A REVISION OF THE GENUS *MEGOLERIA* (LEPIDOPTERA: NYMPHALIDAE, ITHOMIINAE)

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Abstract – The ithomiine genus *Megoleria* Constantino is revised. The genus contains two species, each with three subspecies, of which one, *Megoleria orestilla polylla* **n. ssp.**, is described and named here. We discuss the morphological characteristics of the genus, review its systematics, designate lectotypes for four names, and summarize the biology of each of its constituent taxa. The immature stages of *Megoleria orestilla* (Hewitson), feeding on *Drymonia urceolata* Wiehler, are described for the first time.

Key words: Andes, cloud forest, *Hyposcada*, immature stages, ***Megoleria orestilla polylla*** n. ssp., mimicry, neotropical, *Oleria.*

INTRODUCTION

This paper continues a planned series of publications by the authors (Willmott & Lamas, 2006, 2007) to revise a number of problematic Ithomiinae genera, mainly in the tribes Oleriini, Dircennini and Godyridini. These tribes are the most diverse within the subfamily and are particularly characteristic of Andean cloud forest habitats, where collections over the last few decades have brought to light numerous new taxa. The majority of these genera have not been subject to taxonomic revision since Haensch's review a century ago (Haensch, 1909-10), and virtually all lack any modern synthesis of biological information.

In this paper we revise the systematics of the small, high Andean cloud forest genus *Megoleria* Constantino. Early authors typically placed *Megoleria* species in the related genus *Oleria* Hübner or its junior subjective synonym *Leucothyris* Boisduval (Haensch, 1909), though some authors also treated them in *Hyposcada* Godman & Salvin (Haensch, 1903). Mielke & Brown (1979: 132) noted that *M. susiana* (C. & R. Felder) had been identified by Fox (1961) as a species deserving of a new genus, but continued to treat the species in *Hyposcada*. The genus was finally described by Constantino (1999), who diagnosed it in comparison with *Oleria*. However, recent phylogenetic analyses (Willmott & Freitas, 2006) place *Megoleria* as sister to *Hyposcada*, and the first goal of this paper is, therefore, to re-evaluate the characters that support separation and recognition of *Megoleria* as a distinct genus. We also discuss the taxonomy of both included species, name and describe one new subspecies, describe the life history of *M. orestilla* (Hewitson) for the first time, and summarize known information on the biology and distribution of the genus.

MATERIALS AND METHODS

Specimens were examined in major public and private collections in Europe, North and South America to record distributional data, study morphological variation, assess taxonomic diversity and locate type specimens. The following collection codens and abbreviations are used in the text:

Abbreviations:

AFEN	Andrew F. E. Neild collection, London, UK
AMNH	American Museum of Natural History, New York, NY, USA
BMB	Booth Museum of Natural History, Brighton, UK
BMNH(S)	Natural History Museum, London, UK (supplementary collection)
FLMNH	McGuire Center for Lepidoptera, Florida Museum of Natural History, Gainesville, FL, USA
IAVH	Instituto Alexander von Humboldt, Villa de Leyva, Colombia
JFL	Jean François Le Crom collection, Bogotá, Colombia
JS	Julián Salazar collection, Manizales, Colombia
KWJH	Keith R. Willmott & Jason P. W. Hall collection, Gainesville, USA
LMC	Luis M. Constantino collection, Cali, Colombia
MECN	Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador
MEFLG	Museo Entomológico Francisco Luís Gallego, Universidad Nacional de Colombia, Medellín, Colombia
MHNCA	Museo de Historia Natural, Universidad de Cauca, Popayán, Colombia
MHNUC	Museo de Historia Natural, Universidad de Caldas, Manizales, Colombia
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru
OHM	Olaf H. H. Mielke collection, Curitiba, Brazil
OUM	Oxford University Museum, Oxford, UK
SMF	Senckenberg Museum, Frankfurt-am-Main, Germany
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
SMTD	Staatliches Museum für Tierkunde, Dresden, Germany
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
ZMHU(H)	Zoologisches Museum, Humboldt Universität, Berlin, Germany (Haensch collection)
ZSBS	Zoologisches Sammlung des Bayerischen Staates, Munich, Germany

(D)FW (dorsal) forewing
(V)HW (ventral) hindwing

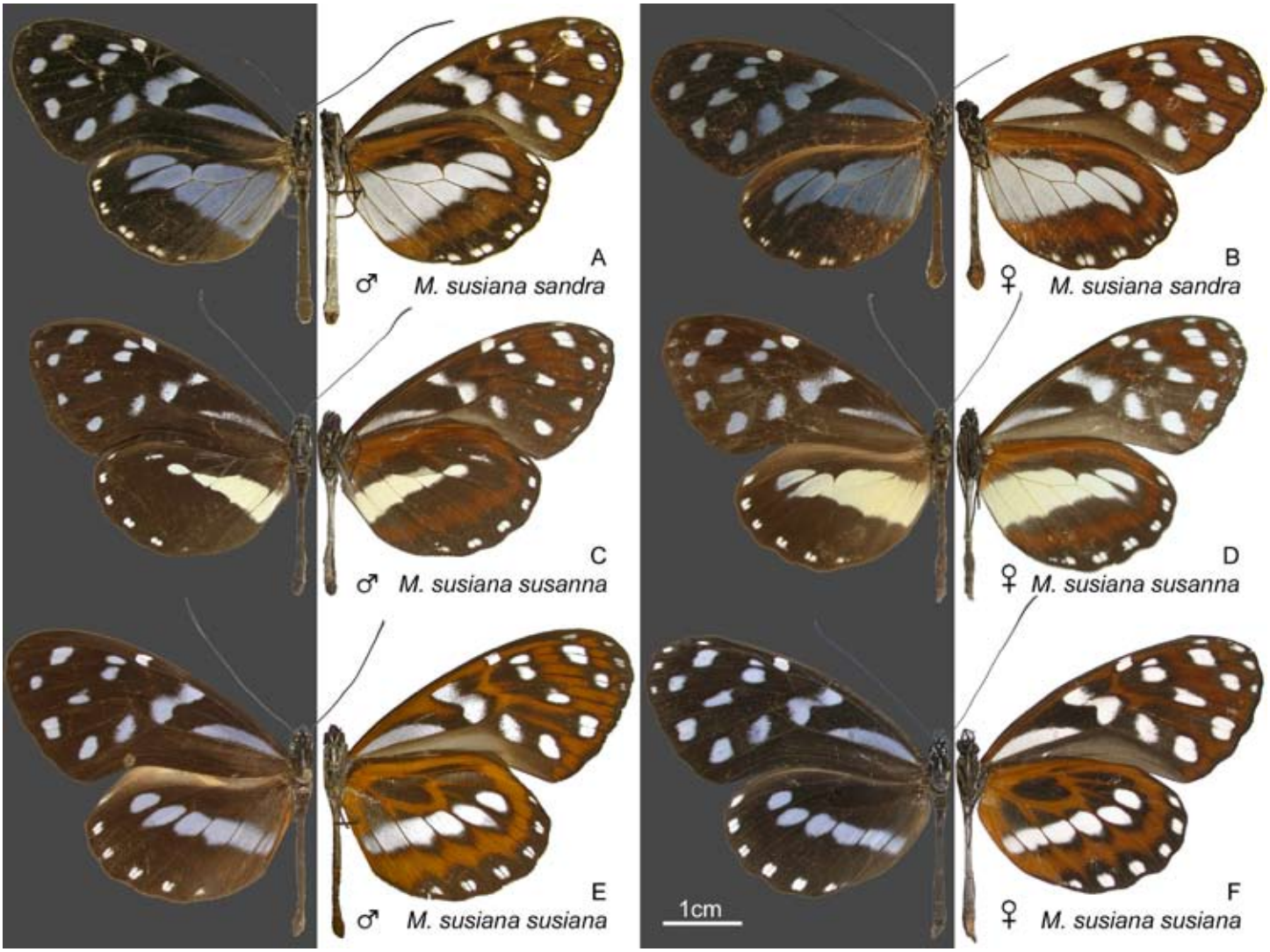

Fig. 1. *Megoleria susiana*. A. *M. susiana sandra*, ♂, Colombia, Cauca, "Vitacoberge". B. *M. susiana sandra*, ♀, Colombia, Cauca, Río Bitaco. C. *M. susiana susanna*, ♂, Colombia, Antioquia, Valdivia. D. *M. susiana susanna*, ♀, Colombia, Caldas, Manizales. E. *M. susiana susiana*, ♂, Colombia, Boyacá, Minas de Muzo. F. *M. susiana susiana*, ♀, Ecuador, Napo, Guacamayos.

Specimen locality data were georeferenced with the help of Brown (1979), the US National Geospatial-Intelligence Agency's and the US Board on Geographic Names' gazetteers available via the GEOnet Names Server (http://earth-info.nga.mil/gns/html/namefiles.htm), the global gazetteer at http://www.fallingrain.com/world/, specimen label GPS data and topographic maps. The distribution map was generated using ESRI ArcGIS 9, with elevation data provided by the Global Land One-km Base Elevation (GLOBE) Project (http://www.ngdc.noaa.gov/mgg/topo/globe.html), and administrative boundaries, coastline and river layers available from http://www.diva-gis.org/. Specimen locality data are available at www.andeanbutterflies.org/database.html.

Field observations on the natural history of *Megoleria* have been made by both authors in Colombia, Ecuador and Peru over the last couple of decades. Fieldwork consisted mainly of sampling ithomiine faunas in little-known regions, elevations or habitats, to provide better distributional data, as well as making observations of adult behaviour. During two ten-week studies of ithomiine immature stages in Ecuador, the immatures of *M. orestilla* were located and reared (see description below). Immatures were collected and reared in plastic bags, with fresh leaves of the natural hostplant provided every 2-3 days. Leaf material was removed from the bag just prior to pupation to permit the pupa to form freely. Photographs were taken of each instar and cast larval skins, head capsules and specimens of larvae and pupae were preserved, where possible, in locally available industrial alcohol (ethanol). Voucher hostplant specimens were collected and are deposited in the BMNH and MECN.

Morphology was studied using standard techniques, with adult abdomens being soaked in hot 10% KOH for 10-15 minutes, dissected and subsequently stored in glycerine. Body morphology and dissections were studied using a binocular microscope at up to 50x magnification. Wing venation was drawn from wings cleared with bleach as well as from uncleared specimens. Hindwing androconia and other wing scales of all species were examined *in situ*, by removal of the right forewing, using binocular microscope at 50x magnification. Male androconial scales were further examined in *M. susiana*, as well as all other ithomiine genera, using a Hitachi S2500 scanning electron microscope, at magnifications of up to 5000x. Wing sections for examination were mounted on stubs with PVA glue and coated with a 20nm layer of gold/palladium (95%/5%) using a Cressington Sputter Coater.

