (3); **1 male**: Tungurahua, Baños, El Tablón, 3000m, III.1999, I. Aldas *leg.*, MBLI; **1 male**: Tungurahua, Runtún,

2900-2950 m, 22.I.2002, J. Wojtusiak *leg.*, TWP.

Etymology: The subspecific name is derived from "leaena", the name of the species with which this taxon has been most often confused.

Comments: This subspecies is known from the upper valley of the Río Pastaza (Tungurahua) south to Morona-Santiago, where it has been recorded from 2100-3000 m, although it is more common in the lower part of this elevational range. Specimens from Morona-Santiago (Gualaceo-Limón road, vía Las Chacras, 2600-2850 m, TWP, KWJH) apparently represent this subspecies, but are excluded from the type series because we have been unable to examine sufficient material to reliably assess variation.

Manerebia inderena mirena Pyrcz & Willmott n. ssp.

Figs. 5A,B, 12G, 17

Diagnosis: This subspecies generally has a slightly wider VHW postdiscal band than *M. i. leaeniva*, a slightly more reddish brown ground colour, and prominent ocelli, in most individuals, in cell Cu2-Cu1 on the DHW and occasionally on the VFW and VHW in cell Cu2-Cu1. The uncus in *M. i. mirena* is usually more noticeably curved ventrally in the middle than in other subspecies, and the saccus is distinctive in always being swollen anteriorly.

Description: MALE (Fig. 5A): **Head**: frons with a tuft of dark brown hair; eyes blackish-brown, smooth; labial palpi covered with blackish-brown hair; antennae dorsally brown, ventrally dirty yellow, club slightly darker than shaft. **Thorax**: dorsal and ventral surface dark brown; legs yellowish-brown. **Abdomen**: dorsal and ventral surface dark brown. **Wings**: forewing (length: 18-19.5 mm; mean: 18.6 mm; n=3) distal margin slightly convex, apex rounded; hindwing with distal margin rounded, with tornal notch almost absent. DFW medium brown; darker brown in discal area. DHW medium brown, slightly darker towards base; a minute white submarginal dot in cell Cu1-M3, a small black ocellus ringed with dark orange with a white pupil in cell 1A-Cu2, a larger similar ocellus in cell Cu2-Cu1. VFW ground colour medium brown, becoming slightly paler from base to apex; thin, indistinct, straight, darker brown postdiscal line in cells Cu2-M2; a row of minute white submarginal dots in cells Cu2-Cu1 to M2-M1; in most individuals the dot in Cu2-Cu1 is replaced by a black ocellus, ringed with orange and with a white pupil, of variable size; indistinct, undulate, darker brown submarginal line from tornus to apex; very thin, straight, dark brown marginal line. VHW medium brown; a wide pale yellowish (more intense at tornus and costa) postdiscal band from apex to tornus, passing through base of cell Cu1-M3, straight and of even width; most individuals have one or two small black submarginal ocelli, with white pupils, in cell 1A-Cu2, and occasionally a larger ocellus in cell Cu2-Cu1, and white submarginal dots in other cells; darker brown, zigzag submarginal line; thin, dark brown marginal line close to and parallel with distal margin. **Male genitalia** (Fig. 12G): uncus curving slightly ventrally near middle, and bent more sharply near base, subunci of medium length; valvae thinning sharply at middle and tapering posteriorly, dorsally grooved, with 4-6 'teeth' at distal tip; aedeagus curving dorsally, with a couple of tiny 'teeth' on left hand side near middle.

FEMALE (Fig. 5B): Similar to male but paler with a fainter pattern on both dorsal and ventral wing surfaces.

Types: **Holotype male**: ECUADOR: Zamora-Chinchi, Valladolid, Quebrada de los Muertos, 2550 m, XI.1999, I. Aldas *leg.*, MZUJ; **Allotype female**: ECUADOR: Loja, Loja-Zumba, km 95-100, 2500-2600 m, 27.XI.1998, P. Boyer *leg.*, PB; **Paratypes (59 males and 1 female)**: ECUADOR: **2 males**: Zamora-Chinchi, Valladolid, no other data, P. Boyer *leg.*, PB; **2 males**: Zamora-Chinchi, km 34 Jimbura-San Andrés rd., 2900 m, 23.IX.1997, K. Willmott *leg.*, KWJH (1), MECN (1); **41 males**: Zamora-Chinchi, Valladolid, Quebrada de los Muertos, 2550 m, XI.1999, I. Aldas *leg.*, TWP (8), MBLI (33); **2 males**: Zamora-Chinchi, Loja - Zamora 2600m, 22.XI.1996, P. Boyer *leg.*, PB; **1 male**: Loja, Loja-Zumba, km 95-100,

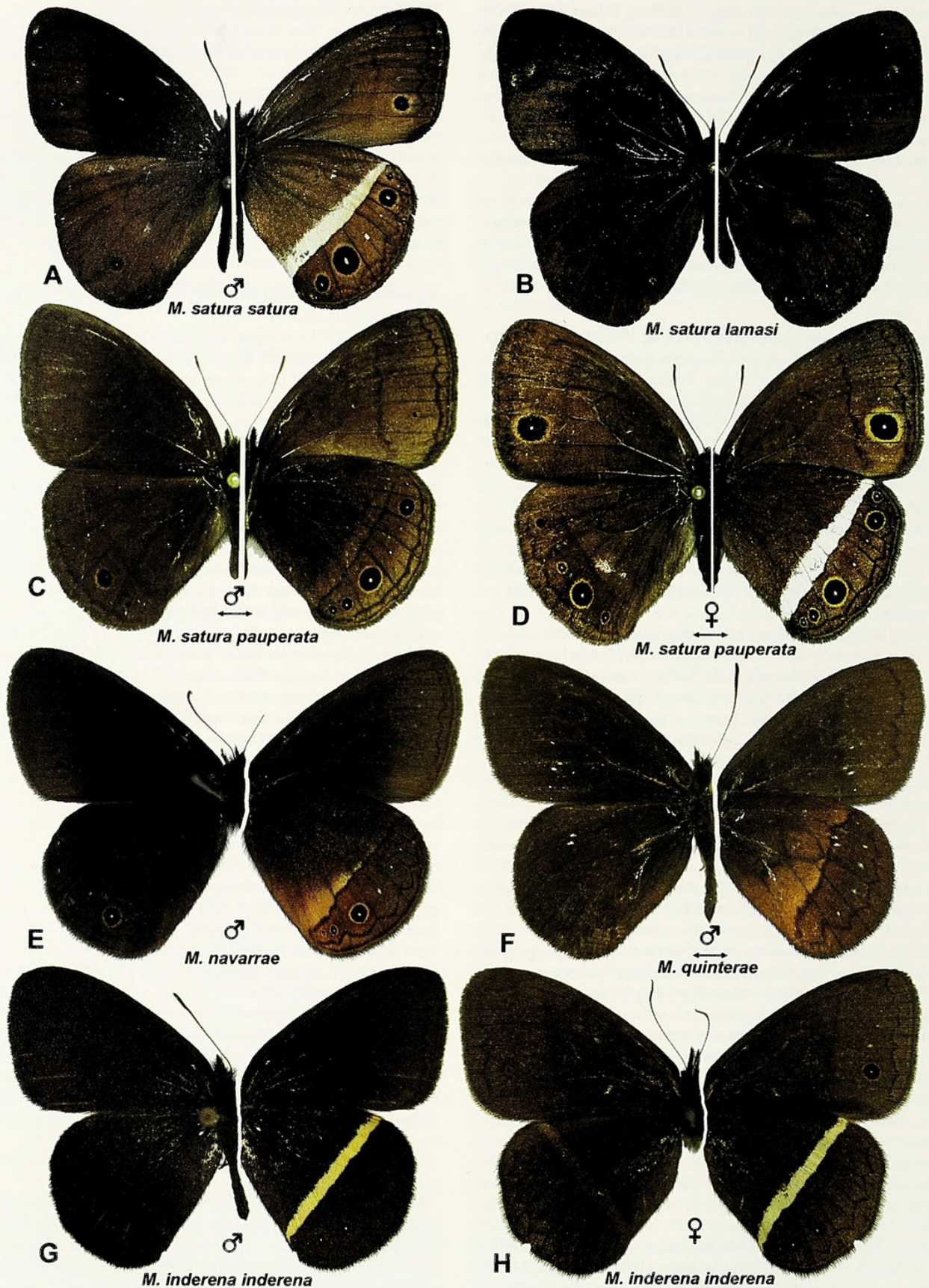


Fig. 3. Adult *Manerebia*, left dorsal view, right ventral view. Double arrows above names indicate image is reflected in vertical plane, so figured wings are righthand pair. A, *M. satura satura* male; B, *M. satura lamasi* n. ssp. male; C, *M. satura pauperata* n. ssp. male; D, *M. satura pauperata* n. ssp. female; E, *M. navarrae* male; F, *M. quinterae* male; G, *M. inderena inderena* male; H, *M. inderena inderena* female. See Appendix 4 for specimen data.

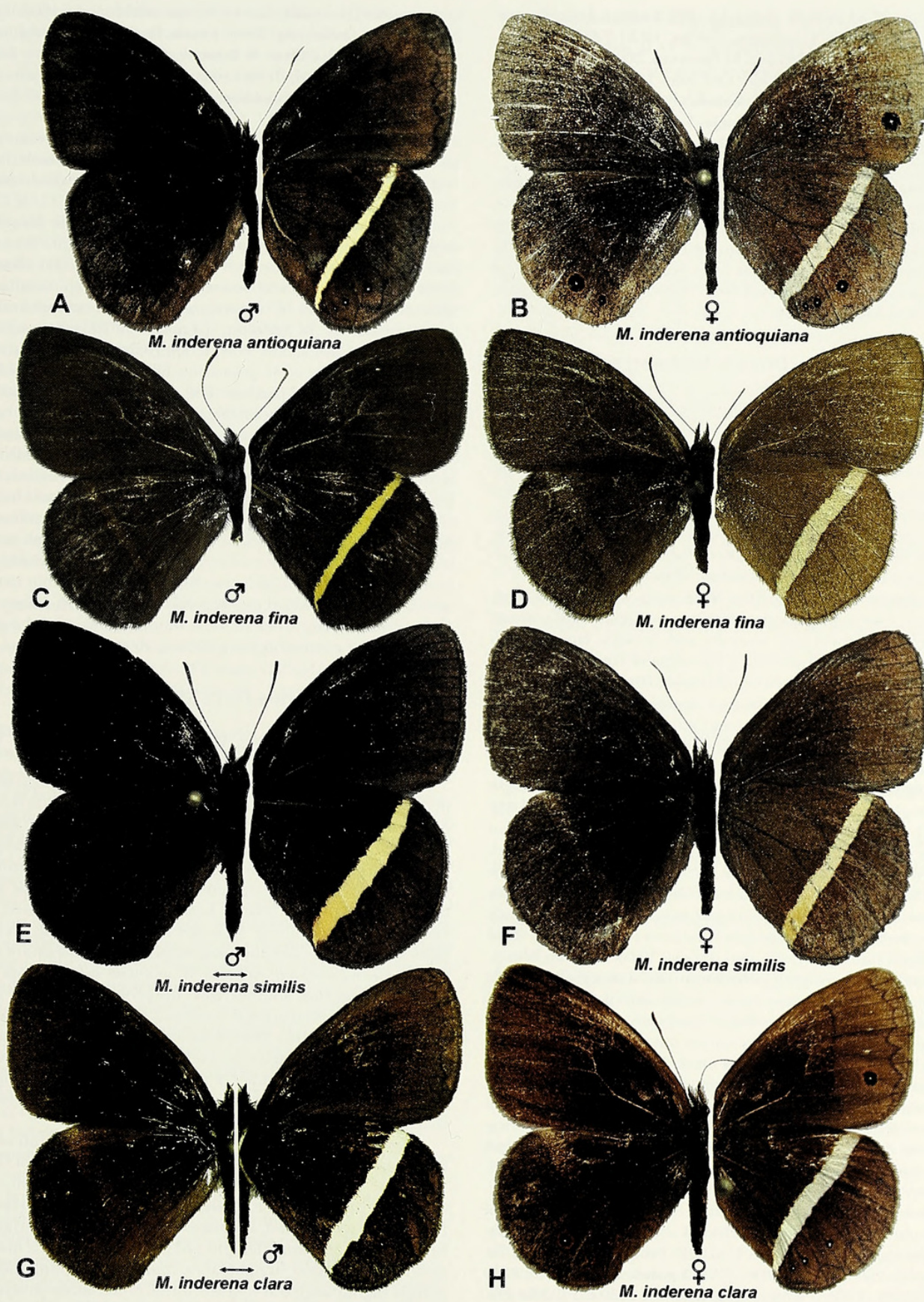


Fig. 4. Adult *Manerebia*, left dorsal view, right ventral view. Double arrows above names indicate image is reflected in vertical plane, so figured wings are righthand pair. A, *M. inderena antioquiiana* n. ssp. male; B, *M. inderena antioquiiana* n. ssp. female; C, *M. inderena fina* n. ssp. male; D, *M. inderena fina* n. ssp. female; E, *M. inderena similis* n. ssp. male; F, *M. inderena similis* n. ssp. female; G, *M. inderena clara* n. ssp. male; H, *M. inderena clara* n. ssp. female. See Appendix 4 for specimen data.

2500-2600m, 27.XI.1998, P. Boyer *leg.*, PB; **2 males**: Loja, Parque Nacional Podocarpus, Cajanuma, 2700m, 10.XI.1996, A. Neild, TWP; **1 male**: Loja, Loja-Zamora, El Basurero, 2600m, 22.XI.1997, P. Boyer *leg.*, PB; **2 males**: Loja, Old road Loja - Zamora, 2800 m, XI.1999, I. Aldas *leg.*, MBLI; **4 males, 1 female**: same data as preceding but 2500 m, MBLI; **1 male**: Loja, Cenén Alto, 2800m, XI.1999, I. Aldas *leg.*, MBLI. PERU: **1 male**: Cajamarca, Tabaconas, I. Aldas *leg.*, TWP.

Etymology: The name "mirena" is composed from the subspecific names "milaena" and "inderena".

Comments: This subspecies occurs from southeastern Ecuador on both slopes of the Andes (Zamora-Chinchi, Loja) to north-eastern Peru (Tabaconas). It has been recorded in cloud forest within a narrow elevational band, from 2500-3000 m, where it may, however, be locally common.

Manerebia golondrina Pyrcz & Willmott n. sp.

Figs. 5D, 12H, 17

Manerebia n. sp. (Pyrcz, Willmott & Hall); Lamas & Viloria (2004: 216, n. 1128).

Diagnosis: This species lacks the pale VHW postdiscal band that occurs in other *Manerebia* species with similar genitalia (*M. inderena*, *M. prattorum* n. sp.). The wing shape, ocelli on the VHW and ocellus on the DHW in cell Cu2-Cu1 are somewhat similar to *M. inderena*. The male genitalia are indistinguishable from those of *M. inderena*, except for lacking lateral 'teeth' on the aedeagus as present in *M. inderena*, a character that varies within other species.

Description: MALE (Fig. 5D): **Head**: frons with a tuft of long, dark brown hair; eyes glabrous, dark brown; labial palpi covered with black and brown hair ventrally and dorsally, laterally with short black and light brown scales, last segment covered with light brown scales and ventrally with short brown hair; antennae brown with white scales at the base of each segment, club only slightly thicker than shaft. **Thorax**: dorsal and ventral surface dark brown; legs paler brown. **Abdomen**: dorsal and ventral surface dark brown. **Wings**: forewing (length: 19-21 mm, mean: 20.1 mm, n=10) distal margin slightly convex, apex rounded; hindwing with distal margin slightly angled at vein M3, with tornal notch almost absent. DFW medium brown; darker brown in discal area, androconial scales not apparent. DHW medium brown, with small black submarginal ocellus ringed with dark orange in cell Cu2-Cu1. VFW ground colour medium brown, darker brown in basal half; very indistinct, darker brown postdiscal line, in cells Cu2-Cu1 to costa; indistinct, slightly undulate, darker brown submarginal line from tornus to apex; distal margin lined indistinctly with dark brown. VHW medium brown, darker towards base; slightly paler brown, thin, straight postdiscal line from apex to tornus; faint, darker brown, undulate submarginal line; a black submarginal ocellus, ringed with dark orange, with a white pupil, in cell Cu2-Cu1, a similar but smaller ocellus in the anterior half of cell 1A-Cu2, and a black dot in the posterior half of the same cell; distal margin lined indistinctly with dark brown. **Male genitalia** (Fig. 12H): uncus bent near base then flat, subunci of medium length; valvae thinning sharply at middle and tapering posteriorly, dorsally grooved, with 4-6 'teeth' at distal tip; aedeagus curving dorsally, laterally smooth.

FEMALE: Unknown.

Types: **Holotype male**: ECUADOR: Carchi, Reserva Forestal Las Golondrinas, 2350 m, 20.V.1999, T. Pyrcz & J. Wojtusiak *leg.* MZUJ; **Paratypes (29 males)**: ECUADOR: **1 male**: same data as the holotype but 2600m, 22.VI.1999, TWP; **3 males**: same data but 2200 m, 22.VI.1999, TWP; **2 males**: same data but 2150 m, 23.VI.1999, TWP; **3 males**: same data but 2000 m, 23.VI.1999, TWP; **1 male**: same data but 2550 m, 02.VII.1999, TWP; **1 male**: same data but 2300 m, 23.VI.1999, TWP; **1 male**: same data but 2200 m, 22.VI.1999, TWP; **1 male**: same data but 27.VI.1999, TWP; **1 male**: same data but 2150 m, 24.VI.1999, BMNH; **2 males**: Carchi, nr. La Carolina, Reserva Las Golondrinas, Santa Rosa, 1700 m, 05.IX.1996, K. Will-

mott *leg.*, KWJH; **1 male**: Carchi, Tulcán - Maldonado, 1300-1600 m, 24.V.1997, A. Jasiński *leg.*, TWP; **1 male**: Carchi, Tulcán-Maldonado km 40 a 50, 2800-3200 m, P. Boyer *leg.*, PB; **2 males**: same locality, 2450 m, 27.VIII.2004, T. Pyrcz *leg.*, TWP; **9 males**: Imbabura, La Carolina, Route de Buenos Aires km 25, 2600m, 05.V.2000, P. Boyer *leg.*, PB (7), TWP (2).

Etymology: The specific name is derived from the name of the private cloud forest reserve where most of the individuals, including the holotype, were collected, the Reserva Las Golondrinas, managed by Fundación Golondrinas.