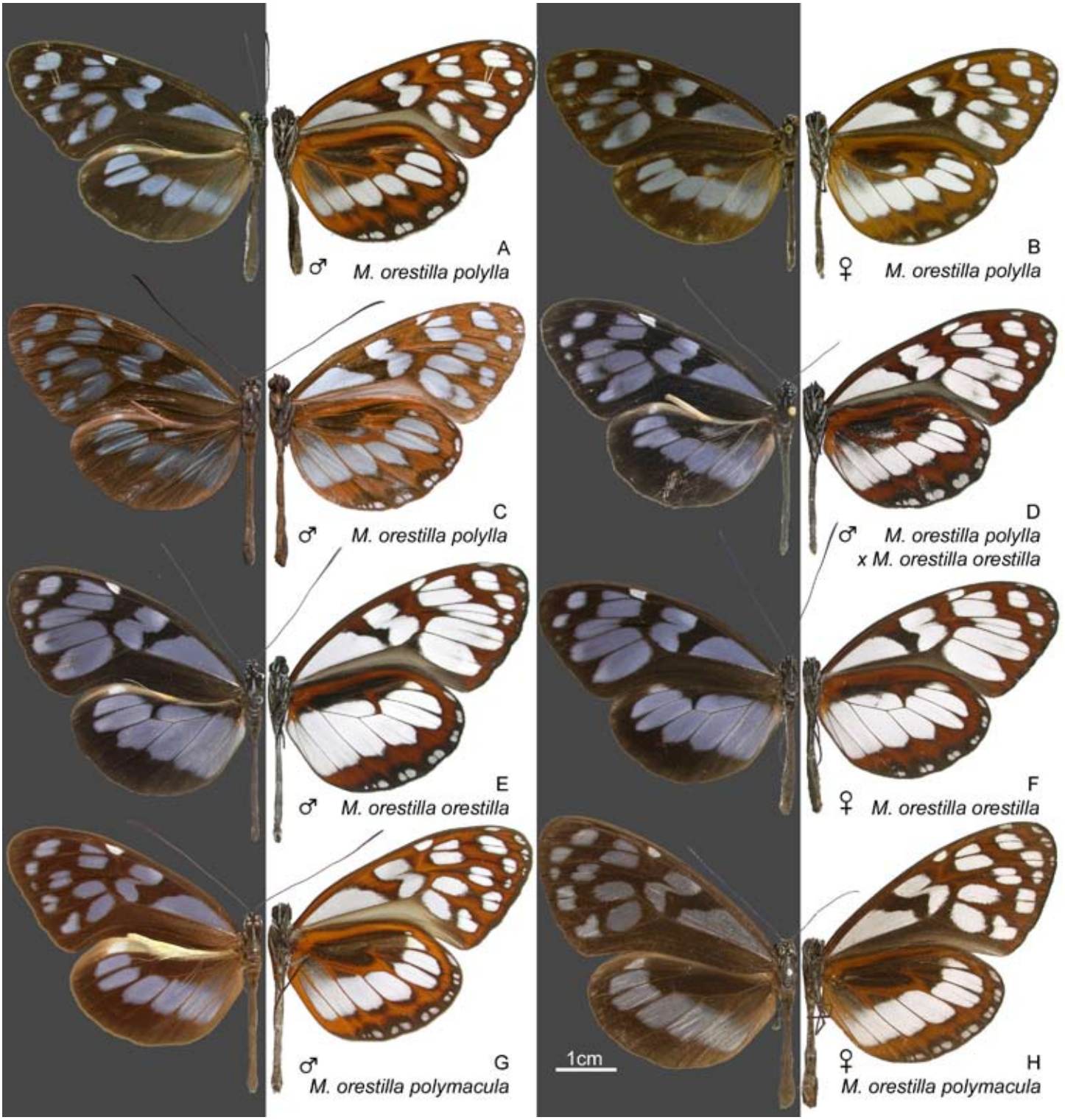

Fig. 2. *Megoleria orestilla*. A. *M. orestilla polylla*, HT ♂, Colombia, Huila, Parque Nacional Las Cuevas. B. *M. orestilla polylla*, ♀, Colombia. C. *M. orestilla polylla*, ♂, Colombia, Antioquia, Municipio de Andes. D. *M. orestilla polylla* x *M. orestilla orestilla*, ♂, Ecuador, Sucumbíos, Río Sucio. E. *M. orestilla orestilla*, ♂, Ecuador, Morona-Santiago, Río Abanico. D. *M. orestilla orestilla*, ♀, Ecuador, Tungurahua, Río Machay. E. *M. orestilla polymacula*, ♂, Bolivia. F. *M. orestilla polymacula*, ♀, Peru, Junín, Chanchamayo.

SYSTEMATICS

Generic characteristics

Adults

Megoleria is aptly named, for these butterflies with their predominantly black wings punctuated by translucent white spots and bands (Figs. 1,2), indeed resemble certain large, Andean members of the genus *Oleria*. All taxa share a common set of pattern elements. The margins of both wings, a FW discal cell band and discocellular band extending down the cubital vein to the anal margin, and a FW postdiscal band, are black. The remainder of the FW discal cell, and a postdiscal and a submarginal row of spots on the FW, are transparent with translucent white shading. The hindwing bears a discal to postdiscal band of variable width, that is either translucent white/transparent, or semi-opaque pale

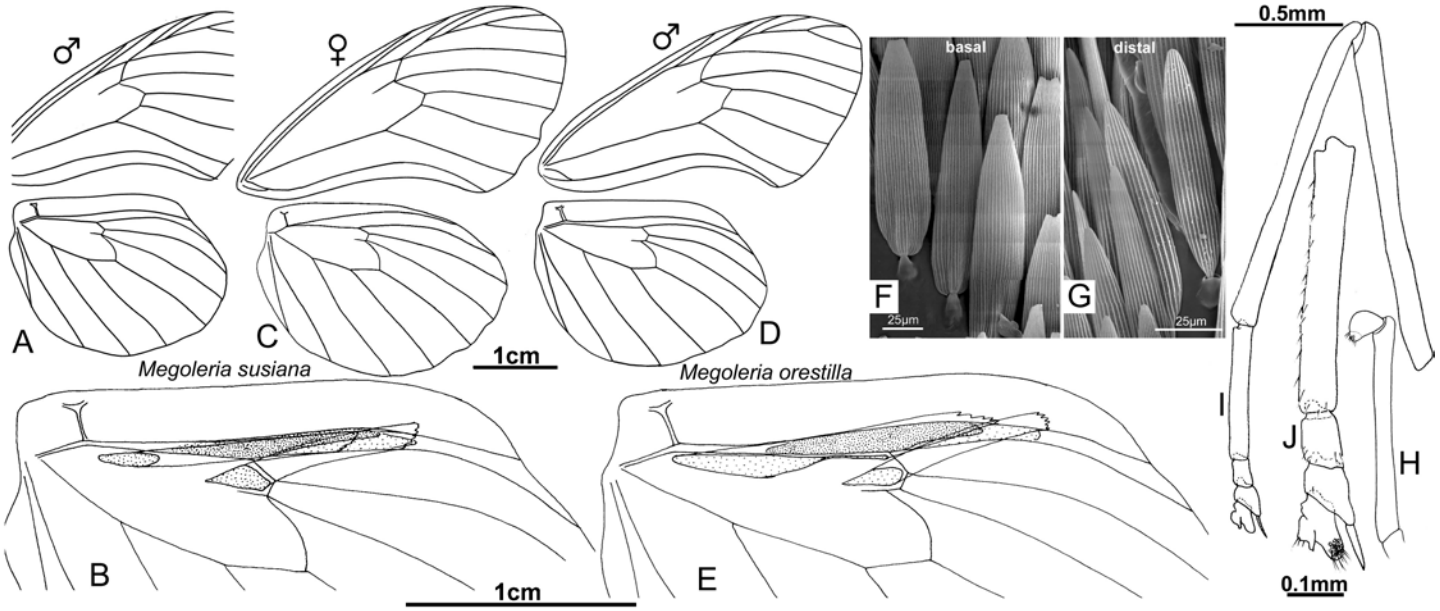

Fig. 3. External morphology. Wing venation and hindwing androconial scale distribution: A,B. *M. susiana susiana*, ♂, Colombia. C. *M. susiana susiana*, ♀, Colombia. D,E. *M. orestilla orestilla*, ♂, Ecuador. Male hindwing androconial scales in cell Rs-Sc+R1, *M. susiana susiana*, Colombia: F. Basal scale patch. G. Distal scale patch. H. *M. susiana susiana*, ♂, foreleg. I,J. *M. susiana susiana*, ♀, foreleg.

yellow. In the majority of taxa these translucent spots or bands are isolated from one another by black markings, forming apparent rows of spots on both wings. A marginal row of paired white spots is present ventrally in both species and dorsally in one species. The ventral surface black markings are lined throughout with rufous scaling.

The male hindwing is slightly convex at apex, at the end of vein Sc+R1, similar to *Hyposcada* (Fig. 3). Both wings have Mr on 3d (males) or 2d (females) near the base of vein M2, or at the base of vein M2, in contrast to *Hyposcada* (in which Mr is also on 3d), where the length of Mr is usually similar to the distance between its base and the base of vein M2. Forewing Mr is notably long, similar in length to 3d. The anterior edge of the HW discal cell is notably short, so that the base of vein M1 is nearer the wing base than the base of vein M3, an apparently unique character within the Oleriini (Fig. 3). As a result of this character, 1d is longer than 2d, whereas in all *Hyposcada* 2d is longer or the veins are similar in length. In contrast to other Oleriini, there is remarkably little sexual dimorphism in wing venation, the female hindwing differing mainly in being more smoothly rounded and concave at the apex.

As in all Ithomiinae, the anterior edge of the male dorsal HW discal cell bears elongate, hair-like androconial scales, which in this genus form two distinct patches (Fig. 3). This "hair pencil" extends anteriorly to cover an area of specialized, pale, dense grayish androconial scales between veins Rs and Sc+R1, an area that extends from approximately the middle of the discal cell to a similar distance distal of the discocellular veins (Figs. 3B, E). The androconial scale patch is differentiated into two distinct scale types beneath the two hair pencils, as in *Hyposcada* and some more basal *Oleria* (Willmott & Freitas, 2006). The more basal scales (Fig. 3F) are approximately twice the length of the distal scales (Fig. 3G), broad at the base and tapering only slightly distally to end at a blunt, squared tip, the pedicel is not visible and the socket is a narrow tube. The more distal scales are proportionally narrower, ending distally in a rounded tip and tapering basally with the pedicel visible, the socket mouth is much broader, appearing like a small cup. Both scale types have distinct vanes with small, indistinct windows.

The antennae extend to just beyond the FW discocellulars and bear sulci on their ventral surface that are placed proximally within each antennomere, as in most Oleriini (Willmott & Freitas, 2006). The palpi and walking legs differ little in morphology from other Oleriini. The male fore-tibiotarsus is reduced to a single rounded segment (Fig. 3H), as in all Oleriini and related tribes. The female foretarsus (Figs. 3I, J) has the fifth segment semi-fused to the fourth segment or distinct (apparently variable), and the third segment bears a pair of spurs. The tegula has the exterior, dorsal half clothed with black scales, the ventral half with white scales. All scales are directed posteriorly and there are dense, long black hairs scattered throughout.

Like most *Oleria*, but in contrast to *Hyposcada*, the male genitalia are asymmetrical, with the uncus in posterior view appearing to be rotated anticlockwise (Figs. 4B, G). The right valva is distinctly longer than the left one and curved more sharply inwards at the posterior tip. The base of the uncus is broad, merging gradually with the tegumen. The appendices angulares, absent in *Hyposcada* and present in *Oleria* as sclerotized projections, are present but unsclerotized (Figs. 4A, F), a unique condition among the Ithomiinae (Willmott & Freitas, 2006). As in all Oleriini, the gnathos is distinct from the appendices angulares, attached at the base of the uncus (Fig. 4B) (Willmott & Freitas, 2006). The medio-ventral inner face of the valva (Figs. 4B, G) is covered with very dense, thick, short hairs, quite distinct from those over the rest of the valva, a unique character within the Ithomiinae. The aedeagus is typical in shape of most Oleriini, narrow with an elongate anterior portion such that the zone is approximately in the middle of the aedeagus (Figs. 4D, I). The vesica everts more or less vertically, and has two thin lines of cornuti on the dorsal and ventral surfaces. The cornuti are very near the base of the vesica, a character of all Oleriini that only occurs sporadically in a few other ithomiine genera (Willmott & Freitas, 2006).

The female abdomen has the eighth sternite plates (lamella postvaginalis) absent or fused with the eighth tergite (Figs. 5A, F). While it is possible to infer that these plates are fused with the eighth tergite in *Hyposcada* through the distribution of setae and pattern of sclerotization, such is not the case with *Megoleria*. The antrum is unsclerotized and slightly asymmetrical, opening to the left (Figs. 5E, J). The ductus seminalis originates near the antrum and the ductus bursae is narrow. The corpus bursae is oval, with small, evenly scattered signa over the entire inner surface, and a smaller, rounded appendix bursae near the anterior tip.

Immature stages

The immature life history of *Megoleria* is described here for the first time, based on observations of *M. orestilla orestilla* in the Reserva Arcoiris, Sector San Francisco, Parque Nacional Podocarpus, Zamora-Chinchipe, Ecuador (Fig. 6).

The egg, first illustrated by Brown & Freitas (1994), is typical of the Oleriini, being oval and relatively elongate, and like all Ithomiinae, the macroscopic chorionic sculpturing is limited to a series of approximately 20 vertical ribs (Figs. 6D, E). All instars have a cylindrical, smooth body, a rounded, unadorned head capsule and lack subdorsal thoracic filaments, as in all Oleriini (see Brown & Freitas, 1994). The first instar is dark green with a black head capsule, typical of the Oleriini, with black legs. Second to third instars are similar, developing a pale gray prothoracic ring and slight lateral yellow scaling on the terminal abdominal segments (Figs. 6F, J, K). In the fourth instar a prominent dirty yellow lateral line from T2 to A10 becomes visible, and the larva is dorsally grayish green (Figs. 6L, M). The fifth instar (Figs. 5N-P) resembles the fourth, except that the head capsule is brown

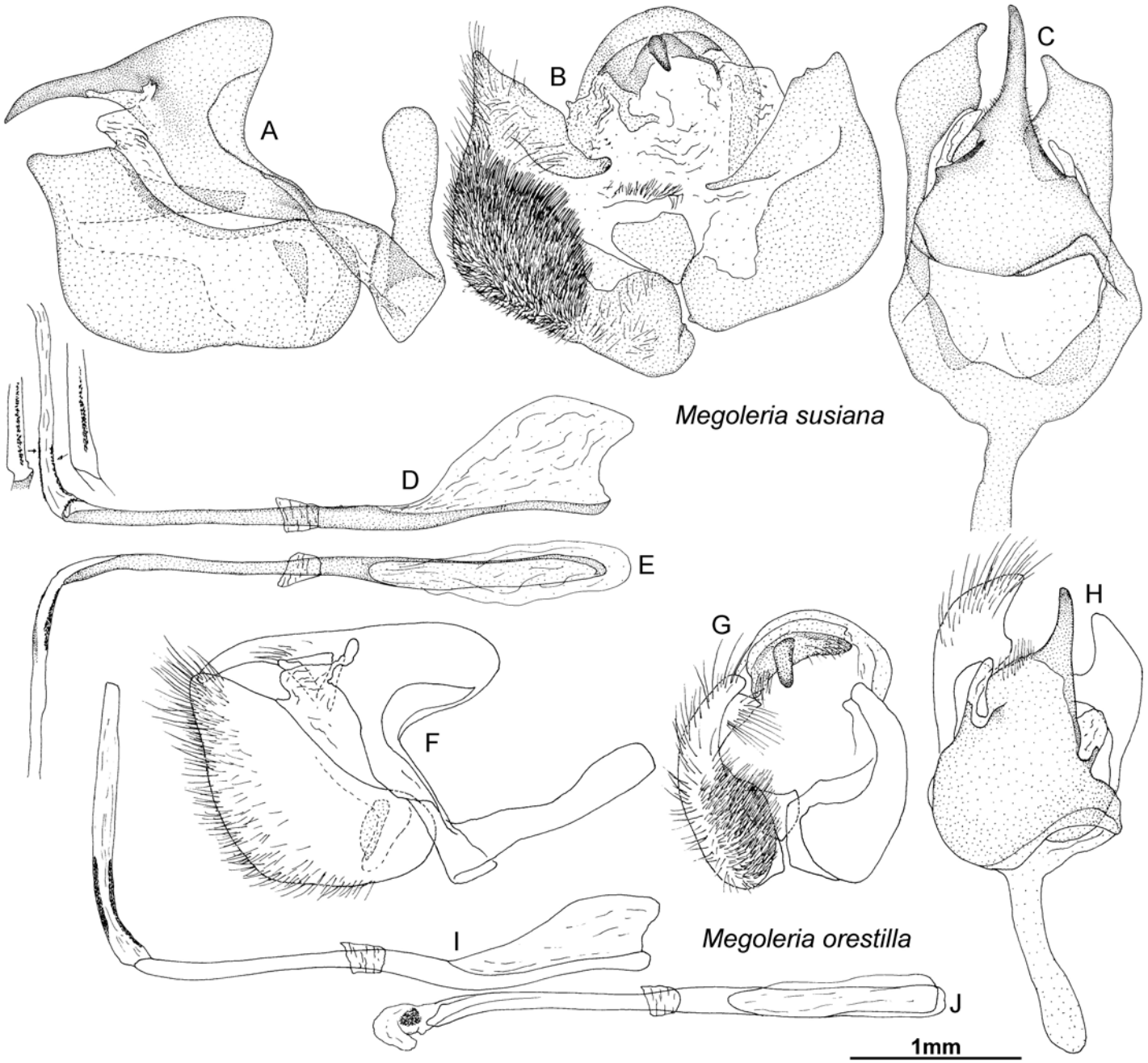

Fig. 4. Male genitalia (stippling present only where necessary to better indicate structure, and setae on valvae partially omitted for clarity): A,F, lateral view; B,G, posterior view; C,H, dorsal view; D,I, lateral view aedeagus; E,J, dorsal view aedeagus. A-E. *M. susiana susiana*. F-J. *M. orestilla orestilla*.

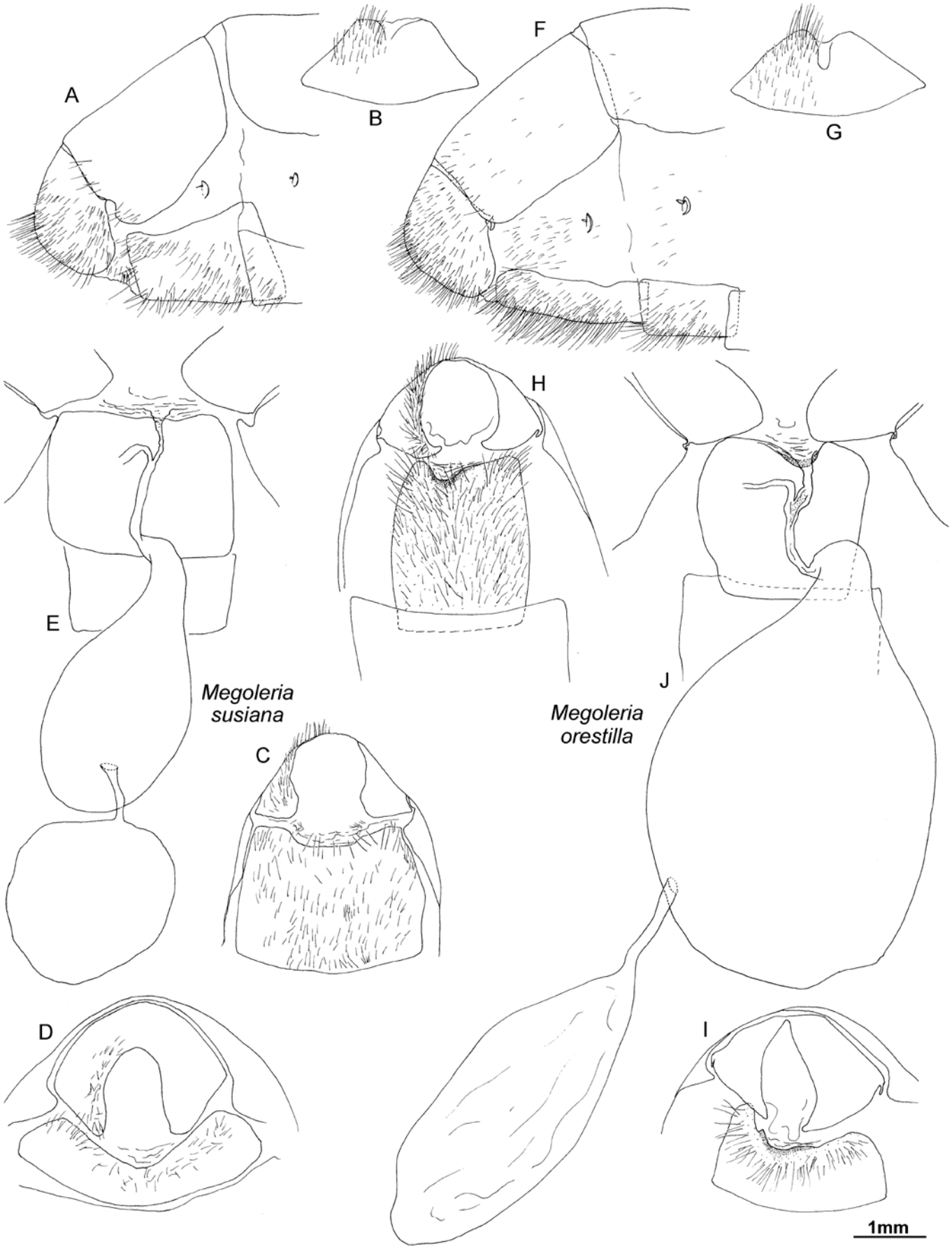

Fig. 5. Female abdomen and genitalia. A,F, lateral view abdomen terminal sclerites; B,G, dorsal view eighth tergite; C,H, ventral view seventh sternite; D,I, posterior view tip abdomen; E,J, dorsal view genitalia. A-E. *M. susiana susiana*. F-J. *M. orestilla polymacula*.