Comments: This species is most closely related to *M. inderena*, with which it is currently not known to be sympatric. We treat it as a distinct species because it occurs at notably lower elevations than *M. inderena fina*, and because of the phenotypic similarity of *M. inderena fina* and *M. inderena inderena* from northeastern and western Ecuador. In addition, specimens of *M. inderena fina* are known from Cotacachi at 3000m, approximately 40 km south of the nearest locality of *M. golondrina*, between which there are no obvious geographical barriers. This species is known to date only from northwestern Ecuador (Fig. 17), an area that is a local centre of endemism for cloud forest satyrines (e.g., *Lasiophila phalaesia alce* Pyrcz, *Corades violacea* Pyrcz, *Pedaliodes phrasicla immaculata* Pyrcz). It is found on the south (Buenos Aires) and north (Las Golondrinas) banks of the Río Mira. It should certainly also occur in southwestern Colombia south of the Río Nariño valley. The two males collected by KRW were both attracted to rotting fish. Other individuals were collected in traps baited with excrement. *Manerebia golondrina* occurs in middle elevation cloud forests from 1600-2600 m, but sampling with baited traps carried out by the first author in the Reserva Las Golondrinas, along an elevational transect, indicated the species to occur most commonly from 2000 to 2600m.

Manerebia prattorum Pyrcz & Willmott n. sp.

Figs. 5E, 12I, 17

Manerebia n. sp. (Pyrcz, Willmott & Hall); Lamas & Viloria (2004: 216, n. 1129).

Diagnosis: This species is easily distinguished from its congeners in the northern Andes by the postdiscal orange band on the DHW only. The only species with somewhat similar pattern is *Manerebia lisa* (Weymer), occurring in central Peru, but in that taxon the band is darker, with blurred edges, narrowing gradually from anal to costal margin. The male genitalia of *M. lisa* show that the two species are not closely related, however, being similar to *M. satura* (see characters grouping *M. satura* with *M. franciscæ*, under the latter species). The size and wing shape of *M. prattorum* are similar to *M. inderena mirena* n. ssp. and *M. undulata milaena* n. sp. n. ssp. *Manerebia prattorum*, however, lacks the ventral magenta or greyish sheen in the distal marginal areas that characterises *M. undulata*, and does not have the DHW submarginal ocelli that occur in *M. inderena mirena*. The male genitalia differ from *M. inderena* and *M. undulata* in having only 2-3 'teeth' at the distal tip of the valva, and from *M. rufanalis* in having a straighter uncus and differently shaped valva (see diagnosis of the latter species).

Description: MALE (Fig. 5E): **Head**: frons with a tuft of short, brown hair; eyes chocolate brown, smooth; labial palpi covered with short, medium brown hair; antennae medium brown, slightly lighter on ventral surface. **Thorax**: dorsal and ventral surface dark brown; legs paler brown. **Abdomen**: dorsal and ventral surface dark brown. **Wings**: forewing (length: 17-17.5 mm; mean: 17.2 mm, n=4) distal margin almost straight, apex rounded; hindwing with distal margin slightly angled at vein M3, tornal notch almost absent. DFW medium brown, darker brown towards base. DHW ground colour medium brown; a broad, orange postdiscal band extending from costa to anterior half of cell 1A-Cu2, basal edge straight, distal edge kinked at vein M3, so that widest point of band is at vein M3. VFW ground colour medium brown, basal half slightly darker, bordered distally by very thin, indistinct, darker brown postdiscal line, that

is slightly inclined towards apex; faint, slightly wavy, darker brown submarginal line from tornus to apex. VHW medium brown; broad whitish postdiscal band from apex to tornus, tapering towards costa and tornus and widest in cells Cu2-Cu1 and Cu1-M3, passing through base of cell Cu1-M3; faint, slightly undulate darker brown submarginal line. **Male genitalia** (Fig. 12I): uncus nearly straight except where bent sharply near base, subunci of medium length; valvae thinning sharply at middle and tapering posteriorly, dorsally grooved, with 2-3 'teeth' at distal tip; aedeagus curving dorsally.

FEMALE: Unknown.

Types: **Holotype male:** PERU: Piura, arriba de Canchaque, 2100 m, 0522/7934, 05.VI.2000, G. Lamas *leg.*, MUSM; **Paratypes (10 males):** PERU: **2 males:** same data as the holotype, MUSM; **2 males:** same data as the holotype except R. Robbins *leg.*, USNM; **1 male:** same data as preceding except 07.VI.2000, USNM; **1 male:** same data as preceding except G. Lamas *leg.*, MUSM; **4 males:** West slopes of Andes, N. Peru, 10 000 ft., June 1912, Pratt, Joicey Bequest, Brit. Mus. 1934-120, BMNH.

Etymology: This species is dedicated to Antwerp Edgar Pratt and his son Felix Pratt, who first collected it almost a century ago.

Comments: *Manerebia prattorum* occurs at 2100-2600 m on the western slopes of the Andes in northwestern Peru, on the west slopes of the Andes, east of the locality of Canchaque and possibly in the valley of Huancabamba (Piura). Specimens potentially representing another undescribed subspecies have also been collected in northwestern Peru (Cajamarca), west of Chiclayo, above the locality of La Florida (Fig. 17).

Manerebia trimaculata (Hewitson, 1870)

Figs. 5F,G,H, 13A, 18

Lymanopoda trimaculata Hewitson (1870: 159). **TL:** Ecuador, Morona-Santiago, St. Rosario. **ST male:** BMNH(T) [examined].

Manerebia trimaculata (Hewitson); Lamas & Vilorio (2004: 216).

Diagnosis: *Manerebia trimaculata* and the related species, *M. undulata* n. sp. and *M. interrupta*, are all characterised by a light greyish or magenta marginal sheen along the distal quarter of the ventral surface of both wings, and a thin, dark brown, undulate line passing through the center of the VHW discal cell. The male genitalia (Fig. 13A) of all three species are distinctive in the uncus being almost straight, so that the dorsal edge of the tegumen and uncus form a smoothly curving line, the subunci are very short and the valva is sharply constricted in the middle to produce the attenuated distal half. This species might arguably be considered conspecific with the west Andean *M. undulata*, but our reasons for keeping them separate are discussed under that species. The VHW yellow band in specimens of the syntypic series is reduced to three spots near the tornus (Fig. 5F), but in other specimens it can be fully developed, but rather irregular at the basal edge (Fig. 5G). *Manerebia trimaculata* is readily distinguished from other similar species by the two or more well developed submarginal ocelli in cells Cu2-Cu1 and Cu1-M3 on the DHW, and usually by the submarginal ocellus in cell Cu2-Cu1 on the VFW. Some specimens of *M. interrupta* have similar but smaller ocelli and are typically smaller in size.

Comments: This species is confined to southeastern Ecuador (Morona-Santiago and Zamora-Chinchipec) (Fig. 18), where it is rather uncommon, and it was omitted entirely by Brown (1944). *Manerebia trimaculata* occurs in relatively intact cloud forests from 2500-2800 m, and in contrast to the closely related *M. interrupta*, it frequents openings within the forest, rarely straying into cleared areas. A single specimen was collected in the Cordillera del Cóndor on the border between Ecuador and Peru (Camp Achupalla, 15 km E. Gualaquiza, 2100-2200 m, MUSM).

Manerebia undulata Pyrcz & Hall, n. sp.

Manerebia undulata is characterised by a thin, dark

brown, undulate line passing through the center of the VHW discal cell, a character only otherwise occurring distinctly and consistently in *M. interrupta* and *M. trimaculata*. Also distinctive is the paler brown or purplish shading around the distal margin of the VHW and apical area of the VFW (also occurring in *M. trimaculata* and *M. interrupta*), and the markedly undulate dark brown VHW submarginal line. The first two of these characters distinguish *M. undulata* from most other west Ecuadorian species (*M. inderena*, *M. germaniae*, *M. ignilineata*). The last two characters also occur in *M. rufanalis* n. sp., but that has distinct male genitalia, with a smoothly arching uncus (not straight), longer subunci and a smooth ventral edge to the valva, which gradually tapers posteriorly. The most closely related species, as indicated by wing pattern and the male genitalia (see discussion under *M. trimaculata*), seem to be *M. interrupta* and *M. trimaculata*. The former occurs at higher elevations and in drier habitats on the western slopes and may be distinguished by its smaller size, the more pointed forewing apex, DHW submarginal ocelli, and uneven VHW postdiscal band (in forms with a full band). *Manerebia undulata* is not known to be sympatric with the eastern slope *M. trimaculata*, with which it might be considered conspecific, but given that *M. undulata* is much commoner at substantially lower elevations, not (or only exceptionally) polymorphic in expression of the hindwing band, and lacks prominent ocelli on the DHW in any subspecies, we treat the two taxa as distinct species.

Unlike *M. trimaculata* and *M. interrupta*, polymorphism of the pale VHW postdiscal band in *M. undulata* is rare or absent (but see discussion under *M. u. undulata*). Two subspecies are recognised.

Manerebia undulata undulata Pyrcz & Hall, (n. sp.)

Figs. 6A,B,C, 13B, 18

Manerebia n. sp. (Pyrcz, Willmott & Hall); Lamas & Vilorio (2004: 216, n. 1125).

Diagnosis: The nominate subspecies has narrower, although somewhat variable, pale VHW postdiscal bands and is slightly larger than *M. undulata milaena* (described below).

Description: **MALE** (Fig. 6A): **Head:** frons with a tuft of brown hair; eyes dark brown, smooth; labial palpi covered with brown hair; antennae dorsally greyish-brown, ventrally orangeish, with whitish scales at base of each segment, tip darker brown. **Thorax:** dorsal and ventral surface dark brown; legs paler brown. **Abdomen:** dorsal and ventral surface dark brown. **Wings:** forewing (length: 17.5-19 mm; mean: 18 mm; n=12) distal margin slightly convex, apex rounded; hindwing with distal margin slightly angled at vein M3, with tornal notch almost absent. DFW medium brown, darker brown in basal half. DHW medium brown, slightly darker towards base; minute black submarginal ocellus with white pupil in cell Cu2-Cu1. VFW ground colour medium brown, slightly darker towards base; thin, distinct, almost straight, darker brown postdiscal line from anal margin to near costa; distinct, undulate, darker brown submarginal line from tornus to apex; very thin, indistinct, dark

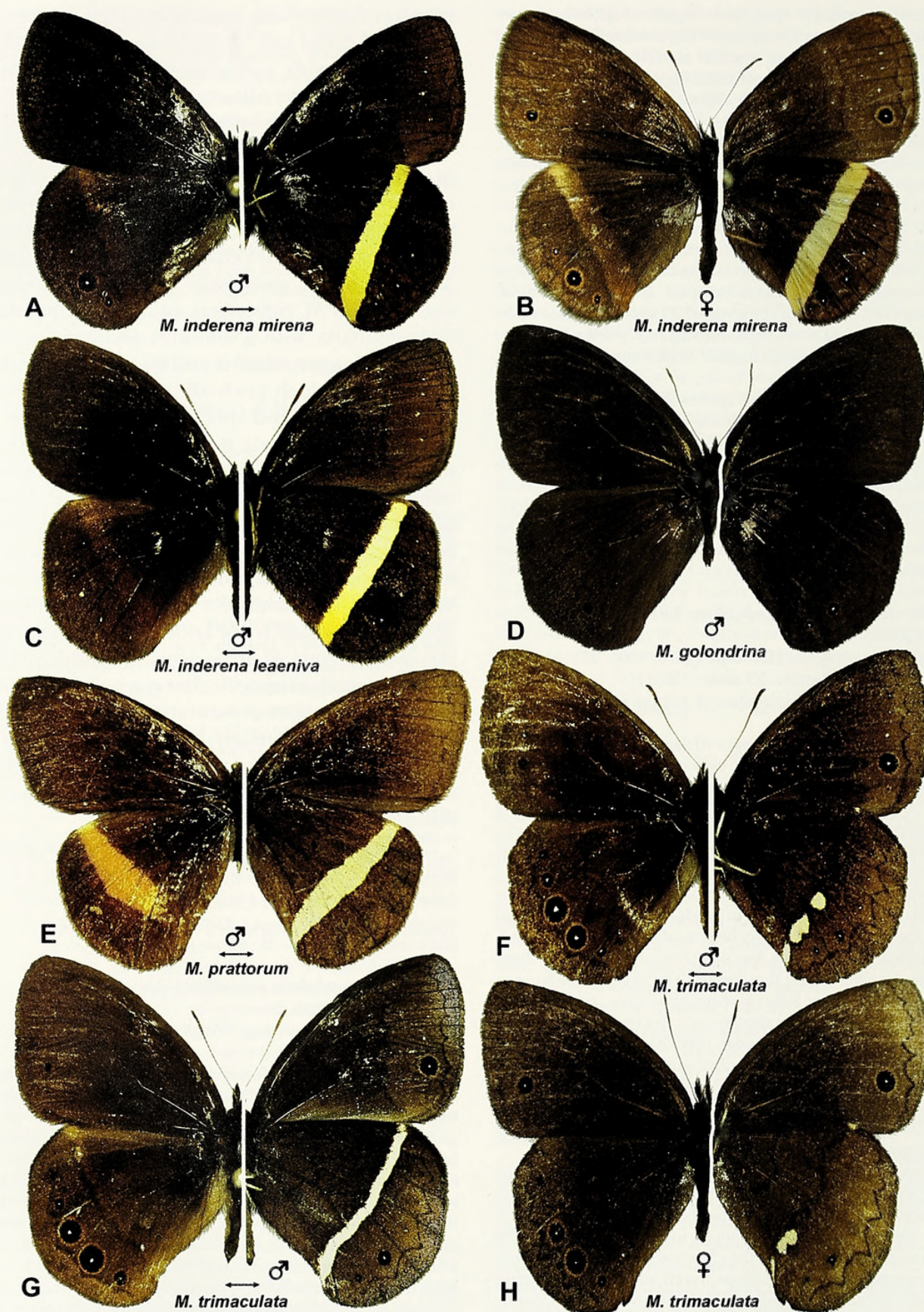


Fig. 5. Adult *Manerebia*, left dorsal view, right ventral view. Double arrows above names indicate image is reflected in vertical plane, so figured wings are righthand pair. A, *M. inderena mirena* n. ssp. male; B, *M. inderena mirena* n. ssp. female; C, *M. inderena leaeniva* n. ssp. male; D, *M. golondrina* n. sp. male; E, *M. prattorum* n. sp. male; F, *M. trimaculata* male (form); G, *M. trimaculata* male (form); H, *M. trimaculata* female. See Appendix 4 for specimen data.

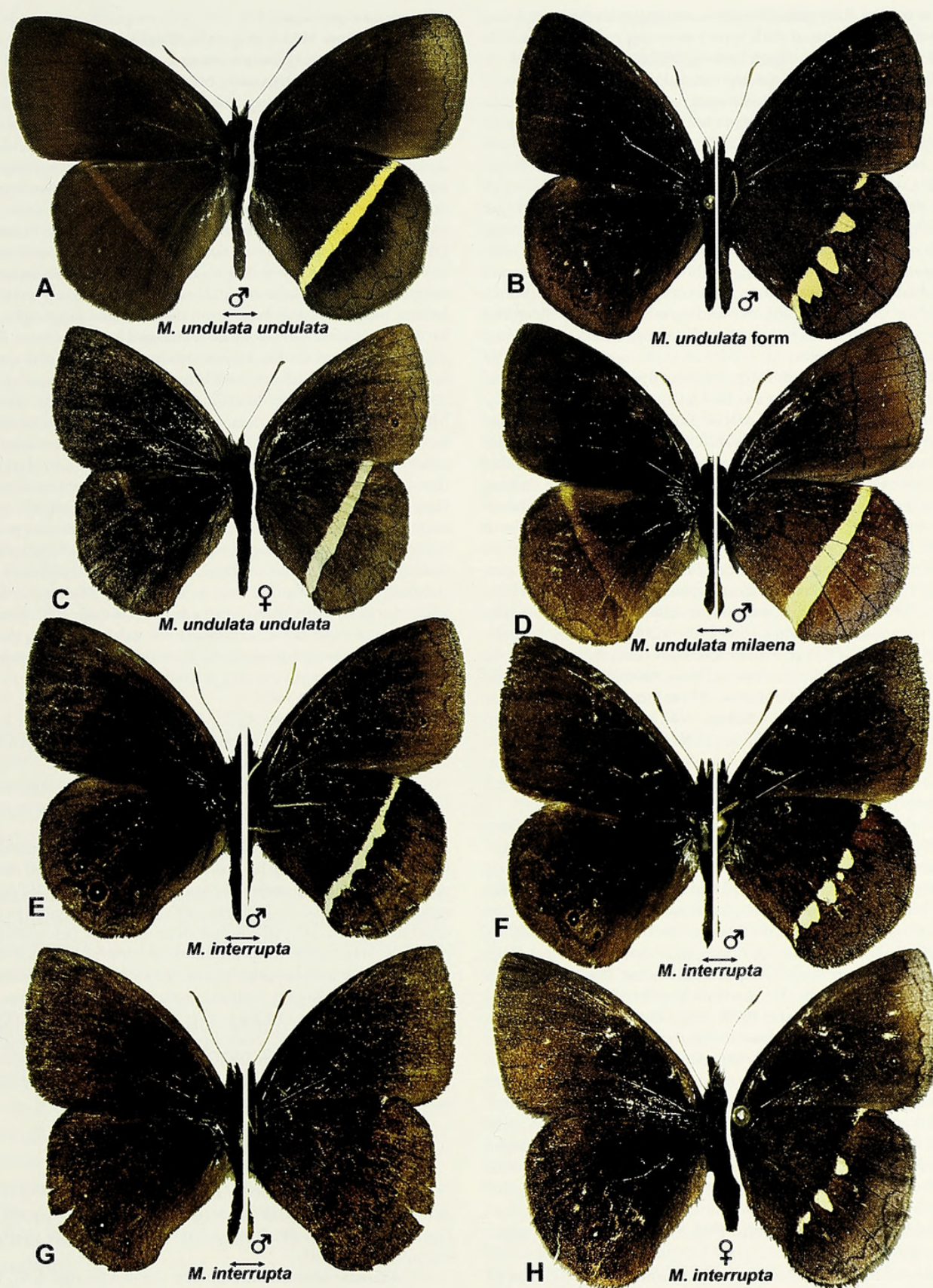


Fig. 6. Adult *Manerebia*, left dorsal view, right ventral view. Double arrows above names indicate image is reflected in vertical plane, so figured wings are righthand pair. A, *M. undulata undulata* n. sp. male; B, *M. undulata undulata* ? male; C, *M. undulata undulata* n. sp. female; D, *M. undulata milaena* n. ssp. male; E, *M. interrupta* male (form); F, *M. interrupta* male (form); G, *M. interrupta* male (form); H, *M. interrupta* female. See Appendix 4 for specimen data.

brown marginal line; pale brownish scaling extending in from distal margin to surround dark brown submarginal line, from cell Cu1-M3 to apex. VHW medium brown; indistinct, undulating dark brown line from costa to anal margin through middle of discal cell; thin, whitish postdiscal band from apex to tornus, passing through base of cell Cu1-M3, slightly convex and thinning slightly towards costa; darker brown, strongly zigzag submarginal line; minute black submarginal ocelli, with white pupils, in cell 1A-Cu2 (two) and cell Cu2-Cu1, white submarginal dots in cells Cu1-M3 and M3-M2; pale brownish scaling extending in from distal margin to surround dark brown submarginal line from tornus to apex; very faint, thin, dark brown marginal line close to and parallel with distal margin. **Male genitalia** (Fig. 13B): uncus straight, with dorsal edge and dorsal edge of tegumen forming a smooth curve, subunci short; valvae thinning sharply at middle and tapering posteriorly, dorsally grooved, with 4-6 'teeth' at distal tip; aedeagus curving dorsally, laterally smooth.