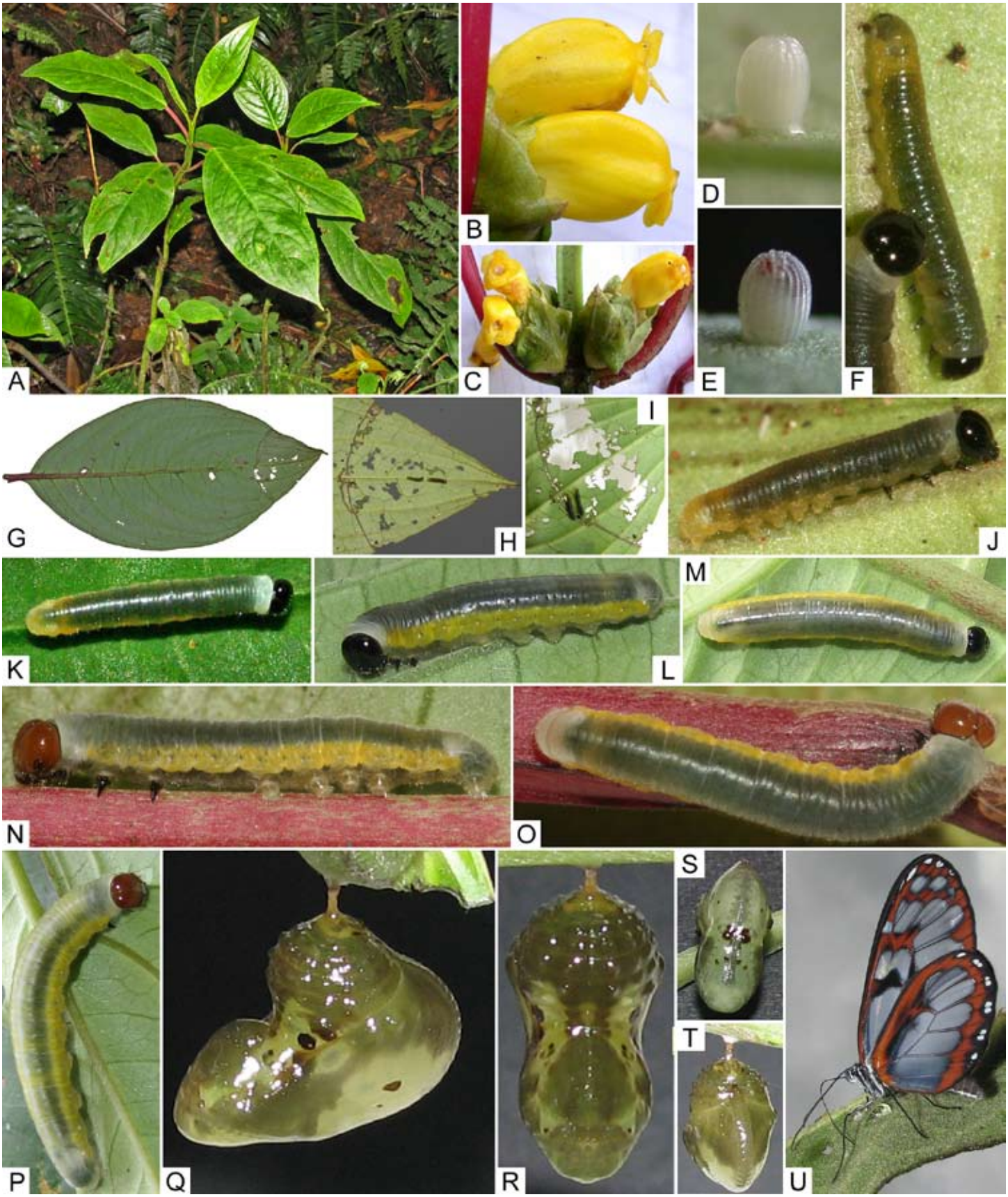

Fig. 6. Immature stages of *M. orestilla orestilla*, Reserva Arcoiris, 2000m, Zamora-Chinchipe, Ecuador. A-C. Larval foodplant *Drymonia urceolata*. D,E. Egg, lateral view, early (D) and on point of eclosion (E). F. 2nd instar larva, dorsolateral view. G-I. Foodplant leaf showing characteristic feeding damage – ventral surface canal isolating leaf tip. J,K. 3rd instar larva, dorsolateral (J) and dorsal (K) views. L,M. 4th instar larva, lateral (L) and dorsal (M) views. N-P. 5th instar larva, lateral (N) and dorsal (O) views, and dorsolateral view (P) just prior to pupation. Q-T. Pupa, lateral (Q), dorsal (R), ventral (S) and posterior (T) views. U. Adult female *M. orestilla orestilla*. Rearing codes for each image given in Appendix 2.

(with black stemmata), a trait that we have otherwise observed among the Oleriini only in the basal *Oleria* species *O. aegineta* (Hewitson, 1869) (Willmott, pers. obs.). The late fifth instar shows an indistinct pale mid-dorsal gray line.

The pupa (Figs. 6Q-T) is a mottled pale olive green and very pale green, the latter color present laterally on the third thoracic and first three abdominal segments, on the wing cases, and ventrally. Unusually, there appear to be no reflective areas (based on photographs examined, taken by Marianne Elias). There is a prominent black lateral spot on abdominal segment 1 (A1), and a less distinct dark brown spot laterally on A2. A brown spot marks the FW discocellulars on the wing case. Like all Oleriini the pupa is sharply bent in lateral view (Fig. 6Q); at approximately 90 degrees the angle is most similar to that of *Hyposcada* pupae. The pupa is largely smooth except for a series of rounded "bumps" scattered around abdominal segments posterior of A3 (Fig. 6R), as in some *Hyposcada*. Head horns are absent, the anterior tip of the pupa being completely rounded (Fig. 6R).

Generic relationships and diagnosis

Megoleria species possess the following unambiguous synapomorphies of the tribe Oleriini (Willmott & Freitas, 2006): 1. Egg with ratio between vertical and horizontal axes between 1.5 and 1.7; 2. Pupa ground color pale green (this is a unique synapomorphy within Ithomiinae, though not all Oleriini species have been examined, and some oleriine species have further derived character states); 3. Sulci on fourth from terminal antennomere of female antenna nearer proximal edge of antennomere; 4. Pale continuous central band on tegula present; 5. Cornuti placed at base of vesica; and 6. Gnathos attached to uncus only, free from appendices angulares (a unique synapomorphy).

Cladistic analyses based on adult characters, immature stage characters (Willmott & Freitas, 2006) and molecular sequence data (Brower *et al*., 2006) all provide support for the monophyly of the tribe, but the relationships of *Megoleria* to remaining genera are less clearly resolved. Brower *et al*. (2006) found *Megoleria* to be basal to remaining Oleriini, but Willmott & Freitas (2006) found it to be sister to *Hyposcada*, albeit with weak and conflicting support from adult and immature stage data partitions. The shared larval hostplant family Gesneriaceae provides the most convincing support for the monophyly of *Megoleria+Hyposcada*, since this plant family is otherwise unknown as a host among the rest of the Ithomiinae, which feed almost exclusively on Solanaceae (Willmott & Freitas, 2006). Some characters of the immature stages, such as the shape of the pupa and presence of abdominal "bumps", may provide additional synapomorphies when sufficient life histories are known.

Constantino (1999) listed the following characters as distinguishing *Megoleria* from *Oleria*: 1. antenna extending distally beyond FW discocellulars; 2. large size (FW length 40-42mm vs 20-25mm); 3. FW vein Cu2 curved rather than straight; 4. FW vein M1 straight (not curved); 5. hindwing distal margin rounded; 6. HW veins M1 and Rs separate at base; and 7. A pair of male DHW androconial hair pencils (rather than a single patch, presumably, though this was not stated). Character 1 also occurs in some *Oleria* (e.g. *Oleria santineza* (Haensch)), as well as all *Hyposcada*. Character 2 is not nearly as marked as suggested, with some specimens of larger *Oleria* (e.g. *O. cyrene* (Latreille) and an undescribed species from Peru) being of similar size to *Megoleria*, while characters 3-6 all occur in both *Hyposcada* and *Oleria*. While character 7 is rare in other oleriines it is not unknown; for example, *Oleria aegineta* (Hewitson, 1869) and *Hyposcada zarepha* (Hewitson, 1869) have the DHW male andoconial hair pencil divided into two patches. Synapomorphies for *Megoleria* identified by Willmott & Freitas (2006) and this study include: 1. The anterior edge of the HW discal cell is notably short, so that the base of vein M1 is nearer the wing base than the base of vein M3; 2. The medio-ventral inner face of the valva is covered with very dense, thick, short hairs, quite distinct from those over the rest of the valva; and 3. The appendices angulares present but unsclerotized. The first synapomorphy is unique within the Oleriini, the last two are unique within the Ithomiinae. Given that both *Hyposcada* and *Megoleria* as currently conceived are monophyletic, that both are easily identified, and that there is some doubt over the sister relationship between the two genera, there is no compelling reason not to maintain the existing generic classification.

Taxonomy

Two species are recognized, with a total of six subspecies, of which one subspecies is described and named here.

Megoleria Constantino, 1999: 60. Type-species, *Ithomia susiana* C. Felder & R. Felder, 1862, by original designation.
("-" denotes a subspecies, "--" denotes a synonym)

susiana (C. Felder & R. Felder, 1862)
-*sandra* Constantino, 1999
-*susanna* (Staudinger, [1884])
orestilla (Hewitson, 1867)
-*polylla* Lamas & Willmott, **n. ssp.**
-*polymacula* (Rosenberg & Talbot, 1914)
--*magnifica* (Tessmann, 1928)
--*speciosa* (Tessmann, 1928)

Key to *Megoleria* taxa:

1. White spots present and distinct on DHW margin; base of FW cell Cu1-M3 black (*susiana*).....2
   White spots absent or only a trace on DHW margin; base of FW cell Cu1-M3 transparent or with transparent spot (*orestilla*) 4
2. HW discal band tapering from anal margin towards apex.....3
   HW discal band approximately even in width..... .....*susiana susiana*
3. HW discal band translucent white.....*susiana sandra*
   HW discal band opaque to semi-opaque pale yellow ....*susiana susanna*
4. FW cells Cu2-Cu1 and Cu1-M3 each with two transparent spots; HW discal cell entirely or almost entirely black.....5
   FW cells Cu2-Cu1 and Cu1-M3 each with single, broad transparent area; HW discal cell posterior half transparent..... .....*orestilla orestilla*
5. HW transparent spots of discal band in cells M3-M2 and M2-M1 of similar width to spot in cell Cu1-M3 ....*orestilla polymacula*
   HW transparent spots of discal band in cells M3-M2 and M2-M1 1.5-2x wider than that in cell Cu1-M3 ....*orestilla polylla*

DISTRIBUTION AND NATURAL HISTORY

Megoleria are confined to the Andes, ranging from western Venezuela to western Colombia and along the eastern Andes to Bolivia, but the two species are sympatric only from southern Colombia to central eastern Ecuador (Fig. 7). Both species occur in undisturbed cloud forest habitats from approximately 1200-2700m, but are most commonly encountered from 1600-2400m.

Known hostplants are in the family Gesneriaceae (e.g., Fig. 6A), a family otherwise used among the Ithomiinae only by the sister genus *Hyposcada*. The immature stages are known only for *M. orestilla* (Fig. 6), and their natural history is described in the account for that species.

Adults are usually uncommon, encountered as solitary individuals flying relatively high, typically from 2-5m above the ground, in shady understorey and midstorey of tall forest. We have never encountered either species feeding on Asteraceae flowers, though *M. orestilla* has been observed feeding on the purple flowers of an unidentified understorey bush. There are no published observations of perching behaviour in males, or of any other aspect of courtship or mating. Both species are involved in mimicry with other ithomiines, mainly within the tribe Oleriini.

SPECIES ACCOUNTS

Megoleria susiana (C. Felder & R. Felder, 1862)
Figs. 1, 3A-C, F-J, 4A-E, 5A-E, 7

Identification, taxonomy and variation: *Megoleria susiana* (Fig. 1) is easily distinguished from *M. orestilla* (Fig. 2) by the conspicuous row of marginal white spots on the DHW from cell Cu2-Cu1 to the apex, and by the absence of a transparent spot or area at the base of FW cell Cu1-M3 and HW cell M1-Rs. The VHW marginal white spots are slightly smaller than in *M. orestilla* and more concentrated towards the center of each cell. Notwithstanding these more obvious differences, Mielke & Brown (1979) and D'Abrera (1984) considered *M. orestilla* to be a subspecies of *M. susiana*, presumably based on apparent allopatry of the various taxa known at that time. Since then, however, additional distribution data demonstrate the two species to be widely sympatric from southern Colombia to central Ecuador. Moreover, on closer inspection there are a number of clear and consistent morphological differences between the two species in wing pattern (as mentioned above), venation and genitalia. The male hindwing cell in *M. susiana* is proportionally smaller than in *M. orestilla* and vein 3d meets Mr at the base of vein M2, rather than more basally (Fig. 3). In *M. susiana* the "footprint" of the basal hair pencil is similar in size to that of the distal hair pencil, whereas in *M. orestilla* the former is approximately twice the width of the latter. In comparison with *M. susiana*, the male genitalic valva of *M. orestilla* (Fig. 4) is more elongate with a distinct attenuated posterior point. The tegumen is more produced anteriorly in *M. susiana*, and in dorsal aspect the uncus and tegumen are more asymmetric. In the female (Fig. 5), the seventh tergite of *M. susiana* extends further ventrally at its posterior corner, and the ostium bursae is indistinct, only weakly indented into the posterior edge of the seventh sternite.

Megoleria susiana shows geographic variation in the extent of black markings on both wings, but especially the hindwing, in the color of the hindwing discal band, the extent of reddish brown markings on the ventral surface, and in the shape and size of the white HW marginal spots, and three subspecies are recognized.

Range and status: Venezuela (Mérida) to eastern Ecuador along the east Andean slopes, and throughout western and central Colombia (Fig. 7). Although currently unknown from northwestern Ecuador, its presence there is not unlikely. Rare, in cloud forest from 1200-2400m.

Specimens examined: **56♂, 50♀**

Megoleria susiana susiana (C. Felder & R. Felder, 1862)
Figs. 1E,F, 3A-C,F-J, 4A-E, 5A-E, 7

Ithomia susiana C. Felder & R. Felder, 1862: 416. **TL**: Colombia, [Cundinamarca], Pandi, 5600'. **Lectotype** ♂, BMNH (here designated) [examined].
Ithomia attalia: Hewitson, 1867: [20] (misidentification).
Hyposcada susiana: Haensch, 1903: 188; Mielke & Brown, 1979: 132.
Leucothyris susiana: Haensch, 1909: 148, pl. 38g, fig. [1].
Oleria susiana: D'Almeida, 1978: 259.
Oleria susiana susiana: D'Abrera, 1984: 242, figs.
Megoleria susiana susiana: Constantino, 1999: 62, fig. 15, 16.

Identification, taxonomy and variation: The nominate subspecies differs from both other subspecies in having the hindwing transparent band of even width, rather than it being broader at the anal margin. The paired white HW marginal spots are elongate parallel with the veins, rather than being circular. Other differences are discussed under the other subspecies. Felder & Felder (1862) described this species based on an unstated number of male and female specimens originating from Pandi, a locality situated southwest of Bogotá, on the western slopes of the Cordillera Oriental.

Range: Venezuela (southern Cordillera de Mérida) to central eastern Ecuador (Tungurahua), apparently occurring in Colombia on both slopes of the Cordillera Oriental.

Habitat and adult ecology: This subspecies occurs from 1400-2000m in cloud forest habitats and appears to be very rare outside of Colombia, the center of its range. In Ecuador, Haensch (1903) collected a single male between Baeza and (Puerto) Napo, on January 16th, most likely in the Cosanga region, while Jason Hall (pers. comm.) collected a single female in secondary forest at Río Machay in July. Despite considerable collecting effort in northern Ecuador we have observed no other specimens in the field, and it is evidently much rarer than its congener. *Megoleria s. susiana* is presumably involved in mimicry with *M. orestilla polylla* n. ssp. and several other species of *Oleria*. Interestingly, with the exception of *O. cyrene*, the other species of *Oleria* that mimic *M. susiana* are sexually dimorphic, with only the female mimicking *M. susiana*. Such species include *O. athalina* (Staudinger, [1884]), *O. radina* (Haensch, 1909), *O. baizana* (Haensch, 1903) and *O. tremona* (Haensch, 1909).

Specimens examined (36♂, 35♀): COLOMBIA.- *Boyacá:* "Minas de Muzo" - (error), 1884-1885, 1♂, (BMNH); *Caquetá:* no specific locality, [specimens not recorded] (JFL); *Cundinamarca:* "Bogotá" - (error), 1♂, 1♀, (BMNH(S)), 1♂ [mislabelled as a "type"], 2♂ [Photographed by D'Abrera], 2♀, (BMNH), 1♂, (OUM), 1♀, (SMNS), (Bates), 1♂, (BMNH(S)), (Lindig), 1♂ [=Pandi; LT *susiana*; B.M. Type No. Rh. 18155], 1♂ [PLT *susiana*; B.M. Type No. Rh. 18156], 1♀ [PLT *susiana*; B.M. Type No. Rh. 18158], (BMNH); "environs de Bogotá" - (error), 1♀, (BMNH), (Apollinaire-Marie), 1918, 1♂, (BMNH(S)); "Region de Bogotá" - (error), (Apollinaire-Marie), 1♂, (BMNH), Dec 1917, 1♂, (BMNH); "Santa-Fé de Bogotá" - (error), 1♀, (BMNH); Monte Redondo, [4°20'N, 73°52'W], [specimens not recorded] (IAVH); Monte Redondo, [4°20'N, 73°52'W], 1420m, Jan Mar Sep Oct, 1♂, 3♀, (ZSBS); *Huila:* Parque Nacional Las Cuevas (=Parque Nacional Natural Cueva de los Guácharos), [c. 1°37'N, 75°55'W], 1800m, (M. Cooper), 15-21 May 1976, 3♂, 3♀, (FLMNH); *Meta:* "Río Meta" - (error), 1♂, (BMNH); *Santander:* Pico de Armas, [6°21'N, 73°30'W], Jan, 2♀, (AMNH); *Tolima:* Aguadita, [5°09'N, 75°07'W], Jun 1914, 1♂, (BMNH); La Marina area, Río Ambeima, [3°43'N, 75°42'W], 1600-1700m, Jun, 1♀, (FLMNH); Río Chili, [4°07.19'N, 75°15.57'W], Apr-Jun 1921, 1♀, (BMNH); *No specific locality:* "Colombia", 1♂, (AMNH), 2♂, 3♀, (BMNH(S)), 1♂, (BMNH), 1♀, (MUSM), 1♂, 2♀, (SMTD), 1♀, (ZMHU(H)), 1♂, 1♀, (ZSBS); "New Granada", 3♂, (BMNH(S)), 1♀, (BMNH), (Watson), 1871, 1♀, (OUM); *Not located:* "Interior of Colombia", (J. Carder), 1♂, (BMNH), (Wheeler), 1♀, (BMNH); Río Magdalena, 1♂, (SMTD). **ECUADOR**.- *Napo:* Baeza, [0°28'S, 77°53'W], 2000m, (Haensch), 1♂, (ZMHU(H)); Guacamayos, [0°37'S, 77°49'W], (I. Aldas), Jul, 1♀, (KWJH); *Tungurahua:* Río Machay, [1°23.75'S, 78°16.3'W], 1600m, (J.P.W. Hall), Jul 1993, 1♀, (KWJH). **VENEZUELA**.- *Táchira:* Mata Mula, Vía Bramón - Delicias, P.N. El Tamá, [7°37.93'N, 72°26.1'W], 1850m, (A. Neild), 17 Nov 1995, 29 Apr 1996, 1♂, 1♀, (AFEN); *No specific locality:* "Venezuela" - (error), 1♀, (BMNH). **NO LOCALITY DATA**.- no data, 1♂, (AMNH), 1♂, 2♂ [PLT *susiana*; B.M. Types No. Rh. 18154, 18157], (BMNH), 1♂, (SMF), (E.W. Mark), 1848-1857, 1♀ ["Probably near Bogota"], (OUM).

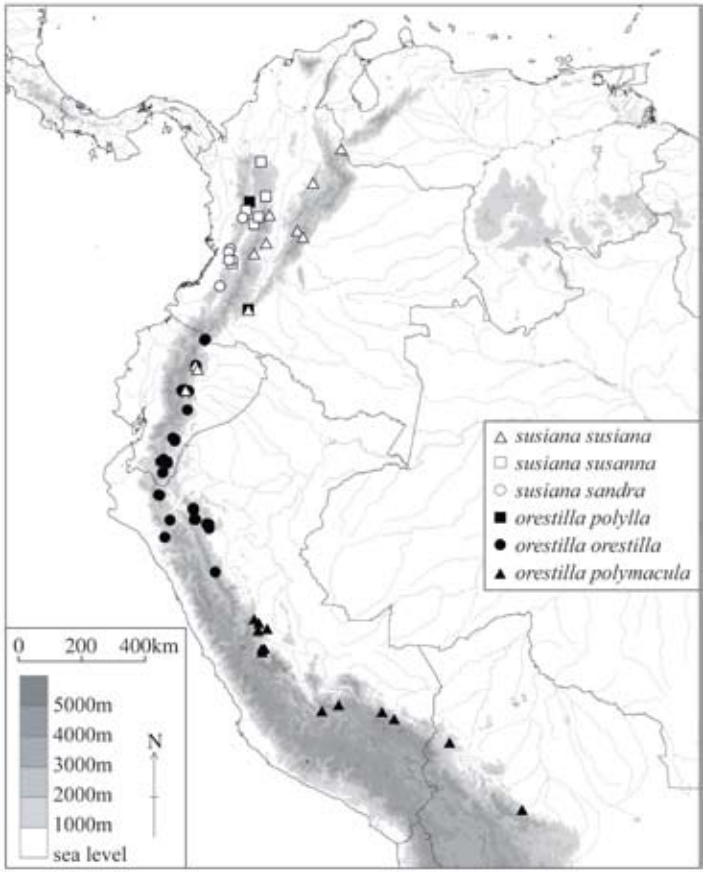

Fig. 7. Localities for *Megoleria orestilla* and *M. susiana*.

Megoleria susiana susanna (Staudinger, [1884])
Figs. 1C,D, 7

Tithorea susanna Staudinger, [1884]: pl. 30, fig. [8]; 1885: 72. **TL**: Colombia, [Chocó], Río Atrato. **Holotype** ♂, ZMHU [examined].
Leucothyris susiana susanna: Haensch, 1909: 148.
Oleria susanna: D'Almeida, 1978: 259; D'Abrera, 1984: 242.
Megoleria susiana susanna: Constantino, 1999: 62, fig. 5, 6.

Identification, taxonomy and variation: This subspecies is distinguished from both other subspecies by the hindwing discal band being tinged pale yellow, and often being opaque, rather than translucent white. This band is also narrower than in *M. susiana sandra* Constantino. The black scaling on the forewing is more extensive than in other subspecies, especially in the discal cell. The ventral rufous markings form a more even submarginal band on the HW and are reduced in the basal half of the VFW. This taxon was described by Staudinger ([1884]) based on a unique male illustrated on his plate 30, collected by E. Kalbreyer, "probably in the valley of the Río Atrato". This rather vague locality possibly refers to a place on the western slopes of the Cordillera Occidental, along the road from Medellín to Quibdó, on the upper reaches of the Río Atrato.

Range: Western and northern Cordillera Central, and northern Cordillera Occidental in Colombia (Antioquia, Caldas, Risaralda, Valle del Cauca).

Habitat and adult ecology: Nothing has been published on the natural history of this taxon, which is rare in collections. Ithomiine co-mimics include *Oleria cyrene cyrene*, the female of an undescribed subspecies of *Oleria radina*, and possibly *Elzunia humboldt* (Latreille, [1809]).