FEMALE (Fig. 6C): Differs from male as follows: ventral surface lighter and duller; an ocellus in cell 1A-Cu2 on the forewing.

Types: *Holotype male*: ECUADOR: Bolívar, Balzapamba, arriba de Santa Lucía, 1700-1750 m, 03.IX.2003, T. Pyrcz leg., MZUJ; *Al-lotype female*: same data as the holotype, MZUJ; *Paratypes* (55 males and 2 females): ECUADOR: 31 males and 1 female: same data as the holotype, TWP (29), BMNH (2 males); 2 males: Bolívar, Balzapamba, arriba de Santa Lucía, 1400-1450 m, 03.IX.2003, T. Pyrcz leg., TWP; 9 males: Loja, Zambí, 2200-2300 m, 08.III.1998, P. Boyer leg., TWP (4), PB (5); 2 males: Loja, Guayquichuma, 28.V.1996, S. Attal & I. Aldas leg., TWP; 1 male: same data but 21.V.1996, TWP; 4 males: Loja, Guayquichuma, 1800-2000 m, 15.IV.1997, A. Jasiński leg., TWP (3), MHNUC (1); 1 male: Zamora - Chinchipe, Zambí, A. Jasiński leg., TWP; 3 males: Cotopaxi, Pilaló, 2500-3000 m, VII.1996, I. Aldas leg., TWP; 1 male: Pichincha, Aloag-Sto. Domingo rd., Tandapi, 1550 m, 10.VIII.1993, J. Hall leg., MECN; 2 males: same data as preceding except 1700 m, 3.VIII.1996, K. Willmott leg., KWJH; 1 male: Pichincha, old Quito-Sto. Domingo rd., nr. Chiriboga, Río Las Palmeras, 1900 m, 14.VIII.1993, J. Hall leg., KWJH; 1 female: Loja, Zambí, P. Boyer leg., PB.

Etymology: The name is the feminine form of the Latin adjective "undulatus", meaning undulate, in reference to the undulate VHW submarginal line.

Comments: We have examined two specimens of *M. undulata* in the TWP recently collected by Stéphane Attal in southwestern Ecuador (Loja) and labelled "Yangana, route de Valladolid, 2600m, 23.V.2000" which have a broken pale VHW postdiscal band (Fig. 6B). A single male in the BMNH from "Ecuador" is similar. These specimens are associated with *M. undulata* rather than *M. interrupta* on the basis of their larger size (30% larger than *M. interrupta*) and rounded forewing apex. It is possible that these specimens represent a local population in which the broken band is monomorphic, given the lack of known specimens with a complete hindwing band from this area and phenotypic stability of the species elsewhere, but more material is required to confirm this.

The nominate subspecies occurs on the western and southwestern slopes of the Ecuadorian Andes, where it may be locally common. It has been recorded from 1400-2300 m.

Manerebia undulata milaena Pyrcz & Willmott, n. ssp.

Figs. 6D, 13C, 18

Manerebia n. sp., n. ssp. (Pyrcz, Willmott & Hall); Lamas & Vitoria (2004: 216, n. 1125b).

Diagnosis: This subspecies is smaller than the nominate. The VHW pale postdiscal bands are wider, and broaden from the costa to tornus. The ventral distal marginal sheen is wider and a purplish, rather than pale brown, colour. The dorsal surface ground colour is also paler, so that the VHW postdiscal band is faintly visible. The male genitalia do not differ consistently from

M. undulata undulata.

Description: MALE (Fig. 6D): **Head:** eyes, labial palpi and antennae as in the nominate subspecies. **Thorax:** dorsal and ventral surface dark brown; legs paler brown. **Abdomen:** dorsal and ventral surface dark brown. **Wings:** forewing (length: 17-18.5 mm; mean: 17.1 mm, n=3) distal margin angled slightly at vein M1, apex rounded; hindwing outer margin almost perfectly rounded with a very slight angle at vein M3, and a slight tornal notch; fringes light brown. DFW medium brown, darker brown in basal half, androconial scales not apparent; a faint, darker, undulate submarginal line. DHW medium brown, slightly darker towards base; very faint, postdiscal band of pale scales reflecting VHW band, stronger at costa; slightly paler yellowish brown, sparse scales in marginal area; darker, zigzag submarginal line. VFW ground colour medium brown, darker towards base; thin, distinct, almost straight, darker brown postdiscal line from anal margin to near costa; distinct, slightly undulate, darker brown submarginal line from tornus to apex; very thin, indistinct, dark brown marginal line; pale purplish grey scaling extending in from distal margin to surround dark brown submarginal line, from cell Cu1-M3 to apex; row of tiny white submarginal dots in cells Cu2-Cu1 to M2-M1. VHW medium brown; indistinct, undulating dark brown line from costa to anal margin through middle of discal cell; thin, yellowish white postdiscal band from apex to tornus, passing through base of cell Cu1-M3, approximately straight and broadening continuously from costa to tornus; darker brown, strongly zigzag submarginal line; pale purplish grey scaling extending in from distal margin to surround dark brown submarginal line from tornus to cel M1-Rs. **Male genitalia** (Fig. 13C): uncus straight, with dorsal edge and dorsal edge of tegumen forming a smooth curve, subunci short; valvae thinning sharply at middle and tapering posteriorly, dorsally grooved, with 4-6 'teeth' at distal tip; aedeagus curving dorsally, laterally smooth.

FEMALE: Unknown.

Types: *Holotype male*: ECUADOR: Loja, Cordillera de Lagunillas, Jimbura - Laguna Negra, 3000-3200 m, 15.V.1998, A. Jasiński leg., MZUJ; *Paratypes:* 2 males: same data as the holotype, TWP.

Etymology: The name is a composite of the names of two other related Ecuadorian *Manerebia* taxa: (*M. inderena*) *mirena* and (*M. inderena*) *leaniva*.

Comments: Unlike *M. undulata undulata*, which is a cloud forest species of intermediate elevations, the type series of *M. undulata milaena* was collected at the tree-line in the Cordillera de Lagunillas range, at 3000-3200 m. Unfortunately, there is virtually no natural vegetation remaining in southwestern Ecuador below 2800m, so it may be impossible to locate the true natural lower elevational limit. A single individual of (apparently) *M. undulata milaena* (in the MUSM), collected further south on the west slopes of the Andes in Peru, east of Chiclayo (Cajamarca), at 2400-2600 m, is excluded from the type series. Specimens of *M. prattorum* from the same locality (see southernmost data point on Fig. 17) represent a subspecies different from that in southern Ecuador, and the same might apply to *M. undulata*.

Manerebia interrupta (Brown, 1944)

Figs. 6E,F, G, H, 13D, 18

Penrosada apiculata form *interrupta* Brown (1944: 257, male genit. Fig. 1618). **TL:** Ecuador, Azuay, Seville de Oro. **HT male:** Ecuador, Azuay, Seville de Oro, 2500 m, 15.II.[19]39. AME [photograph examined].

= *Manerebia keradialeuka* Hayward (1968: 205, figs. 4, 8). **TL:** Ecuador, Azuay, Tarqui. **HT male:** Ecuador, Azuay, Tarqui, 08.V.[19]65, Luis Peña leg. IMLT [examined].

Penrosada apiculata form *curvilinea* (Weymer); Brown (1944: 258) (misidentification).

Manerebia interrupta (Brown); Lamas & Vitoria (2004: 215).

Diagnosis: As in *M. trimaculata*, the VHW yellow band is variably expressed, and varies from complete absence (Fig. 6G), through

a series of semicircular spots (Fig. 6F), to being complete, with an uneven distal edge (Fig. 6E). *Manerebia interrupta* is much smaller than *M. trimaculata*, has a more acute forewing apex, and lacks an ocellus on the VFW in cell Cu1-Cu2. Brown (1944), and presumably earlier workers, misidentified this species in Ecuador as the superficially similar but genitally distinct Colombian *M. apiculata*, and named a form with the band broken into spots as form *interrupta*. Hayward (1968) subsequently named a form without any hindwing band as *Manerebia keradialeuka*. Brown's name *interrupta* thus becomes the first available name for this species, to which *M. keradialeuka* Hayward is a junior synonym (Lamas & Viloria, 2004). Male genitalia as illustrated (Fig. 13D).

Comments: *Manerebia interrupta* appears to be most closely related to *M. undulata* and *M. trimaculata* (see discussion under those species). Although it has not been reported from the same sites as either *M. trimaculata* or *M. undulata*, its closest relatives, it appears to replace each locally at higher elevations and in drier habitats. This species occurs from south-central (Morona-Santiago: Gualaceo-Chiguinda rd.; Gualaceo-Limón road,) to southern Ecuador (Loja: above Catamayo; Cerro Palma, Loja-Zamora rd.) and in northern Peru (Piura: entre Las Minas y El Tambo) on the western slopes of the Andes. It occurs from 2400 m up to the tree-line around 3200 m. Males were found flying low to the ground in areas of recent bamboo regrowth on landslips in elfin forest/páramo mosaic, and also in a dry river gulley through desert scrub on the southwestern slopes. The species is most commonly encountered in drier habitats, such as those of the inter-Andean valleys. We have also observed males hilltopping at Cerro Palma, and occasionally puddling at damp sand. The species appears to be highly seasonal; whereas it was very common along the Gualaceo-Limón road in February (wet season), no individuals were observed in the same locality in August, during the dry season.

Manerebia rufanalis Pyrcz & Hall, n. sp.

This species is distinguished from all others by the rusty suffusion and submarginal ocelli at the tornus of the DHW. The light magenta sheen along the distal margins on the ventral surface, especially at forewing apex and on the hindwing, is also distinctive. The VFW ocellus in cell Cu1-Cu2 is generally, but not always, well developed and is occasionally also apparent in adjacent cells. The VHW yellow band is variable and appears to be relatively wider in smaller specimens. The genitalia are distinctive within the genus, and differ from those of *M. inderena* and *M. undulata* by having an arched uncus and relatively long subunci, similar to species such as *M. leaena* and *M. satura*, while the elongate valva, which lacks 'teeth' at the dorsal edge near the base, similar to *M. inderena* and *M. trimaculata*, has a smoothly upwardly curving (rather than "stepped") basal edge. In addition, the valva always has relatively few (usually 2-3) large 'teeth' at the distal tip.

Manerebia rufanalis rufanalis Pyrcz & Hall, (n. sp.)

Figs. 7A, B, 13E, 19

Manerebia n. sp. (Pyrcz, Willmott & Hall); Lamas & Viloria (2004: 216, n. 1126).

Diagnosis: The nominate subspecies is distinguished from *M. r. fernandina* as discussed below. There is some variation in this taxon,

and some individuals have an additional ocellus on the DHW in cell Cu1-M3.

Description: MALE (Figs. 7A): **Head:** frons with a tuft of dark brown hair; eyes chocolate brown, smooth; labial palpi covered with dark brown hair; antennae dorsally chestnut, ventrally rufous, with white scales at the base of each segment, club same colour as shaft. **Thorax:** dorsal and ventral surface dark brown; legs paler brown. **Abdomen:** dorsal and ventral surface dark brown. **Wings:** forewing (length: 18-21 mm; mean: 19.9 mm; n=8) distal margin slightly angled at vein M2, apex rounded; hindwing slightly angled at vein M3, with slight tornal notch. DFW medium brown, darker brown in basal half. DHW medium brown, slightly darker towards base; a small submarginal black ocellus ringed with orange, with a white pupil, in anterior half of cell 1A-Cu2, a larger similar ocellus in cell Cu2-Cu1; orange-brown scaling along the anal margin, broadening into tornus to extend to edge of ocellus in cell 1A-Cu2. VFW ground colour medium brown, darker in basal half; thin, very faint, straight, darker brown postdiscal line in cells Cu2-M1; black submarginal ocellus ringed with dark yellow, with a white pupil, in cell Cu2-Cu1; three white submarginal dots in cells Cu1-M3 to M2-M1; indistinct, undulate, darker brown submarginal line from tornus to apex; thin, very faint, dark brown marginal line; pale greyish scaling extending from distal margin to surround dark brown submarginal line in cells M3-M2 to costa. VHW medium brown, scattered with very sparse red-brown scales in basal two-thirds, denser along anal margin and costa, particularly at apex; pale yellow postdiscal band (becoming white at basal edge) from apex to tornus, passing through base of cell Cu1-M3, straight and of even width; faint, darker brown, zigzag submarginal line; three small black submarginal ocelli, with a white pupil, in cells 1A-Cu2 and Cu2-Cu1; a white submarginal dot in cell Cu1-M3; thin, dark brown marginal border; pale greyish scaling sparsely extending in from distal margin to just past dark brown submarginal line from tornus to cell M3-M2. **Male genitalia** (Fig. 13E): uncus smoothly arching, subunci relatively long; basal edge of valvae smoothly curving, dorsally grooved, with 2-3 'teeth' at distal tip; aedeagus thin and shallowly curving dorsally, laterally smooth.

FEMALE (Fig. 7B): Similar to male but lighter on both wing surfaces.

Types: **Holotype male:** ECUADOR: Tungurahua, Baños, Runtún, 2600-3000 m, 06.VIII.1998, T. Pyrcz leg., MZUJ; **Allotype female:** ECUADOR: Loja, Old road Loja-Zamora, 2600m, XI.1999, I. Aldas, leg., MBLI; **Paratypes (32 males and 1 female):** ECUADOR: **1 male:** Tungurahua, Baños, TWP; **1 male:** Tungurahua, Baños, V.1995, I. Aldas leg., TWP; **1 male:** Tungurahua, Runtún, 3000m, 21.XI.1998, P. Boyer leg., PB; **1 male:** Tungurahua, Baños-Puyo rd., Río Machay, 1700 m, 19-20.VIII.1993, J. Hall leg., MECN; **1 male:** same data as preceding except 12.IX.1993, KWJH; **1 male:** Napo, Baeza, 1800 m, IX.1996, P. Boyer leg., PB; **1 male:** Zamora-Chinchipe, San Andrés, 2200 m, 13.VIII.1998, T. Pyrcz leg., TWP; **1 male:** Zamora-Chinchipe, región de Valladolid, 2500 m, 25.XI.1993, B. Méry & S. Attal leg., TWP; **1 male:** Zamora-Chinchipe, Río San Francisco, 1400[?] m, 11.XI.1989, A. Crosson-du-Cormier & S. Attal leg., TWP; **1 male:** Zamora-Chinchipe, San Andrés - Calderón, 2200-2600 m, 20.V.1998, A. Jasiński leg., TWP; **1 male:** Zamora-Chinchipe, nr. Valladolid, Quebrada Tapichalaca, 1950 m, 4.XI.1997, K. Willmott leg., KWJH; **1 male:** Zamora-Chinchipe, km 34 Jimbura-San Andrés rd., 2900 m, 23.IX.1997, K. Willmott leg., KWJH; **1 male:** Zamora-Chinchipe, Zamora-Loja rd., nr. Sabanillas, Quebrada San Ramón, 1700 m, 27-29.X.1997, K. Willmott leg., KWJH; **13 males:** Zamora-Chinchipe, Valladolid, Quebrada de los Muertos, 2550 m, XI.1999, I. Aldas leg., TWP (4), MBLI (9); **3 males:** Loja, Old road Loja-Zamora, 2500-2600m, XI-XII.1999, I. Aldas, leg., MBLI; **1 male:** Tungurahua, El Tablón, 3000m, III.1999, I. Aldas leg., MBLI; **1 male:** Tungurahua, Baños, Río Verde, 2300 m, III.1999, G. Velástegui leg., MBLI; **1 female:** Loja, Old road Loja-Zamora, 2600m, XI.1999, I. Aldas, leg., MBLI. PERU: **1 male:** Cajamarca, Tabaconas, VIII.1996,

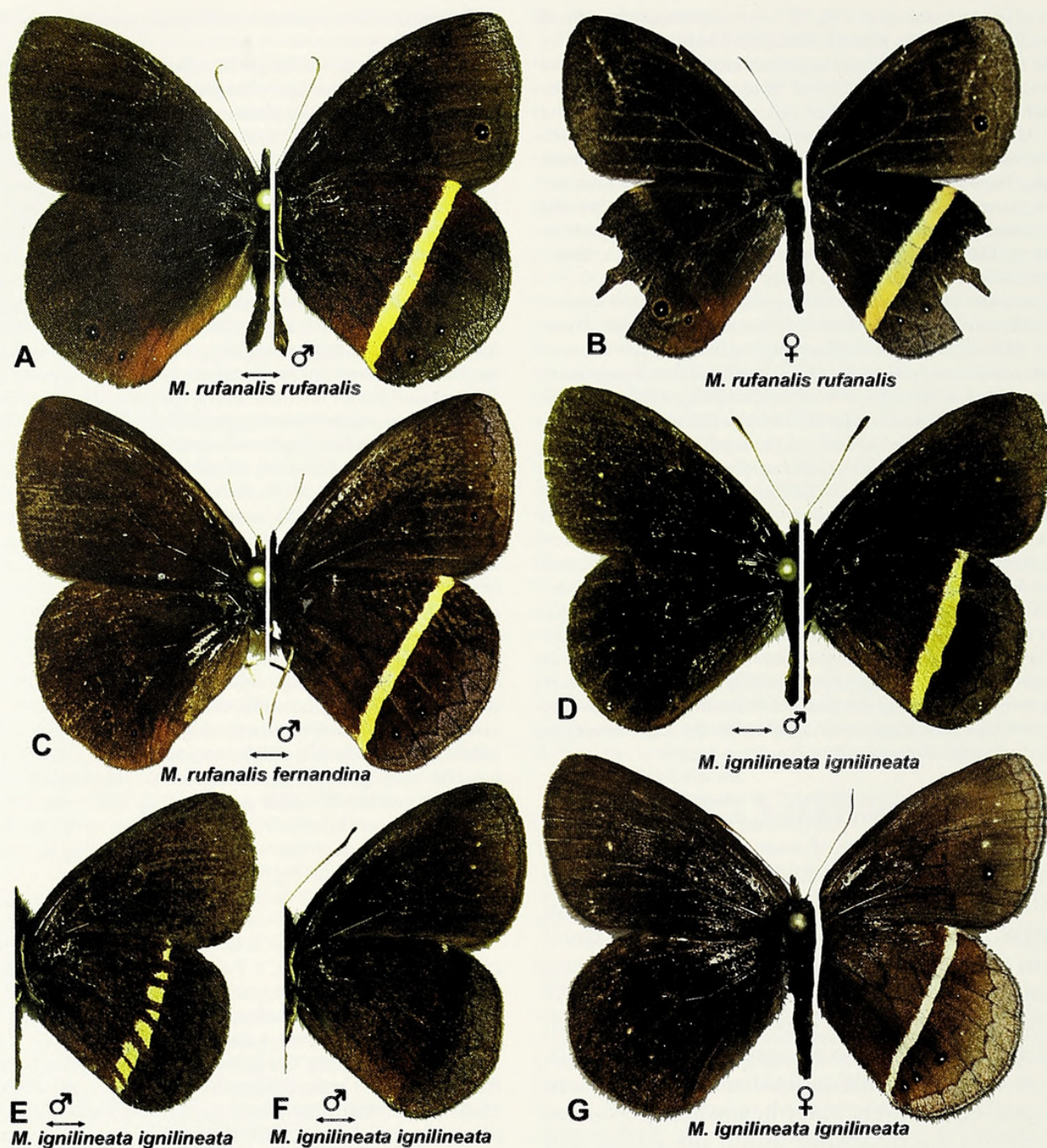


Fig. 7. Adult *Manerebia*, left dorsal view, right ventral view. Double arrows above names indicate image is reflected in vertical plane, so figured wings are righthand pair. A, *M. rufanalis rufanalis* n. sp. male; B, *M. rufanalis rufanalis* n. sp. female; C, *M. rufanalis fernandina* n. ssp. male; D, *M. ignilineata ignilineata* male (form); E, *M. ignilineata ignilineata* male (form); F, *M. ignilineata ignilineata* male (form); G, *M. ignilineata ignilineata* female. See Appendix 4 for specimen data.

I. Aldas leg., TWP.

Etymology: The species name is derived from the Latin “rufus”, reddish brown, referring to the distinctive color in the anal area of the DHW.

Comments: This subspecies is known from the east Andean slopes in central Ecuador to far northern Peru, and it is one of the most common *Manerebia*, occurring in fairly intact cloud forest habitats from 1700–2900 m. Males may often be encountered puddling at stream and river banks, particularly at urine, and are attracted to rotting fish. We have also observed males hilltopping

on open, grassy summits with low bushes, along the Jimbura-San Andrés road.

***Manerebia rufanalis fernandina* Pycr & Willmott, n. ssp.**

Figs. 7C, 13F, 19

Manerebia n. sp., n. ssp. (Pycr, Willmott & Hall); Lamas & Vilorio (2004: 216, n. 1126b).

Diagnosis: This subspecies is slightly smaller than the nominate,

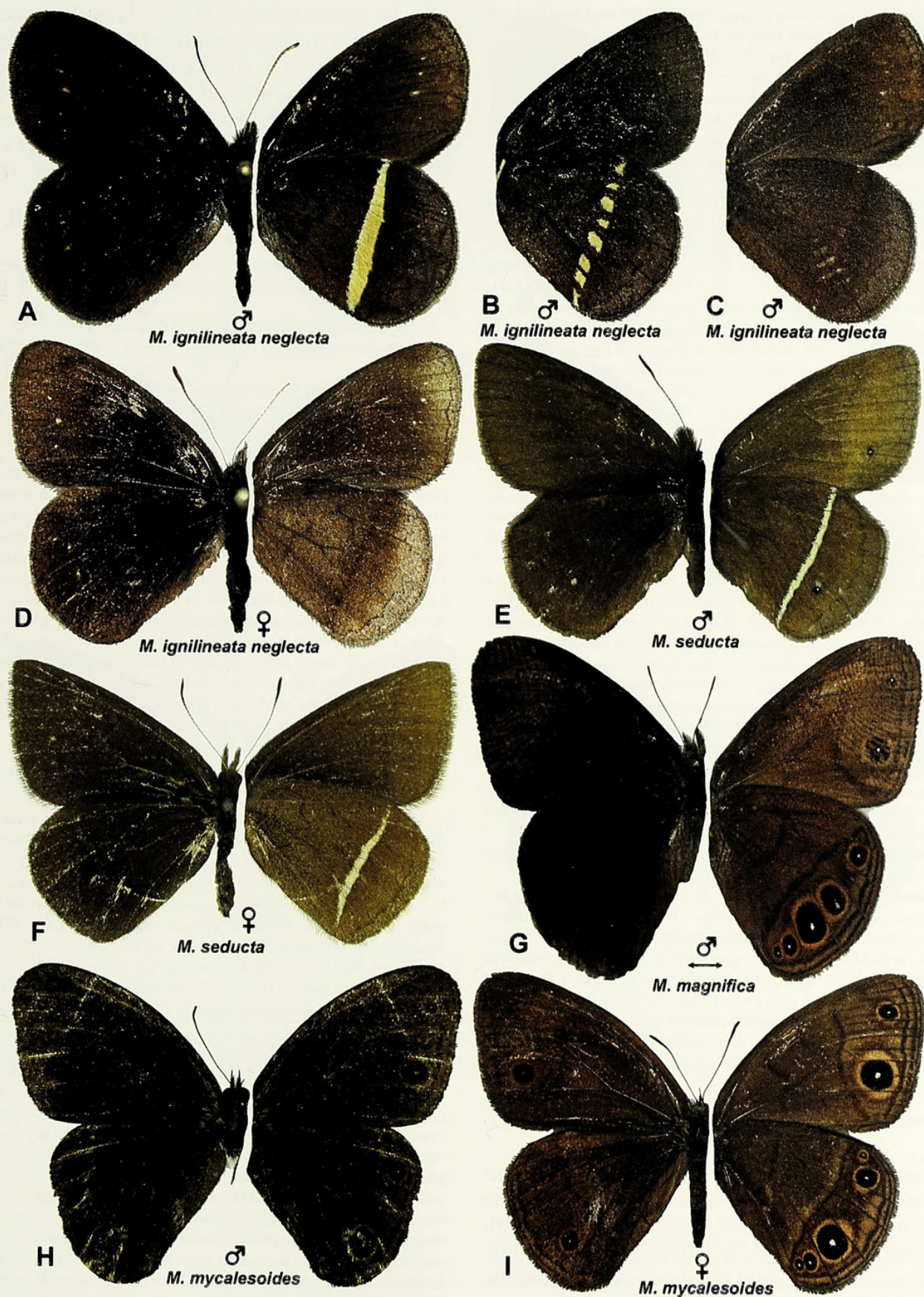


Fig. 8. Adult *Manerebia*, left dorsal view, right ventral view. Double arrows above names indicate image is reflected in vertical plane, so figured wings are righthand pair. A, *M. ignilineata neglecta* male (form); B, *M. ignilineata neglecta* male (form); C, *M. ignilineata neglecta* male (form); D, *M. ignilineata neglecta* male (form); E, *M. seducta* n. sp. male; F, *M. seducta* n. sp. female; G, *M. magnifica* n. sp. male; H, *M. mycalesoides* male; I, *M. mycalesoides* female. See Appendix 4 for specimen data.

has reduced reddish-brown scaling on the DHW anal area and the ocelli are smaller on both wing surfaces.

Description: MALE (Fig. 7C): **Head:** frons with a tuft of dark brown hair; eyes chocolate brown, smooth; labial palpi covered with long, dark brown hair; antennae dorsally chestnut, ventrally orange, with white scales at the base of each segment, club same colour as shaft. **Thorax:** dorsal and ventral surface dark brown; legs paler brown. **Abdomen:** dorsal and ventral surface dark brown. **Wings:** forewing (length: 18 mm, mean: 18 mm, n=1) distal margin slightly angled at vein M2, apex rounded; hindwing slightly angled at vein M3, with slight tornal notch. DFW medium brown, darker brown in basal half. DHW medium brown, slightly darker towards base; two small submarginal black ocelli ringed with orange, with white pupils, in anterior half of cell 1A-Cu2 and in cell Cu2-Cu1; orange-brown scaling in the tornus, not extending to ocellus in 1A-Cu2. VFW ground colour medium brown, darker in basal half; thin, very faint, straight, darker brown postdiscal line in cells Cu2-M1; small black submarginal ocellus ringed with dark orange, with a white pupil, in cell Cu2-Cu1; three white submarginal dots in cells Cu1-M3 to M2-M1; distinct, undulate, darker brown submarginal line from tornus to apex; thin, very faint, darker brown marginal line; pale purplish grey scaling extending from distal margin to surround dark brown submarginal line in cells Cu2-Cu1 to costa. VHW medium brown, scattered with very sparse red-brown scales in basal two-thirds; pale yellow postdiscal band (becoming white at basal edge) from apex to tornus, passing through base of cell Cu1-M3, slightly concave and of even width; faint, darker brown, zigzag submarginal line; two small black submarginal ocelli, with a white pupil, in anterior half of cell 1A-Cu2 and in Cu2-Cu1; a white submarginal dot in cell Cu1-M3; thin, dark brown marginal border; pale purplish grey scaling sparsely extending in from distal margin to just past dark brown submarginal line from tornus to cell M3-M2. **Male genitalia** (Fig. 13F): uncus smoothly arching, subunci relatively long; basal edge of valvae smoothly curving, dorsally grooved, with a single "tooth" at distal tip; aedeagus thin and shallowly curving dorsally, laterally smooth.

FEMALE: Unknown.

Types: **Holotype male:** ECUADOR: Azuay, Girón, San Fernando, 2500 m, 08.V.1998, P. Król *leg.*, MZUJ; **Paratypes: 2 males:** same data as the holotype, TWP.

Etymology: The name is derived from that of the type locality, San Fernando.

Comments: The three types of *M. rufanalis fernandina* are the only known specimens of this species from the western Andes. The type locality of *fernandina* (San Fernando) is in the Cuenca valley, an area of endemism in cloud forest satyrines, generally at the subspecific level (e.g., *Lasiophila phalaesia kroli* Pyrcz, *Pedaliodes xanthosphenisca* ssp. Pyrcz, in prep.). Since a number of other east Andean cloud forest taxa cross over to the western slopes in southern Ecuador (Willmott & Hall, in prep.), this taxon may also occur further south, where little habitat remains at a suitable elevation.

Manerebia ignilineata (Dognin, 1896)

This is the smallest species of *Manerebia*, and is easily distinguished from all other species by the elongate, rounded wings (a character shared with *M. pervaga*), the irregular VHW submarginal line placed relatively far from the distal margin, and the male genitalia. The latter are markedly distinct from all other north Andean species, except *M. seducta*, in the short, squat valva, which is enlarged in the basal half, lacks a dorsal groove, has very large, sparse distal 'teeth', and whose tips flare outwards in ventral view.

Like *M. trimaculata* and *M. interrupta*, this species is polymorphic in the expression of the VHW postdiscal band, and occurs in three fairly discrete forms; one form has a fully developed VHW band (Fig. 7D), the second has the band broken into a row of quadrate spots by dark brown lines on the veins (Fig. 7E), and the last has the band completely absent (Fig. 7F).

Manerebia ignilineata ignilineata (Dognin, 1896)

Figs. 7D, E, F, G, 14A, 20

Lymanopoda ignilineata Dognin (1896: 134). **TL:** Ecuador, Loja, Loja. **HT male:** Ecuador, Loja, Environs de Loja, 1890. BMNH [examined]

Penrosada ignilineata (Dognin); D'Abrera (1988: 824).

Manerebia ignilineata (Dognin); Lamas & Vilorio (2004: 215) (in part).

Diagnosis: The nominate subspecies differs from *M. i. neglecta* as discussed under that taxon. The expression of the VHW pale postdiscal band is polymorphic in both sexes (Figs. 7D, E, F, G). Male genitalia as illustrated (Fig. 14A).

Comments: Dognin's (1896) description of this species is concise but clear, and the holotype male, which has an indistinct, broken VHW postdiscal band intermediate between the specimens figured in Figs. 7E and 7F, is in the BMNH. *Manerebia ignilineata ignilineata* occurs at the cloud forest/páramo ecotone, and in the lower páramo, in southern Ecuador (Morona-Santiago: Gualaceo-Limón; Loja: Jimbura-San Andrés rd.; Loja-Zamora rd.) on the eastern, and in far south, western slopes of the Andes, from 2700-3300 m. The species seems to be very local and seasonal. Males fly usually 1-3 m above dense stands of bamboo growing in páramo intermixed with elfin forest. *Manerebia ignilineata* occurs also in northern Peru, east of the Río Marañón, as a distinct subspecies, *M. ignilineata jalca* Pyrcz (2004).

Manerebia ignilineata neglecta (Brown, 1944), n. stat.

Figs. 8A, B, C, D, 14B, 20

Penrosada lanassa form *neglecta* Brown (1944: 260, male genit. fig. 1619). **TL:** Ecuador, Tungurahua, Minza Chica. **HT male:** Ecuador, Tungurahua, Minza Chica, 08.IV.[19]39, 3200 m, *leg.* F. M. Brown, No. B1619. AME [photograph examined], n. stat.

= *Penrosada lanassa* form *discontinua* Brown (1944: 260, male genit. fig. 1617). **TL:** Ecuador, Tungurahua, Minza Chica. **HT male:** Ecuador, Tungurahua, Minza Chica, 08.IV.[19]39, 3200 m, *leg.* F. M. Brown, No. B1617. AME [photograph examined].

[*Penrosada lanassa* (C. & R. Felder); Brown (1944: 258)]

Manerebia ignilineata (Dognin); Lamas & Vilorio (2004: 215) (in part).

Diagnosis: This subspecies differs from the nominate in the forewing distal margin being nearly straight, except angled slightly at vein M2, instead of convex, and in the hindwing being slightly angled between M1 and M2 and at M3, instead of almost perfectly rounded. It also lacks the shining magenta colour on the distal margin of the VHW and apex of the VFW, and the VHW submarginal line is more zigzag than in the nominate.

Redescription: MALE (Figs. 8A, B, C): **Head:** frons with sparse blackish hair; eyes blackish-brown, smooth; labial palpi covered with black hair; antennae dorsally brown, ventrally dirty yellow, club formed of 10-11 segments, twice width of shaft. **Thorax:** dorsally blackish-brown, ventrally medium brown. **Abdomen:** dorsally blackish-brown, laterally and ventrally medium-brown. **Wings:** forewing distal margin nearly straight except angled slightly at vein M2, apex rounded; hindwing slightly angled between M1 and M2 and at M3, tornal notch absent. Fringes of both fore and hindwings light-brown. DFW medium brown, darker towards base. DHW almost uniform medium brown, except for faint trace of postdiscal band

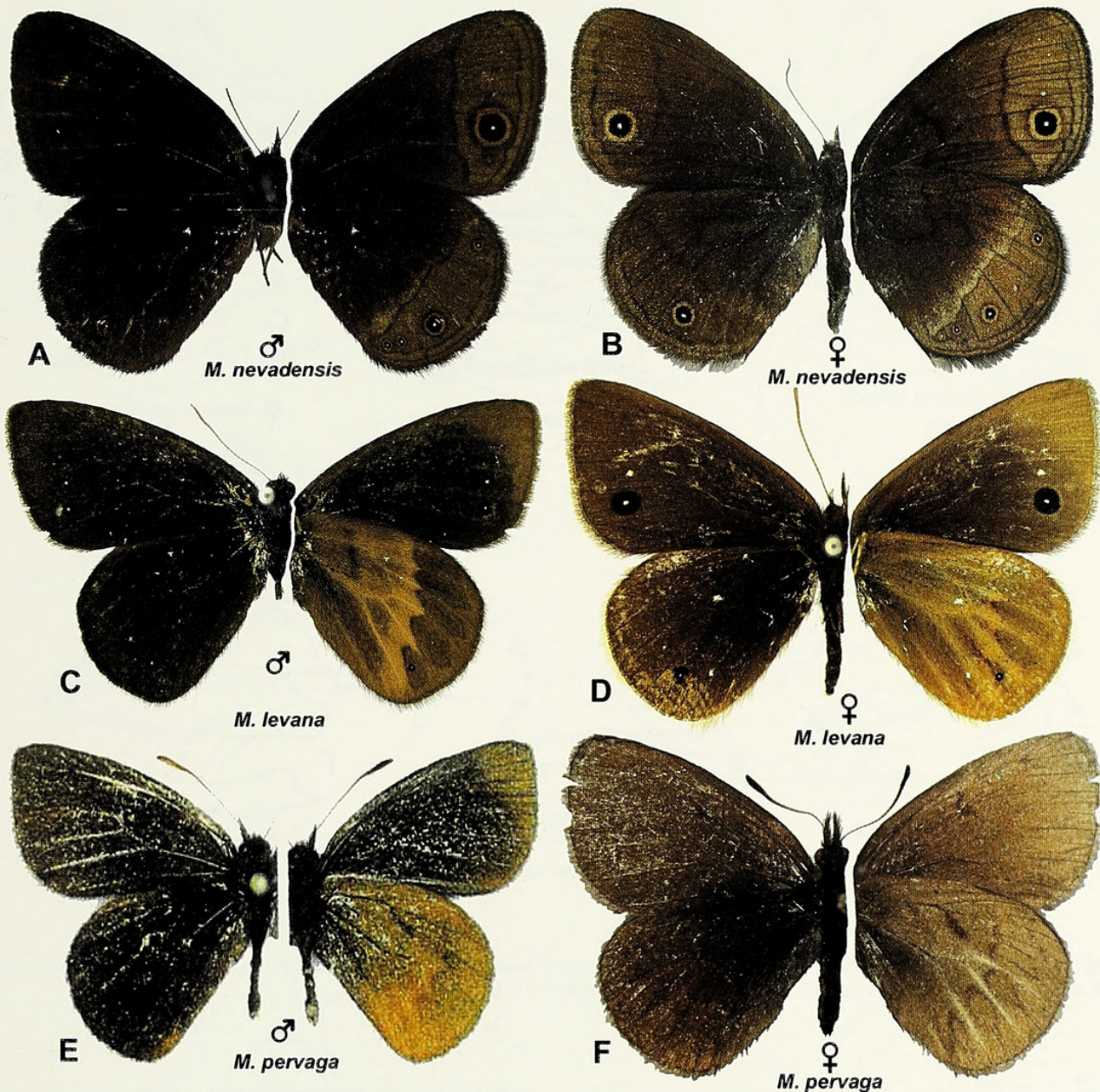


Fig. 9. Adult *Manerebia*, left dorsal view, right ventral view. Double arrows above names indicate image is reflected in vertical plane, so figured wings are righthand pair. A, *M. nevadensis* male; B, *M. nevadensis* female; C, *M. levana* male; D, *M. levana* female; E, *M. pervaga* n. sp. male; F, *M. pervaga* n. sp. female. See Appendix 4 for specimen data.

of pale scales reflecting VHW band, noticeable only towards costal margin. VFW ground colour medium brown, slightly lighter in distal third; two or three tiny, barely noticeable yellow submarginal dots; rufous-brown, slightly undulate submarginal line. VHW medium brown; indistinct, "S"-shaped postdiscal line, a thin (*c.* 1 mm) pale yellow postdiscal band from apex to tornus, nearly straight, passing along distal edge of discal cell at vein M3, in some individuals broken into a series of spots or completely absent; a thin, wavy submarginal darker brown line, area distal to it and immediately basal pale grey with a light magenta sheen. **Male genitalia:** as illustrated (Fig. 14B).

FEMALE (Fig. 8D): Similar to male except with a paler ventral surface.