Specimens examined (5♂, 9♀): COLOMBIA.- *Antioquia:* Mesopotamia, [5°51'N, 75°16'W], 2♀, (AMNH); Valdivia, [7°09'N, 75°27'W], (Pratt), 1897, 3♂, 1♀, (BMNH); *Caldas:* Manizales, [5°05'N, 75°32'W], (A.M. Patiño), 4♀, (BMNH); *Risaralda:* Distrito de Pereira, [4°49'N, 75°43'W], (R.M. Valencia), 1885, 1♀, (BMNH); San Antonio de Chami, [5°20.6'N, 76°00'W], 1650m, (IAVH); no specific locality, (JFL); *Valle del Cauca:* Río Cañas Gordas, [3°21'N, 76°31'W], May, 1♀, (FLMNH); *Not located:* "Cauca", (G. Kalbreyer), 1♂ [= Río Atrato; HT *susanna*], (ZMHU); Río Aguata [possibly = Río Aguacatal], Jul, 1♂, (FLMNH).

Megoleria susiana sandra Constantino, 1999
Figs. 1A,B, 7

Megoleria susiana sandra Constantino, 1999: 62, figs. 3-4, 17.
TL: Colombia, Valle del Cauca, San Antonio, km 14 vía al mar, 2000m. **Holotype** ♂, LMC [examined].

Identification, taxonomy and variation: This recently described subspecies is distinguished by its translucent white hindwing discal band that is broad along the anal margin and tapers towards the apex. Constantino (1999) described this taxon from a series of three males and one female collected in the departments of Valle del Cauca, Cauca, and Risaralda, in southwestern Colombia.

Range: western slope of the central and southern Cordillera Occidental in Colombia (Valle del Cauca, Cauca), possibly extending into extreme northwestern Ecuador.

Habitat and adult ecology: This subspecies has been recorded from 1200-2500m in cloud forest habitats, where it appears to be uncommon. The apparently broad elevational range may reflect erroneous label elevation data, with most specimens having been collected from 2000-2500m. *Megoleria susiana sandra* is mimicked by the female of an undescribed subspecies of *Oleria radina* (Willmott & Lamas, unpub.).

Specimens examined (15♂, 6♀): COLOMBIA.- *Cauca:* Pela Huevo, Tambito, [c. 2°30'N, 76°59'W], 2000m, 11 Feb 1997, 1♂, (MUSM); Tambito, [2°30'N, 76°59'W], 2000m, (W. Chilito), 24 Jul 1997, 1♀, (MHNCA); *Valle del Cauca:* "Vitacoberge" [= Cerro Bitaco?], [3°46'N, 76°38'W], 2300m, (A.H. Fassl), Aug 1909, 1♂ [BMNH(E) # 805942], (BMNH), Jul 1909, 1♂, (BMNH); Alto Calima, [3°53'N, 76°36'W], 1200m, (L. Denhez), 25 Jun 1974, 1♀, (MUSM); Bitaco, [3°46'N, 76°38'W], 2500m, 1♂, (SMF); Cerro San Antonio, [3°29'N, 76°38'W], 2200m, ([A.H. Fassl]), Aug 1908, 1♂, (BMNH); Lago Calima, [3°53'N, 76°36'W], (IAVH); Río Aguacatal, [3°28'N, 76°32'W], 2000m, 1♀, (SMF), 1♂, 1♀, (SMTD), (A.H. Fassl), Nov 1908, 1♀, (SMF); Río Bitaco, [3°46'N, 76°38'W], 2500m, (A.H. Fassl), Dec 1908, 1♂, (SMF), 2300-2400m, ([A.H. Fassl]), Dec 1908, 1♂, (BMNH), 2400m, ([A.H. Fassl]), Dec 1908, 1♀ [BMNH # 805943], (BMNH); San Antonio, above Cali, km 14, [3°29'N, 76°38'W], 2000m, (J. Bechara), 10 Aug 1979, 1♂ [HT *sandra*], (LMC); *No specific locality:* "Colombia", 1♂, (SMTD); *Not located:* "W Colombia", 500m, 1♂, (ZSBS). **NO LOCALITY DATA**.- no data, 1♂, (BMNH).

Other records: COLOMBIA.- *Risaralda:* Cerro Tatamá, [c. 5°04'N, 76°08'W], 1800m, (J. Salazar), 19 Jul 1984, 2♂, (JS) (Constantino, 1999); *Valle del Cauca:* Quebrada El Pital, Lago Calima, [c. 3°53'N, 76°36'W], 1200m, (D. Torres), 23 Sep 1984, 1♂, (MHNUC) (Constantino, 1999).

Megoleria orestilla (Hewitson, 1867)
Figs. 2, 3D,E, 4F-J, 5F-J, 6, 7

Identification, taxonomy and variation: *Megoleria orestilla* is distinguished from *M. susiana* under that species. Recently regarded as conspecific with *M. susiana* (Mielke & Brown, 1979; D'Abrera, 1984; Constantino, 1999), the two species are sympatric and clearly distinct (Lamas, 2004), as discussed under *M. susiana*. Although Piñas (2004) treated *M. orestilla orestilla* in *Oleria*, in his checklist of Ecuadorian Ithomiinae, we presume that this was due to lack of knowledge of Constantino's (1999) description, rather than intended to be a genuine taxonomic change. There is geographic variation in the extent of black markings on both wings, and three subspecies are recognized.

Range and status: Colombia (Cordilleras Central and Oriental) to Bolivia (Cochabamba), along the east Andean slopes. Uncommon to rare, in cloud forest from 1300-2700m.

Specimens examined: **111♂, 73♀**

Megoleria orestilla orestilla (Hewitson, 1867)
Figs. 2, 3D-F, 4F-J, 6, 7

Ithomia orestilla Hewitson, 1867: [20], pl. [11], fig. 160. **TL**: "New Granada" (error) [= Ecuador]. **Lectotype** ♂, BMNH (here designated) [examined].
Hyposcada orestilla: Haensch, 1903: 188.
Leucothyris orestilla: Haensch, 1909: 148, pl. 38g, fig. [4].
Oleria orestilla: D'Almeida, 1978: 254.
Hyposcada susiana orestilla: Mielke & Brown, 1979: 132.

Oleria susiana orestilla: D'Abrera, 1984: 242, figs.
Megoleria susiana orestilla: Constantino, 1999: 62
Megoleria orestilla orestilla: Lamas, 2004: 182.

Identification, taxonomy and variation: The nominate subspecies differs from other subspecies in having the transparent area in FW cells Cu2-M3 undivided, and the posterior half of the HW discal cell and base of cells 2A-Cu1 transparent, rather than black. The black marginal borders tend to become narrower from north to south within the range of the subspecies. Specimens from far northern Ecuador (Sucumbíos) suggest intergradation with *M. o. polylla*, having the hindwing discal cell almost completely black (Fig. 2D), and analogous variation is also present in the same area in presumed co-mimics such as *Oleria cyrene*. Hewitson (1867) described this taxon from an unspecified number of male specimens in his collection, from "New Granada". The illustration and syntype are, however, typical of central and southern Ecuadorian specimens, and given the occurrence in extreme northern Ecuador of specimens apparently intergrading to the Colombian *M. o. polylla*, it seems highly unlikely that *M. o. orestilla* occurs in Colombia, and the type specimen(s) thus appear to have been mislabelled. In order to fix the identity of the name, we designate herein as **lectotype** the male syntype in BMNH bearing the number "B.M. Type No. Rh. 7457".

Range: Ecuador (Napo) to northern Peru (San Martín), along the east slope of the Andes, with intergrades to *M. o. polylla* in far northern Ecuador (Sucumbíos) (Fig. 2B). Constantino (1999) reports the range to extend into southern Colombia, but we have seen no *bona fide* Colombian specimens, and this report may perhaps have been based on the erroneous locality data of the lectotype.

Immature stages: An intensive survey of ithomiine immature stages was conducted at Reserva Arcoiris, Sector San Francisco, Parque Nacional Podocarpus, Zamora-Chinchipe, Ecuador by KRW and Raúl Aldaz in January-February 2002 and, with the further assistance of Marianne Elias, again from September - December 2006. The morphology of the immature stages is described in the generic account. In 2002 a female of *M. orestilla* was observed ovipositing on *Drymonia urceolata* Wiehler (Figs. 6A-C), a common plant within the reserve, leading to intensive searches of this plant for additional immature stage individuals.

Despite searching a very large number of plants, a total of only 13 immature stage individuals were located, comprising eggs (8), 2nd instar (2), 3rd instar (1), 3rd-4th instar (1), and 4th-5th instar (1). Of the 8 eggs found, 4 hatched, of which 3 survived to 1st instar and 1 to 2nd instar. One larva collected as a second instar was parasitized by an unidentified Diptera. The three larvae that died as 1st instars all failed to eat the hostplant, and our general lack of success in rearing the species, with all four larvae found as 2nd-4th instars dying without advancing past the 4th instar, strongly suggests that our rearing conditions were unsuitable. The avoidance of the leaves by first instars, and distinctive feeding behaviour of later instars (described below) suggest that leaf damage initiates some form of chemical defence that renders the leaves toxic to larvae. We therefore advise others attempting to rear this species on *Drymonia urceolata* to use whole potted plants or plants *in situ*, rather than feed larvae with leaves collected from plants.

All four larvae collected in 2006 were found on leaves exhibiting a distinctive pattern of feeding damage: 2nd-3rd instar larvae cut a trench through the underside of the leaf from one side to the other, leaving semi-isolated an approximately triangular section at the tip of the leaf (Figs. 6G, H). Feeding in these and subsequent instars takes place on the underside of the isolated leaf tip, which is eventually entirely consumed, leaving a characteristic leaf shape that can be used to locate larvae in the field. Such behaviour is presumably an adaptation against defensive chemicals mobilized when leaves are damaged, though the identity of such chemicals is unknown.

Based on a limited sample (see Appendix 2), development times are as follows: egg, 10-11 days; 1st instar, at least 5 days; 4th instar, 17 days; 5th instar, 13 days; pupa, 22 days. Total development time from oviposition to eclosion is estimated to be approximately 70-80 days, remarkably long in comparison with other ithomiines. Two species of *Hyalenna* Forbes, for example, reared at the same site, complete this part of the life cycle in 45-50 days (Willmott & Lamas, 2006). It should be noted, however, that no individual was reared from egg to adult, and observed development times may have been retarded by poor food quality.

Dyer *et al*. (2008) also report an undescribed species of *Drymonia* as the larval foodplant of *Megoleria orestilla orestilla* at Yanayacu, Napo Province, northeastern Ecuador, and figure a mature larva in dorsal view.