Comments: Brown (1944) introduced the names *discontinua* and *neglecta* for two individual forms of "*M. lanassa*". The original illustrations of the holotype male genitalia of each, though poorly drawn, show the sparse, large dorsally directed spines at the tip of the valva, the very broad base of the valva, and the short, curved uncus and subunci that occur only in *M. ignilineata*. We have examined photographs of the holotypes of *neglecta* and *discontinua* (provided by Gerardo Lamas), now deposited in the AME, and both names apply to a population of *M. ignilineata* occurring in central Ecuador that appears to be consistently distinct from the nominate. Lamas & Vilorio (2004) placed both names as synonyms of *M. ignilineata*, and since no other authors have dealt with Brown's names, we select *neglecta* as the name for this taxon (**n. stat.**). *Manerebia ignilineata*

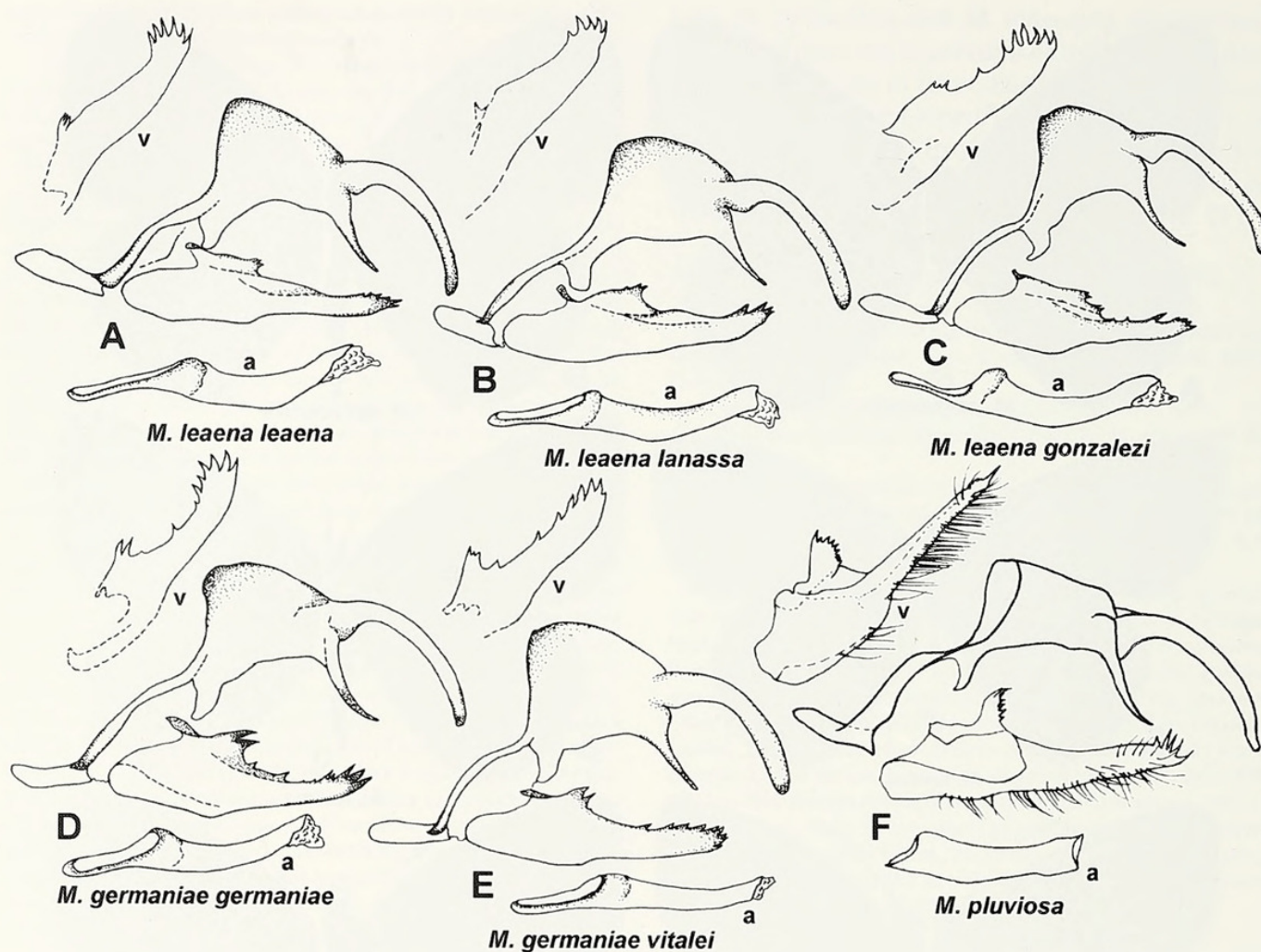


Fig. 10. *Manerebia* male genitalia, lateral view; v = valva ventral view, a = aedeagus lateral view, ad = aedeagus dorsal view. *M. leaena*, *M. germaniae* n. sp., *M. pluviosa* n. sp. See Appendix 5 for specimen data.

neglecta is known from Cañar: Pimo, Gun, Zhud-Alausí km 2, 3100 m; Tungurahua: Minza Chica, 3200 m; Napo: Papallacta-Archidona trail; Pichincha: Quito-Río Toachi trail; Chimborazo: Huigra; Hda. Licay, above Huigra; Bolívar: Pilaló, 3100 m south to Cañar, from 3100-3200 m. It is locally common in the forest-páramo ecotone near Zhud (Azuay), where it flies with *Neopedaliodes parrhoebia* n. ssp. and *Lymanopoda hazelana* n. ssp. (Pyrz, in prep.).

***Manerebia seducta* Pyrcz & Willmott, n. sp.**

Figs. 8E,F, 14C, 20

Manerebia n. sp. (Pyrz, Willmott & Hall); Lamas & Vilorio (2004: 216, n. 1122).

Diagnosis: This species is recognised by the elongate shape of the wings, the white VHW band uniquely lying distal of the discocellulars, and by the small single ocelli on the fore and hindwing (absent in the female). The male genitalia are most similar to *M. ignilineata*, which may be the sister species, and are characterised by the broad base to the valva, with few terminal 'teeth', and elongate aedeagus. *Manerebia seducta* differs principally from *M. ignilineata* by the less reddish ground colour to the wings and more pointed forewing apex. The two species are microsympatric.

Description: MALE: (Fig. 8E): **Head:** frons with a tuft of brown hair; labial palpi covered with dense and long black hair; eyes

blackish, smooth; antennae dorsally brown, ventrally chestnut, white scales at base of each segment. **Thorax:** dorsal and ventral surface dark brown; legs paler brown. **Abdomen:** dorsal and ventral surface dark brown. **Wings:** forewing (length: 23 mm, mean: 23 mm, n=2) elongate, triangular, with almost straight distal margin and sharply pointed apex; hindwing elongate and smoothly rounded, with no tornal notch. DFW uniform medium brown. DHW uniform medium brown. VFW ground colour medium brown, somewhat variable, slightly lighter towards outer margin; irregular dark brown submarginal line; area between it and outer margin suffused with magenta; a minute black ocellus with white pupil in cell Cu2-Cu1. VHW medium brown; barely visible, uneven, dark brown line through middle of discal cell, fading near costa and anal margin; thin, milky white postdiscal band from apex to tornus, with somewhat irregular inner and sharp outer edge; thin, smoothly curving darker brown submarginal line, parallel to distal margin, from tornus to near apex; thinner dark brown marginal line; the area between submarginal line and outer margin suffused with magenta, twice as wide as on the forewing. **Male genitalia:** (Fig. 14C) tegumen slender; uncus arched, subuncus half the length of uncus; valvae stout, sharply thinning at middle with three prominent distal 'teeth' and grooved dorsal surface; aedeagus long, thin and smooth, with a pronounced 'collar' at junction of anterior and

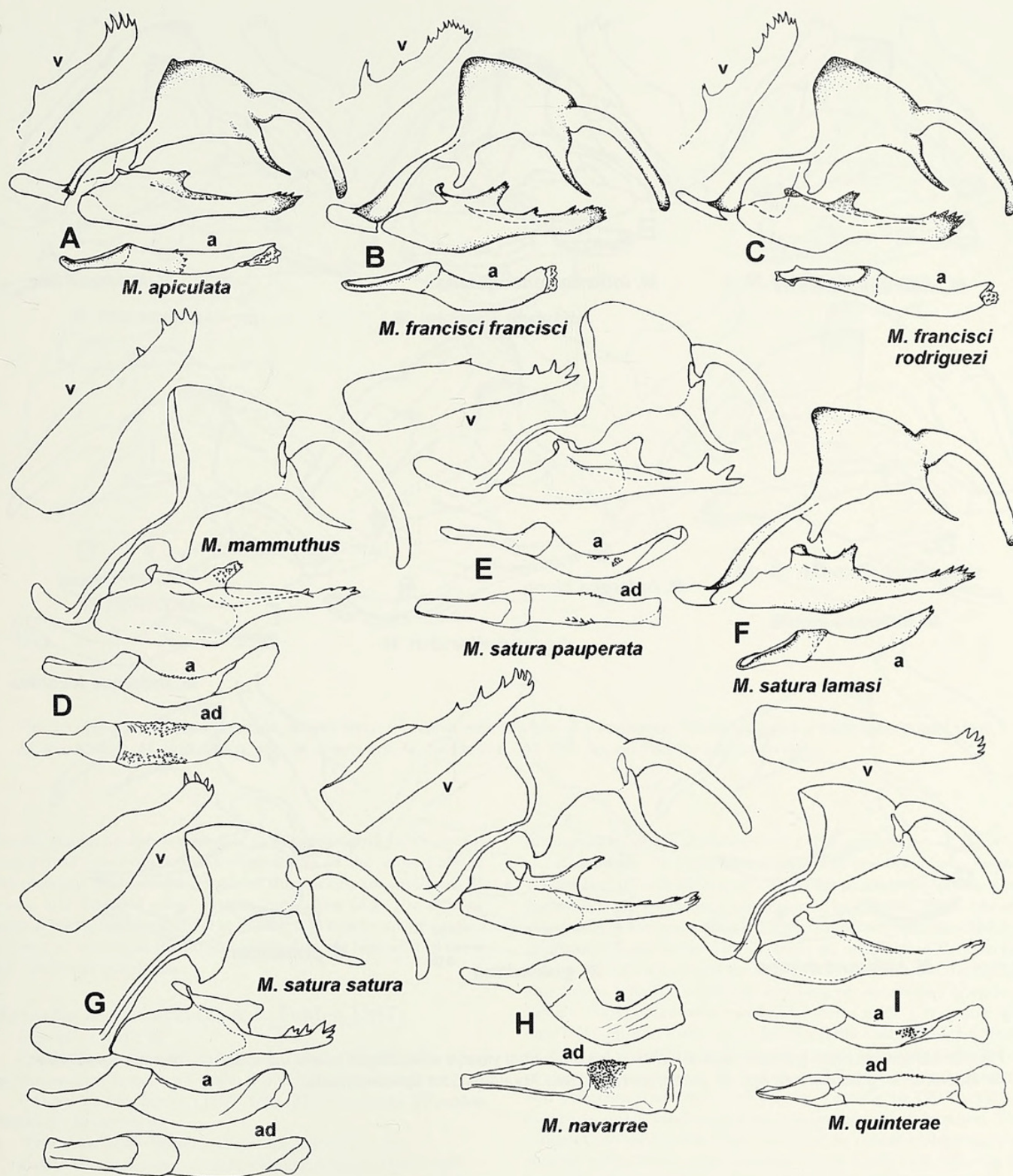


Fig. 11. *Manerebia* male genitalia, lateral view; v = valva ventral view, a = aedeagus lateral view, ad = aedeagus dorsal view. *M. apiculata*, *M. franciscae*, *M. mammothus* n. sp., *M. satura*, *M. navarrae*, *M. quinterae*. See Appendix 5 for specimen data.

posterior portions.

FEMALE: (Fig. 8F) *Head*, *thorax* and *abdomen* as in male. *Wings*: forewing (length: 17.5 mm, n=2) similar to male. DFW and DHW

uniform medium brown. VFW ground colour medium brown; basal two-thirds separated from distal third by sharp vertical boundary, basal two-thirds darker brown; minute paler submarginal dots in

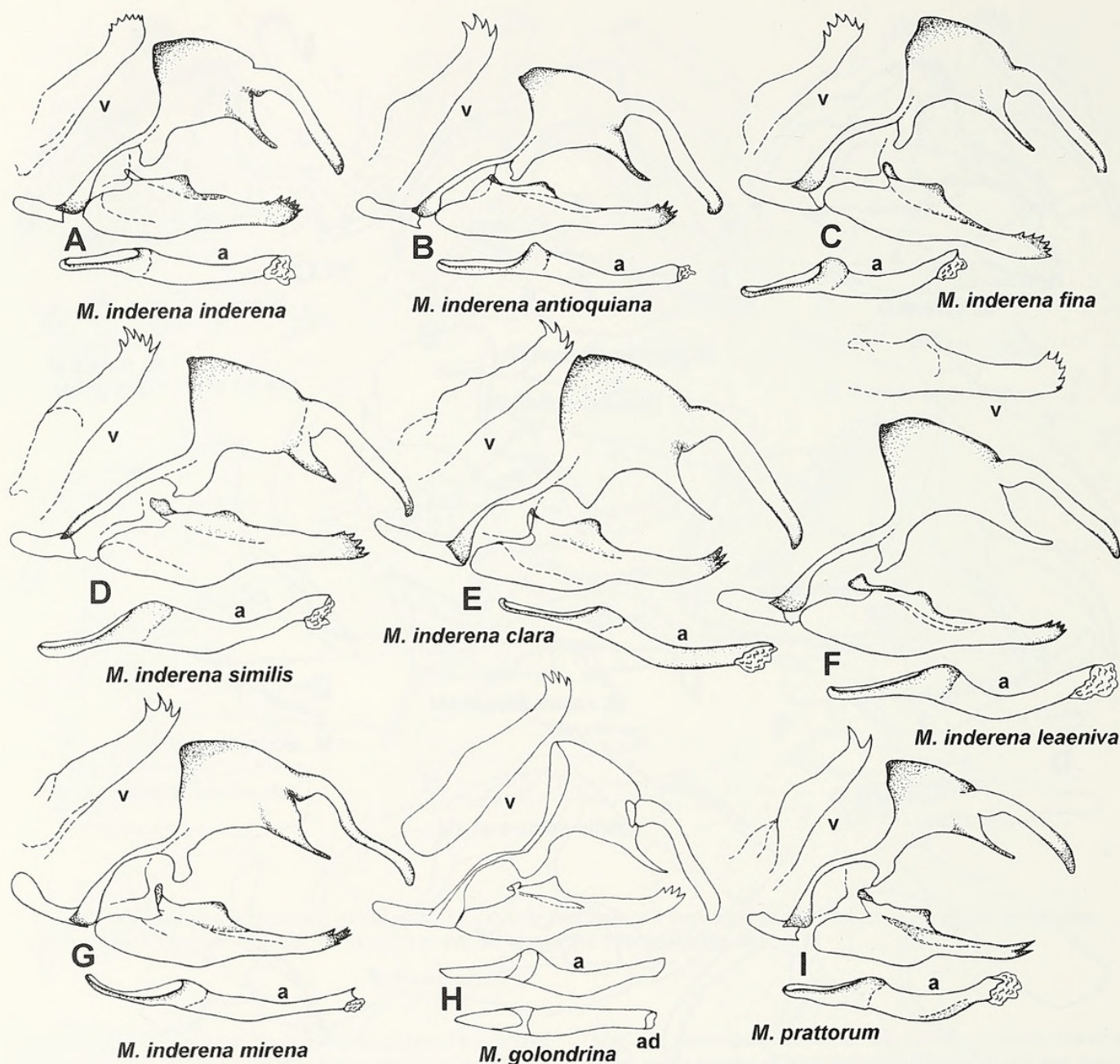


Fig. 12. *Manerebia* male genitalia, lateral view; v = valva ventral view, a = aedeagus lateral view, ad = aedeagus dorsal view. *M. inderena*, *M. golondrina* n. sp., *M. prattorum* n. sp. See Appendix 5 for specimen data.

centers of cells Cu2-Cu1 and Cu1-M3; thin distal marginal border of sparse, pale greyish scales. VHW medium brown; basal half with sparse, long brown hairs and scattered with very sparse paler brown scales; convex, uneven, dark brown line through middle of discal cell, fading near costa and anal margin; thin white postdiscal band from apex to tornus, broadest in cells Cu2-Cu1 to M3-M2, tapering to a point at costa and anal margin, lying distal of discocellulars; thin, smoothly curving darker brown submarginal line, parallel to distal margin, from tornus to near apex; marginal border distal of submarginal line dusted with sparse pale greyish scales.

Types: *Holotype male*: PERU, San Martín, Puerta del Monte, ca. 50 km NE Los Alisos, 3250 m, 22.VIII.1981, L. J. Barkley *leg.*, MUSM;

Allotype female: ECUADOR: Loja, km 20 Jimbura-San Andrés rd., 3300 m, 24.IX.1997, K. Willmott *leg.*, KWJH; *Paratype male*: PERU: San Martín, Parque Nacional Abiseo, Huicungo, Puerta del Monte, 3190-3250 m, 19.VII.1990, M. Medina *leg.*, MUSM.

Etymology: The name of this species is the feminine form of the Latin adjective "seductus", meaning remote or distant, with reference to this species isolated range and rarity.

Comments: The two males of this species were collected in the Central Cordillera in northern central Peru, whereas the only known female specimen was collected in the Cordillera de Lagunillas in extreme southern Ecuador. *Manerebia seducta* thus has a wide, and as yet only roughly defined range. It is apparently a lower

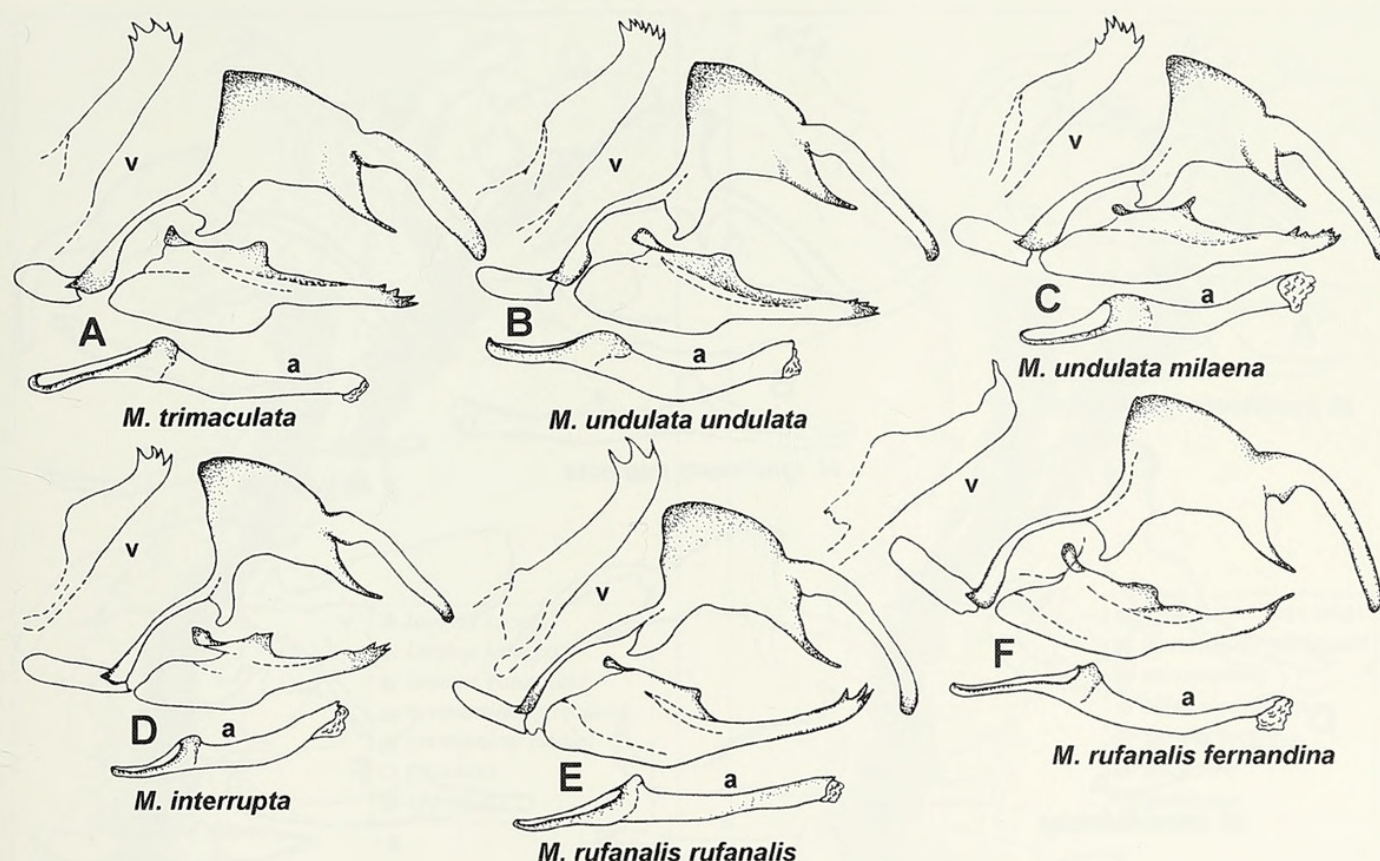


Fig. 13. *Manerebia* male genitalia, lateral view; v = valva ventral view, a = aedeagus lateral view, ad = aedeagus dorsal view. *M. trimaculata*, *M. undulata* n. sp., *M. interrupta*, *M. rufanalis* n. sp. See Appendix 5 for specimen data.

páramo grassland species, similar to *M. ignilineata*, which occurs sympatrically and much more abundantly in the same habitat. The elongate wings of the female of this species are similar to *M. levana*, and those of other páramo butterflies (e.g., the satyrine genus *Lymanopoda*, see Pyrcz *et al.*, 1999), and may be an adaptation to flying or resting in the strong winds that are frequent in these high elevation grasslands.

Manerebia mycalesoides (C. & R. Felder, 1867)

Figs. 8H, I, 14D, 20

Pronophila mycalesoides C. & R. Felder (1867: 473). **TL:** Colombia, Cundinamarca, Bogotá. **ST male:** BMNH(R) [examined]

= *Euptychia lethe* Butler (1867: 465). **TL:** Venezuela. **ST males:** BMNH(R) [examined]

"*Penrosada*" *lethe* (Butler); D'Abrera (1988: 824, fig.).

Pedaliodes mycalesoides (C. & R. Felder); Thieme (1905: 69).

Euptychia mycalesoides (C. & R. Felder); Weymer (1911: 224).

Posteuptychia mycalesoides Forster (1964: 137, fig. 171) (male genitalia).

Manerebia mycalesoides (C. & R. Felder); Lamas & Vilorio (2004: 215).

Diagnosis: *Manerebia mycalesoides* is easily distinguished from all other congeners, except *M. magnifica*, by the large ventral ocelli on both fore and hindwing and wavy, dark, prominent postdiscal line on both VFW and VHW (Figs. 8H, I). The genitalia (Fig. 14D) are distinctive in the elongate distal part of the valva which is strongly curved upwards, ending with several short 'teeth', being most similar to *M. magnifica* and *M. nevadensis*. *Manerebia magnifica* is

distinguished under the account for that species.

Comments: *Pronophila mycalesoides* was described from Bogotá (Colombia) (C. & R. Felder, 1867), but the precise type locality is unknown and the species was not reported by Adams (1986). Shortly afterwards in the same year the same taxon was also described as *Euptychia lethe* by Butler (1867), from an unspecified Venezuelan locality. We have examined the syntypes of both names at the BMNH and *lethe* is a junior subjective synonym of *mycalesoides* (Lamas & Vilorio, 2004). *Manerebia mycalesoides* seems to be a very rare species. It is found in lower cloud forest on the foothills of the Sierra de El Tamá at 1000 m. Nothing was known about the behavior or ecology of this species until Andrew Neild (pers. comm.) observed and collected it at Loma del Viento, Táchira, in 1997, where it flies in an open, windswept area, in association with bamboo. The range of the species has been extended by recent collecting, with records in the Venezuelan Cordillera de la Costa (San Antonio de Los Altos, Colonia Tovar), Sierra de El Tamá (San Vicente de La Revancha, Chorro El Indio), and the west Colombian Río Cauca valley (Popayán). *Manerebia mycalesoides* occurs in premontane rain forest habitats at around 1000 m, where it is a shy inhabitant of shady places within dense forest. Usually only single individuals are encountered, but Pierre Boyer (pers. comm.) observed on one occasion a large group of over ten males in a forest clearing in the Ávila range above Caracas.

Manerebia magnifica Pyrcz & Willmott, n. sp.

Figs. 8G, 14E, 20

Diagnosis: This species differs from its closest relative, *M.*

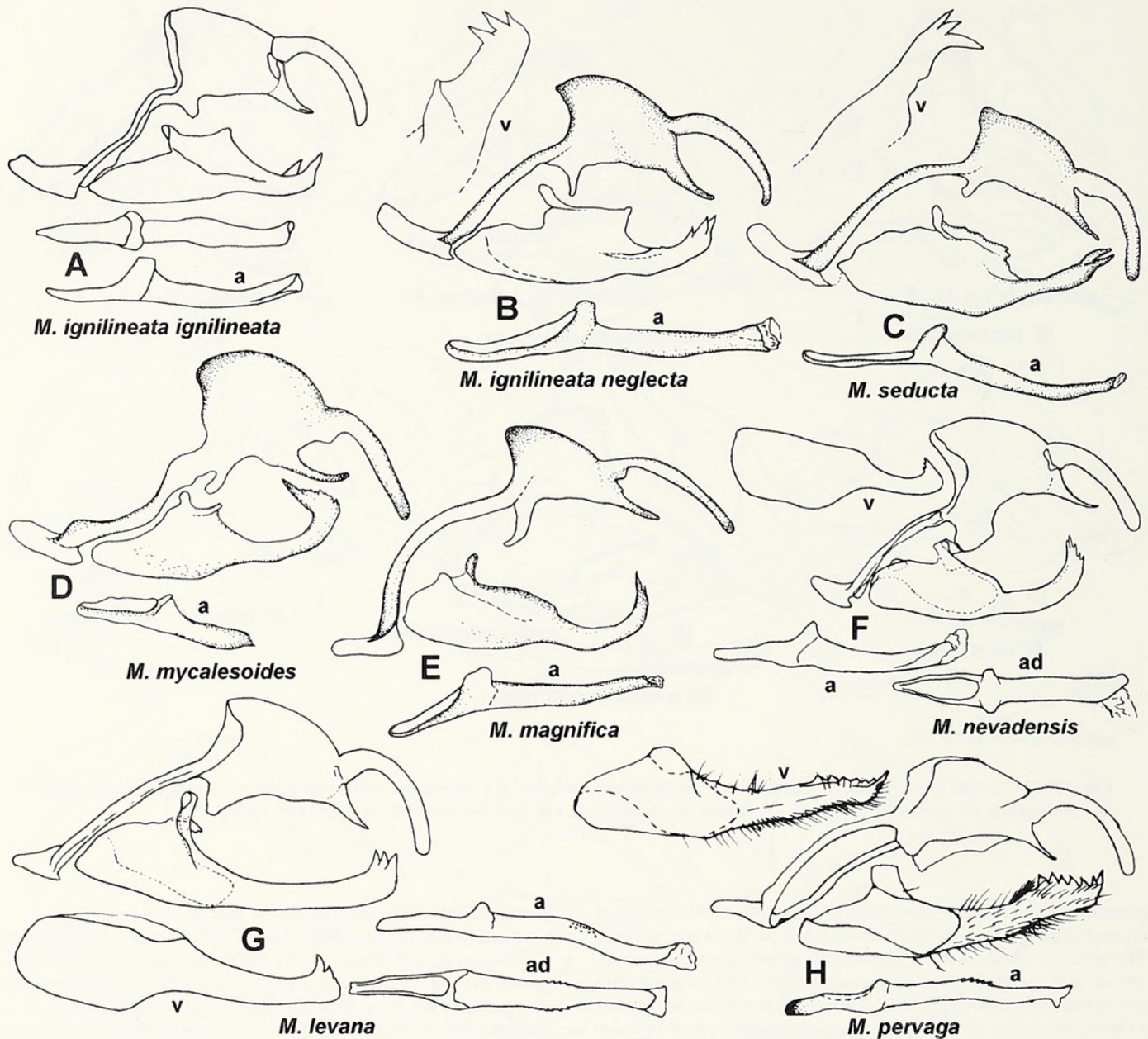


Fig. 14. *Manerebia* male genitalia, lateral view; v = valva ventral view, a = aedeagus lateral view, ad = aedeagus dorsal view. *M. ignilineata*, *M. seducta* n. sp., *M. mycalesoides*, *M. magnifica* n. sp., *M. nevadensis*, *M. levana*. See Appendix 5 for specimen data.

mycalesoides, in the larger size of the VHW submarginal ocelli, with an additional ocellus in cell Cu1-M3, and in their shape being oval instead of rounded. The distal tip of the valva is also less enlarged and recurved.

Description: MALE (Fig. 8G): **Head:** frons with a tuft of black hair; eyes black, smooth; labial palpi covered with long, black hair; antennae dorsally dark brown, ventrally chestnut, with white scales at the base of each segment, club same colour as shaft. **Thorax:** dorsal and ventral surface blackish brown; legs pale brown. **Abdomen:** dorsal surface blackish brown, ventrally grey. **Wings:** forewing (length: 23-24.5 mm, mean: 23.8 mm, n=3) distal margin straight, apex rounded; hindwing with distal margin very slightly angled at vein M3, tornal notch absent. DFW uniform dark brown; andro-

conial scales not apparent; faint blackish submarginal line. DHW dark brown, slightly paler towards distal margin, faint blackish submarginal line. VFW ground colour medium brown; indistinct, darker brown discal line running across discal cell, to base of vein Cu2, continuing towards anal margin; postdiscal line of same colour, bent distally in cell 1A-Cu2 to join submarginal line at tornus; submarginal line, and two dark brown thin marginal lines straight and parallel to outer margin; large (nearly width of cell), rounded, submarginal black ocellus with a white pupil and ringed with orange in cell Cu2-Cu1; another submarginal ocellus, half its size in cell M2-M1. VHW uniform medium brown; dark brown discal line from costa to inner margin, roughly parallel to outer margin, passing through base vein Cu2; dark brown postdiscal line,

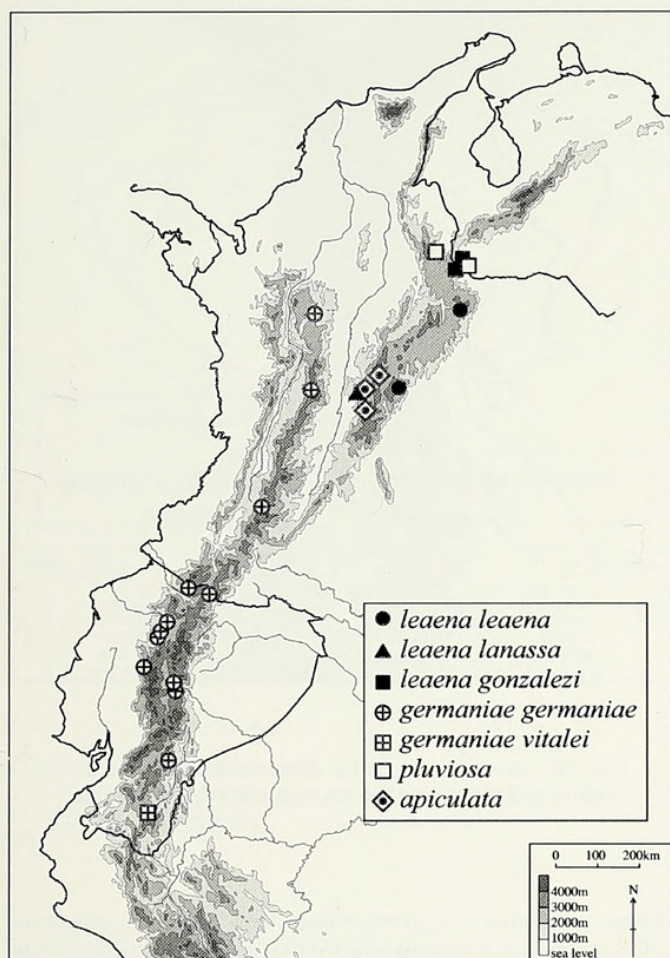


Fig. 15. Locality records for *Manerebia* in the northern Andes: *M. leaena*, *M. germaniae*, *M. pluviosa* and *M. apiculata*

nearly straight, with the extremities curving slightly distally at apex and tornus to merge with a thinner submarginal dark brown line; submarginal line and two marginal lines parallel to outer margin; a series of black submarginal ocelli, four of them oval, two ocelli in cells 1A-Cu2, one each in Cu2-Cu1 and Cu1-M3, one rounded in cell M2-M1, the biggest of which is ocellus in Cu2-Cu1, extends to entire width of cell and nearly half of its length, remaining ocelli diminishing in size anteriorly and posteriorly, with tornal ocellus smallest; all ocelli ringed with orange, pupils in cells 1A-Cu2 and Cu2-Cu1 white, those in cells Cu1-M3 and M2-M1 blue; blue submarginal dot in cell M3-M2. **Male genitalia** (Fig. 14E): tegumen slender; uncus long and arched; subuncus rather short; extended apical part of the valva strongly curved upwards, ended with two 'teeth'; aedeagus straight with a pronounced 'collar' at junction of anterior and posterior portions

FEMALE: Unknown.

Types: **Holotype male:** PERU: Amazonas, Cordillera del Cóndor, alto Río Comaina, PV22, falso Paquisha, 800 m, 25.X.1987, G. Lamas *leg.*, MUSM; **Paratypes: 2 males:** same data as the holotype, MUSM.

Etymology: This species name is the feminine form of the Latin adjective, "magnificus", meaning magnificent, with reference to the impressive submarginal ocelli on the ventral surface.

Comments: This species is clearly most closely related to *M.*

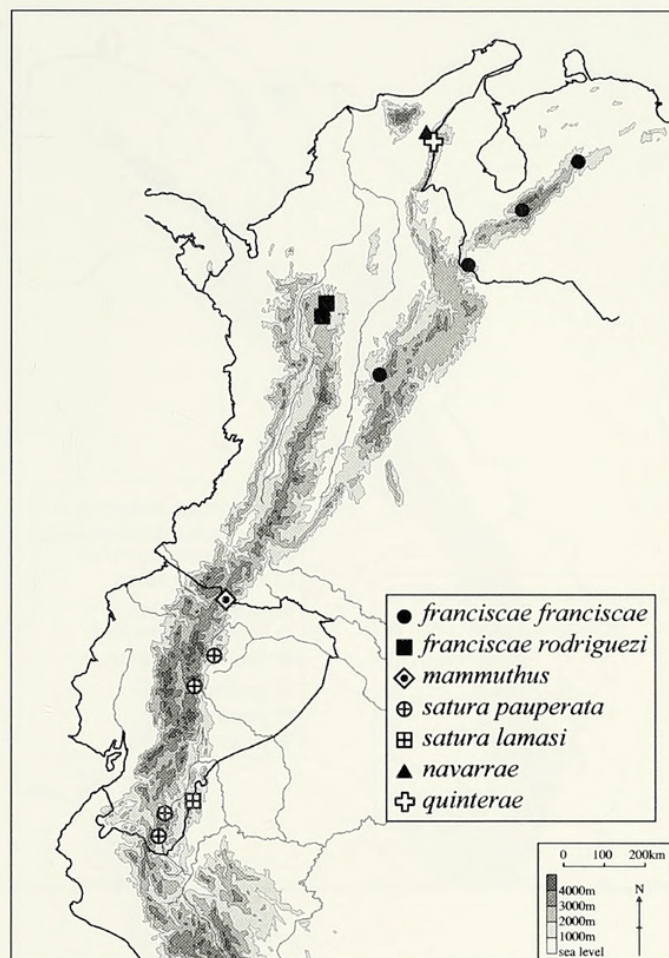


Fig. 16. Locality records for *Manerebia* in the northern Andes: *M. franciscae*, *M. mammuthus*, *M. satura*, *M. navarrae* and *M. quinterae*.

mycalesoides, but the large apparent range disjunction between the two species and slight differences in the male genitalia suggest the two should be treated as distinct for the present. *Manerebia magnifica* is known so far only from the eastern slopes of the Cordillera del Cóndor in Peru, where it occurs in premontane forest. Its apparent absence in the heavily collected Zamora valley further west suggests it may be endemic to this isolated mountain range.

Manerebia nevadensis Krüger, 1925

Figs. 9A, B, 14F, 20

Manerebia nevadensis Krüger (1925: 25). **TL:** Colombia, Sierra Nevada de Santa Marta, 2600m. **LT male** (designated by Pyrcz, 1999: 351): San Lorenzo, Sierra Nevada de Santa Marta, 06.IX.1919, 2600m, E. Krüger *leg.* MZPAN [examined].

Manerebia nevadensis Krüger, Adams & Bernard (1977: 273, fig. 17, male genit. fig. 5); Lamas & Viloria (2004: 215).