Habitat and adult ecology: Haensch (1903) collected this subspecies in Ecuador on Volcán Tungurahua and near Baeza (Napo), from January to March, and reported it to be rather rare. In our experience, despite being relatively scarce in collections, both sexes of the nominate subspecies can be locally common in the interior of undisturbed cloud forest. The taxon is most abundant between 1600-2400m, though apparently occurs as low as 1300m in river valleys. The only known larval hostplant in southern Ecuador, *Drymonia urceolata*, is very common in shady understorey, especially near streams, along the edges of steep rivers and in damp gullies, where it grows up to 2m in height. *Megoleria orestilla orestilla* occurs in similar habitats, typically observed as solitary individuals flying from 2-5m and rarely up to 8m, rather higher than the majority of Oleriini. We once observed a female at 1430 hrs ovipositing near a stream on this species of hostplant in damp, shady understorey, 5m above the ground (the plant was growing on the side of a steep slope). A total of 4 eggs were laid singly on the underside of leaves 2-3cm from the leaf edge, not near veins or areas of leaf damage (as in some ithomiines). We have observed males feeding on flowers of a small, non-Asteraceae understorey tree, but have never observed the species feeding on the weedy Asteraceae that are otherwise highly attractive to most montane ithomiines, including *Oleria*. We have also observed males occasionally feeding on bird excrement. This subspecies flies with and is an accurate mimic of numerous ithomiines. These include not only a number of *Oleria* species, such as *O. athalina*, *O. tremona*, *O. makrena* (Hewitson, 1854), *O. fasciata* (Haensch, 1903), *O. cyrene*, *O. derondina* (Haensch, 1909), *O. santineza* and *O. olerioides* (D'Almeida, 1952), but also isolated members of *Godyris* Boisduval, *Hyalenna*, *Hyposcada*, *Ithomia* Hübner, *Napeogenes* Bates, *Patricia* Fox, *Greta* Fox and *Pteronymia* Butler & Druce.

Specimens examined (95♂, 52♀): "**COLOMBIA**".- *No specific locality:* "New Granada" - (error), 1♂ [LT *orestilla*; B.M. Type No. Rh. 7457], (BMNH). **ECUADOR**.- *Loja:* environs de Loja, [4°04'S, 79°12'W], 1889, 1♀, (BMNH), (Gaujon), 1886, 1♂, (BMNH); *Morona-Santiago:* Chigüinda, [3°17.6'S, 78°40.6'W], 1600m, (Buckley), 2♂, (BMNH(S)), (C. Buckley), 1♂, 1♀, (BMNH); km. 9.5 Chigüinda-Gualaquiza rd., hillside, [3°14.63'S, 78°40.11'W], 1750m, (K.R. Willmott), 12 Oct 2007, 1♂, (FLMNH); Río Abanico, [2°08'S, 78°12'W], 1600m, (K.R. Willmott), Nov, 1♂, (KWJH); *Napo:* Baeza, [0°28'S, 77°53'W], 2000m, 1♂, (FLMNH), 1♂, (ZMHU(H)), 1♂, (ZSBS), (C. Penz), 12 Aug 1990, 1♂, (MECN); El Arrayán, [c. 0°28.5'S, 77°52.5'W], 2200m, (K.R. Willmott), Oct, 1♂, (KWJH); *Pastaza:* "Río Pastaza" - (error), 1♂, (SMTD); "Sarayacu, Río Bobonaza" - (error), (C. Buckley), 1879, 1♀, (BMB); "Upper Río Pastaza" - (error), 1♂, 1♀, (SMTD); Abitagua, Río Pastaza, [1°27'S, 78°09'W], 1200m, Apr, 2♀, (USNM); *Sucumbíos:* El Higuerón, [0°30.9'N, 77°32.2'W], 2400m, (K.R. Willmott), Nov, 1♀, (KWJH); Quebrada El Garrapatal, [0°29.3'N, 77°33.2'W], 2100-2200m, (K.R. Willmott), 31 Dec 2001, 1♂, 1♀, (BMNH); Río Sucio, nr. La Bonita, [0°28.5'N, 77°33.3'W], 1800-2000m, (K.R. Willmott), 15 Dec 2001, 1♂, (KWJH); *Tungurahua:* "Ambato" = upper Río Pastaza, [1°24'S, 78°25'W], (A. Vásconez), 6♂, 5♀, (BMNH(S)), 1♂, 1♀, (BMNH); "env[irons] d'Ambato" = upper Río Pastaza, [1°24'S, 78°25'W], (I. Blanc), 1♀, (BMB), 6♂, 4♀, (BMNH(S)), (I. Blanc), 3♂, 2♀, (BMNH); Baños a Canelos, (M. de Mathan), Sep-Oct 1894, 1♂, (BMNH(S)), 1♀, (BMNH); Baños, [1°24'S, 78°25'W], 1500-2100m, (M.G. Palmer), 1♂, (BMNH(S)); Baños, [1°24'S, 78°25'W], 1800m, 1♂, (SMF), 1♂, (ZSBS), Jun, 1♀, (AMNH), (M.G. Palmer), 1♂, (BMNH), Apr 1912, 1♂, 3♀, (BMNH); Las Minas de Ulba, 2300m, Dec, 1♂, 1♀, (AMNH); Río Blanco, [1°23'S, 78°20'W], 1650-2000m, 1♂, (FLMNH); Río Machay, [1°23.75'S, 78°16.3'W], 1700m, (K.R. Willmott & J.P.W. Hall), Aug, 1♀, (KWJH); Río Topo, [1°25'S, 78°10'W], 1300m, Jul, 1♂, (USNM); Volcán Tungurahua, [c. 1°24'S, 78°25'W], 1♂, 1♀, (ZMHU(H)); *Zamora-Chinchipe:* "Zamora" - (error), (O.T. Baron), 2♂, (BMNH); Casa Simpson, Reserva Tapichalaca, above Valladolid, [4°29.4'S, 79°07.5'W], 2420m, (K. Willmott), 30 November 2005, 1♀, (FLMNH); Quebrada Honda trail, Reserva Tapichalaca, [4°28.35'S, 79°07.3'W], 1900-2000m, (K. Willmott), 30 November 2005, 1♂, 1♀, (FLMNH); San Francisco, casa de Arcoiris, km 23 Loja-Zamora rd., [3°59.4'S, 79°05.7'W], 2000-2100m, (K. Willmott), 28 November 2003, 1♂, (KWJH); San Francisco, casa de Arcoiris, km 23 Loja-Zamora rd., [3°59.4'S, 79°05.7'W], 2000-2150m, (K.R. Willmott), 04 Feb 2002, 1♂, (BMNH), 1♀, (KWJH), (R. Aldaz), 07 Feb 2002, 1♂, (KWJH), 13 Jan 2002, 1♂, (KWJH); San Francisco, casa de Arcoiris, km 23 Loja-Zamora rd., [3°59.4'S, 79°05.7'W], 2100m, (K.R. Willmott), 10 Oct 2006, 1♂, (FLMNH), 15 Oct 2006, 1♀, (FLMNH), 26 Oct 2006, 1♂, (FLMNH), 4 Dec 2006, 1♀ [KW-330], (FLMNH), 4 Nov 2006, 1♂, (FLMNH); Zamora, [4°04'S, 78°58'W], (O.T. Baron), 1♂, (BMNH(S)); *No*

specific locality: "Ecuador", 5♂, (BMNH(S)), 1♂, (FLMNH), 1♂, (SMF), 1♂, (SMTD), (Buckley), 1♂, (BMNH(S)), (C. Buckley), 1♂, (BMNH); *Not located:* Oriente, 1♀, (AMNH). **PERU**.- *Amazonas:* 5 km W Pomacochas, [5°50'S, 78°00'W], 2000m, (G. Lamas), 16-17 Dec 1975, 1♂, (MUSM); 8 km N Pedro Ruiz, [5°54'S, 77°58'W], 1600m, (B. Calderón), Dec 2004, 1♂, 1♀, (MUSM); Alva, nr. Chachapoyas, 3 May 1974, 2♂, (MUSM); Chachapoyas, [6°14'S, 77°53'W], (M. de Mathan), 1889, 1♀, (BMNH); Huambo, [6°34'S, 77°23'W], 1600m, IVth Trim. 1889, 1♂, 1♀, (BMNH); Inguilpata, [6°14'S, 77°57'W], 2300m, (B. Calderón), Aug 1999, 1♂, (MUSM); La Orilla, Río Huamanpata, N.E. Nueva Esperanza, [6°25'S, 77°24'W], (B. Calderón), 15 Jan 1985, 3 Feb 1985, 3♂, (MUSM); Mendoza, [6°24'S, 77°29'W], 1800m, (M. Büche), Jul 1994, 1♀, (MUSM); Pomacochas, [5°49'S, 77°58'W], 2300m, (B. Calderón), Dec 2004, 4♂, 4♀, (MUSM); *Cajamarca:* Hacienda Taulís, [6°54'S, 79°03'W], 1700m, (H.-W. Koepcke), Feb, Apr, 2♂, (ZSBS); Manchara, [5°20'S, 79°14'W], 2120m, (A. & E. Pratt), 1912, 1♂, (BMNH); Naranja, [6°16'S, 78°51'W], 2300m, (G. Lamas), 6 Nov 1998, 1♂, (MUSM); Río Tabaconas, [5°19'S, 79°17'W], 1800m, (A.E. & F. Pratt), 1912, 2♂, 1♀, (BMNH(S)); Río Tabaconas, [5°19'S, 79°17'W], 1820m, (A.E. & F. Pratt), 1912, 2♂, 2♀, (BMNH); Río Tabaconas, [5°19'S, 79°17'W], 1900m, (A.E. & F. Pratt), 1912, 1♂, (MUSM); *La Libertad:* Cumpang, Tayabamba-Ongón, [8°12'S, 77°10'W], 2400-2700m, (T. Parker), 21 Oct 1979, 1♂, (MUSM); *San Martín:* Las Palmas, Huicungo, Parque Nacional Abiseo, 2100-2680m, (M. Medina), 8 Aug 1990, 2♀, (MUSM). **NO LOCALITY DATA**.- no data, 1♀, (FLMNH), 1♂, 1♀, (SMF).

Other records: ECUADOR.- *Morona-Santiago:* El Boliche, km 8.5 Chigüinda-Gualaquiza rd., [3°15.84'S, 78°39.8'W], 1800m, (K. Willmott), 10 Oct 2007; Granadillos-Qbda. Tres Chorros trail, [3°11.38'S, 78°45.1'W], 2030m, (K. Willmott), 13 Oct 2007; Río Abanico, [2°08'S, 78°12'W], 1600m, Oct, Dec (Willmott & Hall, unpub.); *Napo:* Baeza, [0°28'S, 77°53'W], 2000m, (Haensch, 1903); *Sucumbíos:* Quebrada El Garrapatal, [0°29.3'N, 77°33.2'W], 2200m, (Willmott & Hall, unpub.), 21 December 2001; *Tungurahua:* Río Ulba, [1°26.5'S, 78°23.5'W], 2400m, Nov, (Willmott & Hall, unpub.); Volcán Tungurahua, [c. 1°24'S, 78°25'W], Jan Mar, (Haensch, 1903); *Zamora-Chinchipe:* La Pituca, Zamora-Romerillos rd., [4°08.5'S, 78°57.3'W], 1300-1700m, May; San Francisco, casa de Arcoiris, km 23 Loja-Zamora rd., [3°59.4'S, 79°05.7'W], 2100m, (K. Willmott), 11 Oct 2006, 12 Nov 2006, 14 Oct 2006, 1♂, 15 Nov 2006, 17 Oct 2006, 1♂, 19 Oct 2006, 1♂, 20 Sep 2006, 22 Oct 2006, 1♂, 23 Oct 2006, 25 November 2003, 27 Oct 2006, 1♀, 5 Dec 2006, 3♂, (Willmott & Hall, unpub.).

Megoleria orestilla polylla Lamas & Willmott, **n. ssp.**
Figs. 2A-C, 7

Megoleria orestilla n. ssp.: Lamas, 2004: 182.

Description and diagnosis: This subspecies is distinguished from its closest neighbour, *M. orestilla orestilla*, by having more extensive black on both wings, resulting in the HW translucent discal band narrowing (instead of broadening) from apex to anal margin, the transparent areas in FW cells Cu2-M3 being divided in two by a vertical black line, and the FW black discal band being broader. The FW pattern is similar to *M. o. polymacula*, but the hindwing translucent discal band in that subspecies is approximately even throughout the wing, whereas in *M. o. polylla* it is broadest in cells M3-M1.