Diagnosis: *Manerebia nevadensis* superficially resembles some subspecies of *M. satura* in wing pattern, but the male genitalia (Fig. 14F) are strongly distinct from that species, instead indicating a relationship with *M. mycalesoides* and *M. magnifica*. All three of these species have a pronounced 'collar' at the junction of the anterior and posterior portion of the aedeagus, upturned tip to the valva and short subuncus, similar to certain southern Andean *Manerebia*

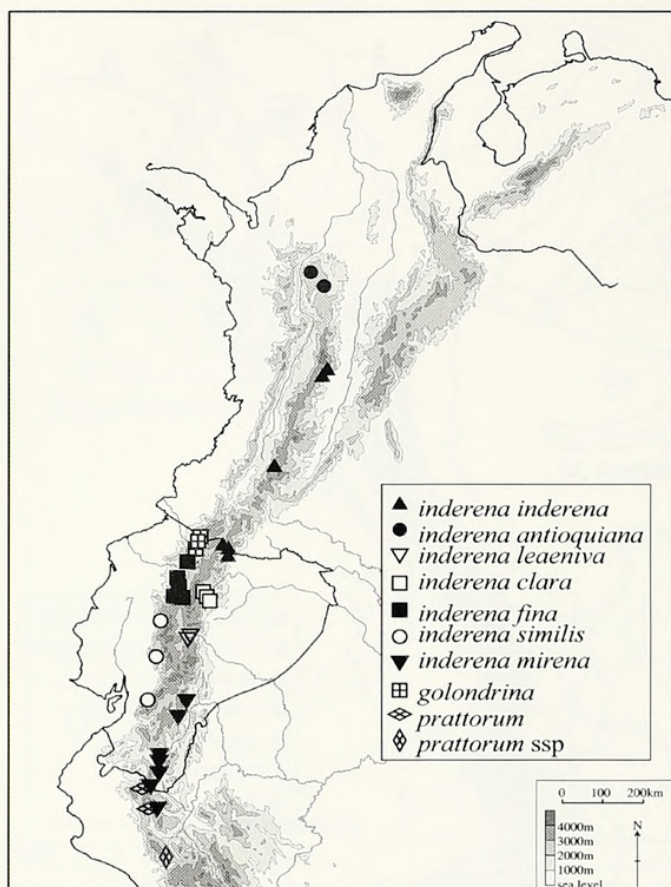


Fig. 17. Locality records for *Manerebia* in the northern Andes: *M. inderena*, *M. golondrina* and *M. prattorum*.

(e.g., *M. cyclopina* Staudinger).

Comments: This species is endemic to the Sierra Nevada de Santa Marta, where Adams & Bernard (1977) and Pyrcz (1999) report that it occurs from 2500–3000 m. It is an elusive butterfly, with a skipping flight, preferring to remain inside dense bamboo clumps and seldom coming to the edges.

Manerebia levana (Godman, 1905)

Figs. 9C, D, 14G, 20

Lymanopoda levana Godman (1905: 188, pl. 10, fig. 10). **TL:** Colombia, Cundinamarca, Bogotá. **ST male:** Colombia, Cundinamarca, Bogotá. BMNH [examined].

Penrosada levana (Godman); Adams (1986: 307); Pyrcz (1999: 367).

Manerebia levana (Godman); Lamas & Vioria (2004: 215).

Diagnosis: This is a small, very distinctive species, superficially resembling only *M. pervaga* and to some extent *M. navarrae*. The VHW postdiscal band is yellowish, indistinct, oblique and marked at its distal edge by a thin, dentate and dark brown line, dividing the wing into an yellow-orange area basally and a chestnut area distally. The ventral submarginal ocelli are much reduced, with only a small one in cells 1A–Cu2 on the VHW and VFW. Further distinguishing characters are discussed under *M. pervaga*. The male genitalia resemble only those of *M. pervaga*. These two species are unique within *Manerebia* in having a highly elongate distal portion of the valva and elongate aedeagus, bearing two dorso-lateral patches of spines in the middle of the posterior section. The relationships of

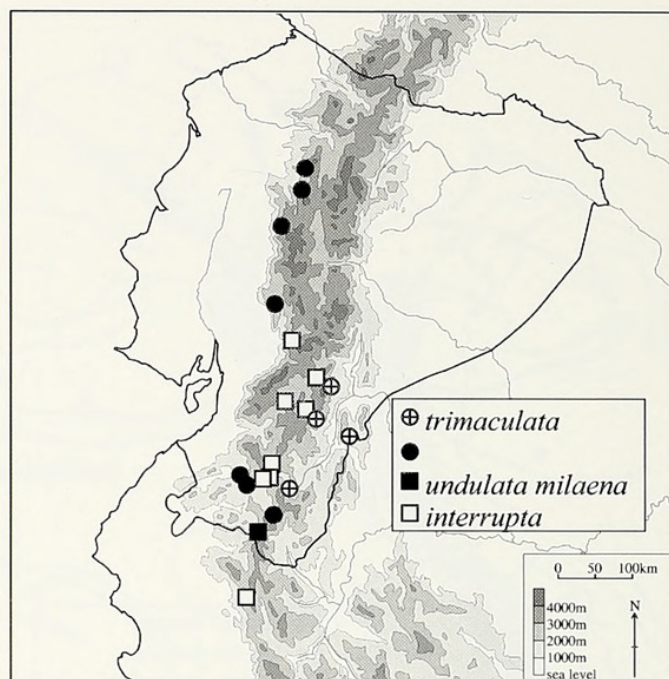


Fig. 18. Locality records for *Manerebia* in the northern Andes: *M. trimaculata*, *M. undulata* and *M. interrupta*

the species to other congeners are uncertain. *M. levana* is geographically variable and it remains possible that distinct subspecies will be recognised in future. Male genitalia as illustrated (Fig. 14G).

Comments: Although Adams (1986) reports this species from Panama, based on specimens in the BMNH, these are definitely mislabelled. The species is known from both slopes of the Colombian Cordillera Oriental in the Bogotá region (Cerro Monserrate) from 2700–3300 m, and Adams (1986) found it in páramo grassland between bamboo-filled gullies at the tree-line. Krüger (1924) described the female of this species (Pyrcz, 1999).

Manerebia pervaga Pyrcz & Vioria, n. sp.

Figs. 9E, F, 14H, 20

Manerebia n. sp. (Pyrcz & Vioria); Lamas & Vioria (2004: 216, n. 1121).

Diagnosis: This species differs from *M. levana* in several characters. The VHW is more uniformly coloured in the male, while the female is uniformly brown, lacking the yellowish colouring of *M. levana*. Both sexes lack tornal ocelli on both wings and the dark postdiscal line on the VHW is more basally positioned, being present in cell 2A–Cu2 (absent in *M. levana*). The female has a strongly dentate thin brown marginal line that is more basally positioned, and the forewing, and to a lesser extent the hindwing, are much more rounded than in *M. levana*. Finally, both sexes have a dark discocellular streak between the bases of veins M2 and M1 on the hindwing (also on the forewing in the female) that is unique in the genus.

Description: MALE (Fig. 9E): **Head:** frons with a tuft of dark brown hair; eyes dark coffee brown, smooth; labial palpi slightly longer than head, with light brown and black hairs; antennae with club twice as broad as shaft, orange brown, darker dorsally. **Thorax:** moderately hairy, more densely on ventral surface, dorsally blackish brown, ventrally brown; legs medium brown. **Abdomen:** dark brown, lighter on ventral surface, especially at posterior tip. **Wings:** forewing (length: 16.5–17.5; mean: 17 mm; n=3) triangular, tornus

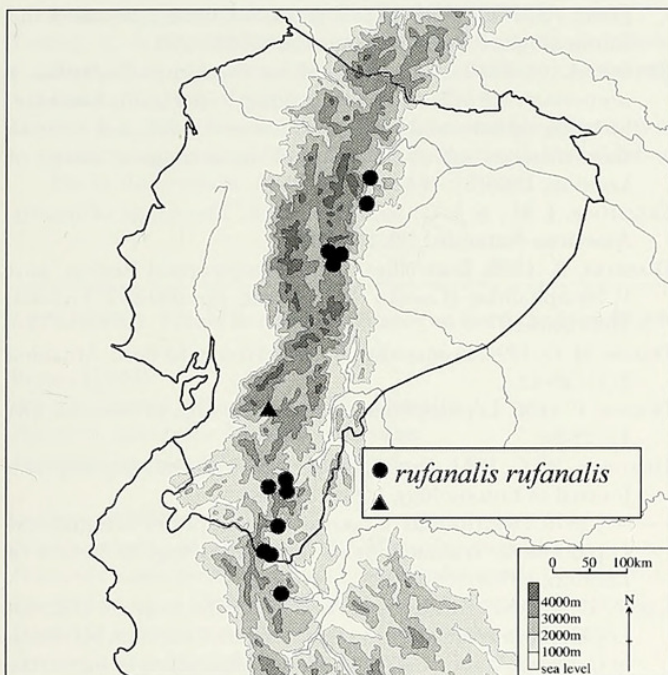


Fig. 19. Locality records for *Manerebia* in the northern Andes: *M. rufanalis*

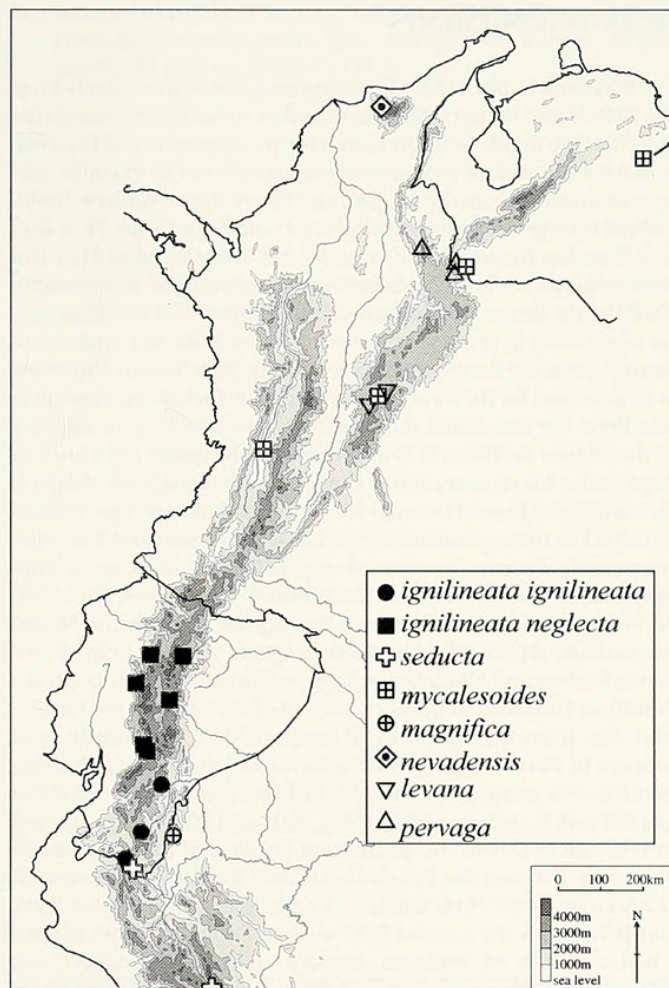


Fig. 20. Locality records for *Manerebia* in the northern Andes: *M. ignilineata*, *M. seducta*, *M. mycalesoides*, *M. magnifica*, *M. nevadensis*, *M. levana* and *M. pervaga*.

obtuse; hindwing rounded, tornus moderately pointed, anal margin straight; dorsal surface of both wings hairy in basal half and along anal margin. Dorsal surface ground colour coffee brown; diffuse orange patch on DHW tornus. VFW ground colour chocolate brown, slightly darkened at base; costal margin lighter; distal margin, apical, and subapical region ochraceous brown (with reddish tone towards anterior edges), as well as base of costal margin region. VHW ground colour yellowish brown, darker at basal region; light suffusion of orange towards posterior postdiscal region, forming diffuse irregular wedge bordered distally with thin dark brown dentate postdiscal line, fading anteriorly and posteriorly and parallel to distal margin, in cells 2A-Cu2 to M2-M1. **Male genitalia** (Fig. 14H): similar to *M. levana* with elongate distal tip to valva, except dorsal 'teeth' at distal tip of valva more extensive, extending anteriorly; aedeagus similar to *M. levana*, elongate, with two dorso-lateral patches of spines in middle of posterior section.

FEMALE (Fig. 9F): **Head**: frons with a tuft of brown hair; eyes medium brown, smooth; labial palpi 2.5 times length of head, with long brown hair; antennae with club three times as thick as basal segments, shaft dorsally and ventrally light brown, club ventrally orange, dorsally blackish brown. **Thorax**: moderately hairy, more densely on ventral surface, dorsally blackish brown, ventrally brown; legs medium brown. **Abdomen**: dorsally blackish brown, laterally and ventrally medium brown. **Wings**: forewing (length: 16.5-17.5 mm; mean: 17 mm; n=2) costa slightly arched, apex blunt, distal margin and tornus rounded. Hindwing overall triangular, with apex, tornus and margins smoothly rounded. Dorsal surface uniform medium brown; fringes light grey. VFW greyish brown, darker brown in basal half; darker brown streak over discocellulars between bases of veins M1 and M2. VHW greyish brown, darker brown at base and posterior of discal cell; darker brown streak over discocellulars between bases of veins M1 and M2; postdiscal dark brown line composed of lunular streaks incurved basally in cells M2-M1 to 1A-Cu2, approximately parallel to distal margin; faint dark brown

submarginal 'V'-shaped streaks in cells M1-Rs to 1A-Cu2.

Material examined: Holotype male: VENEZUELA: Táchira, Parque Nacional El Tamá, Venezuela, 3100-3350 m, 16-18.II.1992, A. Viloria & J. Camacho leg., MALUZ; **Allotype female**: COLOMBIA: Norte de Santander, Cerro Oroque, 3850 m, 12.VI.1965, J. Bechyné leg., MIZA; **Paratypes (3 males)**: VENEZUELA: **1 male**: same data as the holotype, MALUZ; **1 male**: Páramo El Tamá, 2600m, 12.II.1983, M. Vivas leg., MIZA; COLOMBIA: **1 male**: Norte de Santander, Páramo El Tamá via Herrán, XII.1993, J. F. Le Crom leg., JFLC; **1 female**: same data as allotype, MIZA.

Etymology: The name is the feminine form of the Latin adjective "pervagus", meaning wandering, in reference to the flight of this species in the páramo grassland.

Comments: *Manerebia pervaga* is known from the Sierra de El Tamá on the Venezuela/Colombia border and the Cerro Oroque in Norte de Santander in Colombia. It occurs in open páramo covered with low growing *Chusquea* thickets from 3200-3850 m. This is higher than that reported for any other congeners, even páramo species like *M. seducta*, *M. ignilineata* and *M. levana*. *Manerebia pervaga* shares with the last two of these species its small size and dull, cryptic colours, which may be adaptations to páramo habitats and not necessarily indicate any close affinity. This species seems to be seasonal and has only been found flying during the dry season, on days with bright, direct sunlight.

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APPENDIX 1. Errors in main references on north Andean *Manerebia*

Brown (1944):

Penrosada leaena = *Manerebia inderena leaeniva*

Penrosada apiculata = *Manerebia interrupta*

Penrosada lanassa = *Manerebia ignilineata*

D'Abrera (1988):

Penrosada leaena (dorsal surface) = *Manerebia undulata*

Penrosada leaena (ventral surface) = *Manerebia* n. sp., Peru (Pyrz, in prep.)

Penrosada lanassa (dorsal surface) = *Manerebia rufanalis rufanalis*

Penrosada lanassa (ventral surface) = *Manerebia satura satura*

Penrosada sp. = *Manerebia satura pauperata*

Euptychia jovita = *Manerebia satura pauperata*

Penrosada lethe = *Manerebia mycalesoides*

Adams (1986):

Penrosada inderena male holotype = *Penrosada inderena* female paratype

APPENDIX 2. Distribution of taxa along hypothetical elevational transects

Approximate elevational range	Ecuador, Zamora-Chinchi, E. slope	Ecuador, Pastaza, E. slope	Colombia, Choachí, E. cordillera, E. slope	Colombia, El Tamá E. cordillera, NE tip
1000-1400m	<i>magnifica</i>	-	<i>mycalesoides</i>	<i>mycalesoides</i>
1400-1800m	<i>satura pauperata</i>	<i>satura pauperata</i>	<i>franciscæ franciscæ</i>	<i>franciscæ franciscæ</i>
1800-2200m	<i>rufanalis rufanalis</i>	<i>rufanalis rufanalis</i>	-	-
2200-2600m	<i>trimaculata</i>	-	-	-
2600-3000m	<i>inderena mirena</i>	<i>inderena leaeniva</i>	<i>leaena leaena</i>	<i>leaena gonzalezi</i>
2800-3200m	<i>germaniae vitalei</i>	<i>germaniae germaniae</i>	<i>apiculata</i>	<i>pluviosa</i>
3000-3400m	<i>ignilineata ignilineata</i>	<i>ignilineata neglecta</i>	<i>levana</i>	<i>pervaga</i>
3200-3600m	<i>seducta</i>	-	-	<i>pervaga</i>
Total species	8	5	5	5

APPENDIX 3. Distribution of taxa by country

Species	Subspecies	Ecuador	Colombia	Venezuela	North Peru
<i>leaena</i>	<i>leaena</i>	-	+	-	-
	<i>lanassa</i>	-	+	-	-
	<i>gonzalezi</i>	-	+	+	-
<i>germaniae</i>	<i>germaniae</i>	+	+	-	+
	<i>vitalei</i>	+	-	-	-
<i>pluviosa</i>		-	+	+	-
<i>apiculata</i>		-	+	-	-
<i>navarrae</i>		-	+	+	-
<i>golondrina</i>		+	+	-	-
<i>satura</i>	<i>pauperata</i>	+	-	-	-
	<i>lamasi</i>	+	-	-	+

APPENDIX 3 (Cont)

Species	Subspecies	Ecuador	Colombia	Venezuela	North Peru
<i>mammuthus</i>		+	+	-	-
<i>franciscæ</i>	<i>franciscæ</i>	-	+	+	-
	<i>rodriguezi</i>	-	+	-	-
<i>ignilineata</i>	<i>ignilineata</i>	+	-	-	+
	<i>neglecta</i>	+	-	-	-
<i>inderena</i>	<i>inderena</i>	-	+	-	-
	<i>antioquiæna</i>	-	+	-	-
	<i>leæniva</i>	+	-	-	-
	<i>clara</i>	+	-	-	-
	<i>similis</i>	+	-	-	-
	<i>finæ</i>	+	+	-	-
	<i>mirena</i>	+	-	-	+
<i>pratrorum</i>		-	-	-	+
<i>trimaculata</i>		+	-	-	+
<i>undulata</i>	<i>undulata</i>	+	-	-	-
	<i>milaena</i>	+	-	-	+
<i>interrupta</i>		+	-	-	+
<i>rufanalis</i>	<i>rufanalis</i>	+	-	-	+
	<i>fernandina</i>	+	-	-	-
<i>quinteræ</i>		-	+	+	-
<i>nevadensis</i>		-	+	-	-
<i>levana</i>		-	+	-	-
<i>pervaga</i>		-	+	+	-
<i>mycalesoides</i>		-	+	+	-
<i>magnifica</i>		+	-	-	+
<i>seducta</i>		+	-	-	+
TOTAL 23	37	sp12/ssp22	sp14/ssp20	sp7/ssp7	sp11/ssp11

APPENDIX 4. Figured specimens

Species	Subspecies	Locality	Sex	Type	Coll.	Fig.
<i>leæna</i>	<i>leæna</i>	Colombia, Cundinamarca: Guasca-Gachetá	M		BMNH (A&B)	1A
	<i>leæna</i>	Colombia, Cundinamarca: "Bogotá"	F		TWP	1B
	<i>lanassa</i>	Colombia, Boyacá: W below Arcabuco	M		BMNH (A&B)	1C
	<i>lanassa</i>	Colombia, Boyacá: W below Arcabuco	F		BMNH (A&B)	1D
	<i>gonzalezi</i>	Venezuela, Táchira: Sierra de El Tamá	M	PT	TWP	1E
<i>germaniae</i>	<i>germaniae</i>	Ecuador, Cotopaxi: Pilaló	M	HT	MZUJ	1F
	<i>germaniae</i>	Ecuador, Cotopaxi: Pilaló	F	AT	TWP	1G
	<i>vitalei</i>	Ecuador, Zamora: Loja-Zamora old rd.	M	HT	MZUJ	1H
<i>pluviosa</i>		Venezuela, Táchira: San Vicente de la Revancha	M	PT	TWP	2A
<i>apiculata</i>		Colombia, Cundinamarca: "Bogotá"	M		BMNH	2B
<i>apiculata</i>		Colombia, Cundinamarca: "Bogotá"	F		MIZPAN	2C
<i>franciscæ</i>	<i>franciscæ</i>	Venezuela, Mérida: above La Montaña	M	PT	BMNH (A&B)	2D
	<i>franciscæ</i>	Venezuela, Mérida: above La Montaña	F	PT	BMNH (A&B)	2E
	<i>rodriguezi</i>	Colombia, Antioquia: Guarné	M	HT	MZUJ	2F
	<i>rodriguezi</i>	Colombia, Antioquia: El Retiro	F	AT	TWP	2G
<i>mammuthus</i>		Ecuador, Sucumbíos: El Higuerón	M	HT	AME	2H
<i>satura</i>	<i>satura</i>	Peru, Puno: Carabaya, Santo Domingo	M		BMNH (R)	3A
	<i>lamasi</i>	Peru, Amazonas: Alfonso Ugarte	M	HT	MUSM	3B
	<i>pauperata</i>	Ecuador, Zamora: Loja-Zamora rd. km 40	M	HT	MZUJ	3C
	<i>pauperata</i>	Ecuador, Zamora: Loja-Zamora rd. km 40	F	AT	TWP	3D
<i>navarrae</i>		Colombia, César: S. de Valledupar, Finca Altamira	M	PT	BMNH (A&B)	3E
<i>quinteræ</i>		Venezuela, Zulia: E. above Manaure	M	PT	BMNH (A&B)	3F
<i>inderena</i>	<i>inderena</i>	Colombia, Tolima: S above Cajamarca	M	HT	BMNH (A&B)	3G
	<i>inderena</i>	Colombia, Tolima: S above Cajamarca	F	PT	BMNH (A&B)	3H
	<i>antioquiæna</i>	Colombia, Antioquia: El Retiro	M	HT	MZUJ	4A
	<i>antioquiæna</i>	Colombia, Antioquia: El Retiro	F	AT	TWP	4B

APPENDIX 4 (Cont)

Species	Subspecies	Locality	Sex	Type	Coll.	Fig.
	<i>finia</i>	Ecuador, Pichincha: Aloag-Santo Domingo rd.	M	PT	KWJH	4C
	<i>finia</i>	Ecuador, Pichincha: Volcán Pasochoa	F	PT	KWJH	4D
	<i>similis</i>	Ecuador, Bolívar: Balzapamba, arriba de Sta. Lucía	M	HT	MZUJ	4E
	<i>similis</i>	Ecuador, Azuay: Molleturo	F	PT	TWP	4F
	<i>clara</i>	Ecuador, Napo: Baeza	M	PT	TWP	4G
	<i>clara</i>	Ecuador, Napo: Hda. San Isidro	F	AT	PB	4H
	<i>mirena</i>	Ecuador, Loja: Cajanuma	M	PT	TWP	5A
	<i>mirena</i>	Ecuador, Loja: km 95-100 Loja-Zumba rd.	F	AT	PB	5B
	<i>leaeniva</i>	Ecuador, Tungurahua: El Tablón	M	PT	TWP	5C
<i>golondrina</i>		Ecuador, Carchi: Santa Rosa, Las Golondrinas	M	PT	KWJH	5D
<i>prattorum</i>		Peru: "West slopes of Andes"	M	PT	BMNH(R)	5E
<i>trimaculata</i>		Ecuador, Zamora-Chinchipe: Río San Francisco	M		TWP	5F
<i>trimaculata</i>		Ecuador, Zamora-Chinchipe: Loja-Zamora rd.	M		TWP	5G
<i>trimaculata</i>		Ecuador, Morona-Santiago: km 37 Limón-Gualaceo	F		KWJH	5H
<i>undulata</i>	<i>undulata</i>	Ecuador, Pichincha: Tandapi	M	PT	KWJH	6A
	<i>undulata</i> ?	Ecuador, Loja: Yangana, Valladolid rd.	M		TWP	6B
	<i>undulata</i>	Ecuador, Bolívar: Balzapamba, arriba de Sta. Lucía	F	AT	TWP	6C
	<i>milaena</i>	Ecuador, Loja: Jimbura-Laguna Negra rd.	M	HT	MZUJ	6D
<i>interrupta</i>		Ecuador, Azuay: Sigüig-Granadillas	M		TWP	6E
<i>interrupta</i>		Ecuador, Azuay: Sigüig-Granadillas	M		TWP	6F
<i>interrupta</i>		Ecuador, Azuay: Sigüig-Granadillas	M		TWP	6G
<i>interrupta</i>		Ecuador, Azuay: Sayausí	F		TWP	6H
<i>rufanalis</i>	<i>rufanalis</i>	Ecuador, Tungurahua: Runtún	M	HT	MZUJ	7A
	<i>rufanalis</i>	Ecuador, Zamora-Chinchipe: Loja-Zamora old rd.	F	AT	MBLI	7B
	<i>fernandina</i>	Ecuador, Girón: San Fernando	M	HT	MZUJ	7C
<i>ignilineata</i>	<i>ignilineata</i>	Ecuador, Morona-Santiago: Gualaceo-Limón rd.	M		TWP	7D
	<i>ignilineata</i>	Ecuador, Loja: Loja	M		TWP	7E
	<i>ignilineata</i>	Ecuador, Loja: Loja-Zamora rd.	M		TWP	7F
	<i>ignilineata</i>	Ecuador, Morona-Santiago: Gualaceo-Limón rd.	F		TWP	7G
	<i>neglecta</i>	Ecuador, Bolívar: Pilaló	M		TWP	8A
	<i>neglecta</i>	Ecuador, Cañar: Zhud	M		TWP	8B
	<i>neglecta</i>	Ecuador, Bolívar: Pilaló	M		TWP	8C
	<i>neglecta</i>	Ecuador, Cañar: Zhud	F		TWP	8D
<i>seducta</i>		Peru, San Martín: Puerta del Monte	M	HT	MUSM	8E
<i>seducta</i>		Ecuador, Loja: Jimbura-San Andrés rd.	F	AT	KWJH	8F
<i>magnifica</i>		Peru, Amazonas: Falso Paquisha	M	HT	MUSM	8G
<i>mycalesoides</i>		Venezuela, Miranda: Altos de Pipe	M		AFEN	8H
<i>mycalesoides</i>		Venezuela, Táchira: Loma del Viento	F		AFEN	8I
<i>nevadensis</i>		Colombia: S. Nevada de Santa Marta, El Campano	M		BMNH(A&B)	9A
<i>nevadensis</i>		Colombia: Sierra Nevada de Santa Marta	F	PLT	MIZPAN	9B
<i>levana</i>		Colombia: "Interior of Colombia"	M		BMNH	9C
<i>levana</i>		Colombia, Tolima: Río Chili	F		BMNH	9D
<i>pervaga</i>		Venezuela, Táchira: Sierra de El Tamá	M	HT	MALUZ	9E
<i>pervaga</i>		Colombia, Norte de Santander: Cerro Oroque	F	PT	MIZA	9F

APPENDIX 5. Male genitalic dissections

Species	Subspecies	Locality	Type	Coll.	Dissection#	Fig.
<i>leaena</i>	<i>leaena</i>	Colombia, Cundinamarca: "Env. Bogotá"		BMNH	6443	
	<i>leaena</i>	Colombia, Cundinamarca: Choachi		TWP	02/02.05.1999	10A
	<i>leaena</i>	Colombia, Cundinamarca: Choachi		BMNH	6441	
	<i>leaena</i>	Colombia, Cundinamarca: Guasca-Gachetá		BMNH	6442	
	<i>leaena</i>	Colombia, Boyacá: Sierra Nevada del Cocuy		BMNH		
	<i>leaena</i>	No data: "¿Ecuador/Quito"	LT	BMNH		
	<i>lanassa</i>	Colombia, Cundinamarca: Facatativa		TWP	04/07.04.1999	10B
	<i>lanassa</i>	Colombia: Santander		TWP		
	<i>lanassa</i>	Colombia, Cundinamarca: "Bogotá"	HT	BMNH	29877	
	<i>gonzalezi</i>	Venezuela, Táchira: Sierra de El Tamá	PT	TWP	05/07.04.1999	10C

APPENDIX 5 (Cont.)

Species	Subspecies	Locality	Type	Coll.	Dissection#	Fig.
<i>germaniae</i>	<i>germaniae</i>	Colombia, Cauca: Puracé	PT	TWP		
	<i>germaniae</i>	Ecuador, Pichincha: Quito-Sto. Domingo old rd.	PT	KWJH	PENROS 12	
	<i>germaniae</i>	Ecuador, Pichincha: Yanacocha	PT	KWJH		
	<i>germaniae</i>	Ecuador, Pichincha: above Chiriboga	PT	BMNH	6451	
	<i>germaniae</i>	Ecuador, Cotopaxi: Pilaló	PT	TWP	01/26.01.1999	10D
	<i>germaniae</i>	Ecuador, Tungurahua: El Tablón	PT	MBLI		
<i>pluviosa</i>	<i>vitalei</i>	Ecuador, Zamora-Chinchi: Loja-Zamora rd.	PT	MBLI	2003-12-23	10E
		Venezuela, Táchira: Sierra de El Tamá	PT	TWP		10F
<i>apiculata</i>		Colombia, Cundinamarca: Zipaquirá		TWP	05/30.03.1999	11A
<i>franciscæ</i>	<i>franciscæ</i>	Venezuela, Mérida: Mérida	PT	BMNH	6436	
	<i>franciscæ</i>	Venezuela, Táchira: Sierra de El Tamá		TWP	01/02.05.1999	11B
	<i>franciscæ</i>	Colombia, Cundinamarca: Pacho		TWP		
<i>mammuthus</i>	<i>rodriguezi</i>	Colombia, Antioquia: El Retiro	PT	TWP	01/21/12/2003	11C
		Ecuador, Sucumbíos: El Higuerón	HT	KWJH	PENROS 8	11D
<i>mammuthus</i>		Ecuador, Sucumbíos: El Higuerón	PT	KWJH	MAN 1	
<i>satura</i>	<i>pauperata</i>	Ecuador, Napo: Sierra de los Huacamayos	PT	TWP	02/31.03.1999	11E
	<i>pauperata</i>	Ecuador, Pastaza: "Env. d'Ambato"	PT	BMNH	6455	
	<i>pauperata</i>	Ecuador, Zamora-Chinchi: Loja-Zamora rd.	PT	KWJH	PENROS 9	
	<i>lamasi</i>	Peru, Amazonas: Alfonso Ugarte	PT	MUSM	06/27.04.2002	11F
	<i>ssp</i>	Peru, Cajamarca: La Balsa		MUSM		
	<i>satura</i>	Peru, Puno: Santo Domingo		BMNH	6454	11G
	<i>satura</i>	No data: "Cauca valley, Colombia" - error		BMNH	6437	
		Colombia, César: Sierra de Perijá	PT	BMNH	29913	11H
<i>navarrae</i>		Colombia, César: Sierra de Perijá	PT	MA		
<i>quinterae</i>		Venezuela, Zulia: E. above Manaure	PT	BMNH	6445	11I
<i>inderena</i>	<i>inderena</i>	Colombia, Caldas: Páramo de Letras		TWP		
	<i>inderena</i>	Colombia, Tolima: S. above Cajamarca		BMNH	6453	
	<i>inderena</i>	Colombia: Rurillo		TWP	09/30.03.1999	12A
	<i>inderena</i>	Ecuador, Sucumbíos: Qbda. de Piedras		KWJH	PENROS 13	
	<i>inderena</i>	Ecuador, Sucumbíos: El Higuerón		KWJH	PENROS 19	
	<i>antioquiensis</i>	Colombia, Antioquia: El Retiro	PT	TWP	05/11.12.2003	12B
	<i>finá</i>	Ecuador, Pichincha: Nono-Nanegalito rd.	PT	TWP	03/31.03.1999	12C
	<i>finá</i>	Ecuador, Pichincha: Qbda. Molino	PT	KWJH	PENROS 3	
	<i>finá</i>	Ecuador, Pichincha: Aloag-Sto. Domingo rd.	PT	KWJH	PENROS 6	
	<i>finá</i>	Ecuador, Pichincha: Aloag-Sto. Domingo rd.	PT	KWJH	PENROS 4	
	<i>finá</i>	Ecuador, Pichincha: Volcán Pasochoa	PT	TWP		
	<i>similis</i>	Ecuador		BMNH	6439	
	<i>similis</i>	Ecuador, Bolívar: Balzapamba	PT	TWP	04/25.01.1999	12D
	<i>clara</i>	Ecuador, Napo: Río Chonta	PT	KWJH		
	<i>clara</i>	Ecuador, Napo: Baeza	PT	TWP	06/25.01.1999	12E
	<i>leaveniva</i>	Ecuador, Tungurahua: Volcán Tungurahua	PT	TWP	08/07.04.1999	12F
	<i>leaveniva</i>	Ecuador, Tungurahua: Río Verde Chico	PT	TWP		
	<i>leaveniva</i>	Ecuador, Tungurahua: Baños	PT	BMNH	6457	
	<i>leaveniva</i>	Ecuador	PT	BMNH	6456	
	<i>leaveniva</i>	Ecuador, Morona-Santiago: Limón-Gualaceo rd.		KWJH	PENROS 2	
<i>golondrina</i>	<i>mirena</i>	Ecuador, Zamora-Chinchi: Jimbura-S. Andrés rd.	PT	KWJH	PENROS 14	
	<i>mirena</i>	Ecuador, Zamora-Chinchi: Jimbura-S. Andrés rd.	PT	TWP		
	<i>mirena</i>	Ecuador, Zamora-Chinchi: Valladolid	PT	MBLI		
	<i>mirena</i>	Ecuador, Zamora-Chinchi: Valladolid	PT	MBLI		
	<i>mirena</i>	Ecuador, Loja: Cajanuma	PT	TWP	01/31.03.1999	12G
	<i>mirena</i>	Peru, Cajamarca: Tabaconas	PT	TWP		
	<i>mirena</i>	Peru, Cajamarca: Hacienda Udima	PT	MUSM		
	<i>prattorum</i>	Ecuador, Carchi: Santa Rosa, Res. Golondrinas	PT	KWJH	PENROS10	12H
	<i>prattorum</i>	Peru: "W. Slopes of Andes"	PT	BMNH	6448	
	<i>prattorum</i>	Peru: "W. Slopes of Andes"	PT	TWP	03/02.05.1999	12I
	<i>prattorum</i>	Peru, Piura: Canchaque	PT	MUSM		
	<i>trimaculata</i>	Ecuador, Zamora-Chinchi: Loja-Zamora rd.		TWP	03/07.04.1999	13A
	<i>trimaculata</i>	No data		BMNH	6447	
<i>undulata</i>	<i>undulata</i>	Ecuador, Loja: Guayquichuma	PT	TWP	09/07.04.1999	13B
	<i>undulata</i>	Ecuador, Pichincha: Río Las Palmeras	PT	KWJH	PENROS 7	
	<i>undulata</i>	Ecuador, Pichincha: Tandapi	PT	KWJH	PENROS 18	
	<i>undulata</i>	Ecuador, Cotopaxi: Pilaló	PT	TWP		
	<i>milaena</i>	Ecuador, Loja: Jimbura-San Andrés rd.	PT	TWP	03/25.01.1999	13C

APPENDIX 5 (Cont.)

Species	Subspecies	Locality	Type	Coll.	Dissection#	Fig.
<i>interrupta</i>	<i>milaena</i>	Peru, Cajamarca: Hacienda Udimá		MUSM		
<i>interrupta</i>		Ecuador, Azuay: Gualaceo-Chiguinda rd.		KWJH	PENROS 15	
<i>rufanalis</i>		Ecuador, Loja: Loja-Cuenca rd.		TWP	04/30.03.1999	13D
	<i>rufanalis</i>	Ecuador, Tungurahua: Río Machay	PT	KWJH	PENROS 1	
	<i>rufanalis</i>	Ecuador, Loja: Cajanuma	PT	TWP		
	<i>rufanalis</i>	Ecuador, Zamora-Chinipe: Qbda. San Ramón	PT	KWJH	PENROS 17	
	<i>rufanalis</i>	Ecuador, Zamora-Chinipe: Jimbura-S. Andrés rd.	PT	KWJH	PENROS 16	
	<i>rufanalis</i>	Ecuador, Zamora-Chinipe: "Zumba"	PT	TWP		
	<i>rufanalis</i>	Ecuador, Zamora-Chinipe: San Andrés	PT	TWP		
	<i>rufanalis</i>	Peru, Cajamarca: Tabaconas	PT	TWP	07/31.03.1999	13E
	<i>fernandina</i>	Ecuador, Azuay: Girón	PT	TWP	10/25.01.1999	13F
<i>ignilineata</i>	<i>ignilineata</i>	Ecuador, Loja: Jimbura-San Andrés rd.		KWJH	PENROS 20	14A
	<i>neglecta</i>	Ecuador, Cotopaxi: Pilaló		TWP	10/07.04.1999	14B
<i>seducta</i>		Peru, San Martín: Abiseo	PT	MUSM	01/22.06.2002	14C
<i>mycalesoides</i>		Venezuela, Barinas: Uribante		JFLC	74/1996	14D
<i>mycalesoides</i>		Venezuela, Táchira: Sierra de El Tamá		TWP		
<i>mycalesoides</i>		Venezuela, Miranda: Altos de Pipe		AFEN	NEILD 01	
<i>magnifica</i>		Peru, Amazonas: Falso Paquisha	PT	MUSM	07/27.04.2002	14E
<i>nevadensis</i>		Colombia: Sierra Nevada de Santa Marta		MA		
<i>nevadensis</i>		Colombia: Sierra Nevada de Santa Marta		BMNH	6444	14F
<i>levana</i>		Colombia, Cundinamarca: "Bogotá"		TWP		
<i>levana</i>		Colombia, Cundinamarca: "Env. Bogotá"		BMNH	6446	14G
<i>pervaga</i>		Venezuela, Táchira: Sierra de El Tamá	HT	MALUZ		14H



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