Type material: *Holotype* ♂: Parque Nacional Las Cuevas (=Parque Nacional Natural Cueva de los Guácharos), [c. 1°37'N, 75°55'W], 1800m, (M. Cooper), 15 May 1976, (FLMNH).

Etymology: An arbitrary combination of letters, formed from the initial part of the word *polymacula*, and the final part of the word *orestilla*; a feminine noun in apposition.

Taxonomy and variation: This taxon shares all of the diagnostic characters for this species as discussed under the introduction for *M. susiana*, and apparent intergrades to *M. o. orestilla* occur in northeastern Ecuador (Sucumbíos). We have also examined a photograph of one male from Antioquia (cordillera Central), in the MEFLG (Fig. 2C), and a female with no precise data, in the MUSM (Fig. 2B), which we tentatively associate with this subspecies. Both differ slightly from the holotype (Fig. 2A) in having the translucent hindwing discal band broaden at the anal margin, and both have a transparent spot at the posterior edge of the hindwing discal cell. Given the isolation between the Colombian cordilleras Central and Oriental, and the presence of different groups of potential co-mimics in each of these areas, it is perhaps likely that the Antioquia specimen represents a distinct taxon. However, given the lack of material we do not describe it here.

Range: Southeastern Colombia, from Huila to, presumably, near the border with Ecuador.

Habitat and adult ecology: Little is known of the natural history of this rare taxon. The holotype was collected at 1800m along with a small series of *M. susiana susiana*, suggesting these taxa may fly together and be involved in mimicry.

Specimens examined (2♂, 1♀): COLOMBIA.- *Antioquia:* Municipio de Andes, [5°39.08'N, 75°52.24'W], 1357m, (J. Urbina), 12 Apr 1978, 1♂ [no. 8437], (MEFLG); *Huila:* Parque Nacional Las Cuevas (=Parque Nacional Natural Cueva de los Guácharos), [c. 1°37'N, 75°55'W], 1800m, (M. Cooper), 15 May 1976, 1♂ [HT *polylla*], (FLMNH); *No specific locality:* "Colombia", 1♀, (MUSM).

Megoleria orestilla polymacula (Rosenberg & Talbot, 1914)
Figs. 2G,H, 5F-J, 7

Leucothyris polymacula Rosenberg & Talbot, 1914: 673. **TL**: Peru, [Pasco], Huancabamba. **Holotype** ♀, BMNH [examined].
Leucothyris magnifica magnifica Tessmann, 1928: 121, pl. 5, fig. 2. **TL**: Peru, [Pasco], Pichis road, between Eneñas and Dos de Mayo, 1500 m. **Lectotype** ♂, ZMHU (here designated) [examined].
Leucothyris magnifica speciosa Tessmann, 1928: 121. **TL**: Bolivia, [La Paz], San Antonio [de Chicalulu], 1800m. **Lectotype** ♂, ZMHU (here designated) [examined].
Oleria magnifica: D'Almeida, 1978: 252.
Oleria speciosa: D'Almeida, 1978: 259.
Oleria magnifica magnifica: D'Abrera, 1984: 246.
Oleria magnifica speciosa: D'Abrera, 1984: 246.
Oleria polymacula: D'Almeida, 1978: 256; D'Abrera, 1984: 246.
Megoleria susiana polymacula: Constantino, 1999: 62
Megoleria susiana speciosa: Constantino, 1999: 62
Megoleria orestilla polymacula: Lamas, 2004: 182.

Identification, taxonomy and variation: This subspecies is distinguished by the relatively narrow but even translucent HW discal band, in addition to characters discussed under the other subspecies. Tessmann (1928) described *Leucothyris magnifica* from Pasco, Peru, apparently unaware of Rosenberg & Talbot's (1914) description of *Leucothyris polymacula* from the same department, and we regard the two names as synonyms. We can also see no significant differences between Peruvian and Bolivian specimens, and so follow Lamas (2004) in regarding *Leucothyris magnifica speciosa* as a further synonym of *polymacula*. The main characters used by Tessmann to justify recognition of two subspecies were the width of the hyaline discal band on the HW (wider in *magnifica*, narrower in *speciosa*), and the thicker black line along HW vein M3 in *speciosa*. However, both traits vary slightly in series we have examined, apparently without geographic correlation.

Range: Peru (Pasco) to Bolivia (Cochabamba), along the eastern slope of the Andes.

Habitat and adult ecology: This subspecies is known from 1400-2700m in cloud forest, where it is apparently uncommon (Peru) to rare (Bolivia). It is similar in behaviour to *M. o. orestilla*. Ithomiine co-mimics include *Oleria athalina*, *O. attalia* (Hewitson, 1855), *O. deronda*, *O. fasciata*, *O. olerioides* and an undescribed species of *Oleria* (Lamas & Willmott, unpub.). In addition, there are several accurate mimics from other genera, including *Hyposcada taliata* (Hewitson, 1874), *H. attilodes* Kaye, 1918, *Velamysta peninna* (Hewitson, 1855), *Napeogenes glycera* Godman, 1899, *N. harbona* (Hewitson, 1869), *Ithomia ellara* (Hewitson, 1874), *I. eleonora* Haensch, 1905, and *I. praeithomia* Vitale & Bollino, 2003.

Specimens examined (14♂, 20♀): BOLIVIA.- *Cochabamba:* Yungas del Espíritu Santo, [17°06'S, 65°40'W], (P. Germain), 1888-1889, 1♂, (BMNH); *La Paz:* San Antonio [de Chicalulu], Yungas, [14°35'S, 68°23'W], 1800m, (Garlepp), 1895-1896, 1♂ [LT *speciosa*], (ZMHU); *No specific locality:* "Bolivia", 1♂, (BMNH). **PERU**.- *Cuzco:* Ccasapata, [13°24'S, 73°10'W], 2400m, (P. Parrillo), 2♀, (MUSM); entre Intipunco y Wiñaywayna, Santuario Histórico Machu Picchu, [13°10.5'S, 72°32'W], 2700m, (O. Mielke), 27 Oct 2001, 1♀, (MUSM); Marcapata, [13°26'S, 70°55'W], 1370m, 2♀ [4500 ft], (BMNH); *Junín:* 0-1 km S Mina Pichita, [11°05'S, 75°25'W], 2100m, (G. Lamas), 12 Sep 2001, 1♂, 2♀, (MUSM); 1 km S Mina Pichita, [11°05'S,

75°25'W], 2100m, (G. Lamas), 21 Aug 2003, 1♂, (ZMHU), 28 Jun 2004, 1♀, (ZMHU); 1-3 km S Mina Pichita, [11°05'S, 75°25'W], 2100m, (G. Lamas), 16-17 Oct 1989, 3♀, (MUSM); 1-3 km SW Mina Pichita, [11°05'S, 75°25'W], 2100m, (G. Lamas), 24, 26 Aug 1988, 2♂, 2♀, (MUSM); Chanchamayo, [11°04'S, 75°19'W], 1♀, (BMNH); Mina Pichita, [11°05'S, 75°25'W], 2000m, (O. Mielke & M. Casagrande), 16,17 Oct 1989, 1♀, (OHM); Quebrada Siete Jeringas, [11°12'S, 75°24'W], 1700m, (G. Lamas, J.J. Ramírez), 15 Nov 2003, 1♀, (MUSM), 28 Jun 2004, 1♀, (MUSM), 8 Nov 2003, 1♂, (MUSM); *Pasco:* Cushi, [9°58'S, 75°42'W], 1900m, (W. Hoffmanns), 1♀, (BMNH); Eneñas-Dos de Mayo, [c. 10°20'S, 75°13'W], (G. Tessmann), 1♂ [LT *magnifica*], (ZMHU); Huancabamba, [10°23'S, 75°33'W], 1900m, 1♂ [PT *polymacula*; B.M. Type No. Rh. 7458], 1♀ [HT *polymacula*; B.M. Type No. Rh. 18159], 1♀ [PT *polymacula*; B.M. Type No. Rh. 7459], (BMNH); Pozuzo, [10°07'S, 75°32'W], 1520-1820m, (native collector), 1♂, (BMNH); *Puno:* Uruhuasi, [13°42'S, 70°28'W], (H. & C. Watkins), Apr May 1910, 1♂ [PT *polymacula*; B.M. Type No. Rh. 7532], 1♂ [PT *polymacula*; B.M. Type No. Rh. 7533], (BMNH), Mar Apr 1910, 1♂ [PT *polymacula*; B.M. Type No. Rh. 7534], (BMNH).

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Appendix 1. Genitalia dissections examined of *Megoleria*. * indicates a figured specimen.

Taxon	Sex	Locality	Collection	Dissection
M. orestilla orestilla	♂	Ecuador: Napo, El Arrayán	*KWJH	Oleria-42
M. orestilla orestilla	♀	Ecuador: Sucumbíos, El Higuerón	KWJH	Oleria-51
M. orestilla polymacula	♂	Peru: Junín, Pozuzo	BMNH	7225
M. orestilla polymacula	♀	Peru: Junín, Chanchamayo	*BMNH	7226
M. susiana susanna	♂	Colombia: Antioquia, Valdivia	BMNH	7227
M. susiana susanna	♀	Colombia: Antioquia, Distrito de Pereira	BMNH	7228
M. susiana susiana	♂	Colombia: "Interior of Colombia"	*BMNH	6683
M. susiana susiana	♀	Colombia: "Bogotá"	*BMNH	6684

Appendix 2. Rearing records for *Megoleria orestilla orestilla* at Reserva Arcoiris, 2000m, Zamora-Chinchipe, Ecuador. Image numbers (Fig. 6) are listed under Rearing Code. Collectors are: KW: Keith Willmott; RA: Raúl Aldaz; ME: Marianne Elias. Dates of developmental stages are the last dates on which that stage was recorded.

Taxon ID status	Rearing code (Fig.)	Collector	Stage found	N	Date found	Plant location	Height on plant	Location on plant	Date egg	Date 1st instar	Date 2nd instar	Date 3rd instar	Date 4th instar	Date 5th instar	End date pupa	Last stage	Sex	Fate	Comments
Likely	KRW-284 (6K)	KW	3/4	1	03/02/2002	damp, shady primary forest understorey near stream	0.5	under leaf					07/02 2002			4		died	
Likely	KRW-285 (6D)	KW	egg	1	03/02/2002	damp, shady primary forest understorey on steep slope beside trail	5	under leaf 2-3cm from leaf edge, not near vein or damaged portion	13/02 2002	18/02 2002						2		died	oviposition at 1430hrs
Likely	KRW-286	KW	egg	1	03/02/2002	damp, shady primary forest understorey on steep slope beside trail	5	under leaf 2-3cm from leaf edge, not near vein or damaged portion								egg		failed to hatch	oviposition at 1430hrs
Likely	KRW-286	KW	egg	1	03/02/2002	damp, shady primary forest understorey on steep slope beside trail	5	under leaf 2-3cm from leaf edge, not near vein or damaged portion	14/02 2002	18/02 2002						1		died	ovip. at 1430hrs; larva didn't eat
Likely	KRW-287	KW	egg	1	03/02/2002	damp, shady primary forest understorey on steep slope beside trail	5	under leaf 2-3cm from leaf edge, not near vein or damaged portion	14/02 2002	18/02 2002						1		died	ovip. at 1430hrs; larva didn't eat
Likely	KRW-295 (6E)	KW	egg	1	13/02/2002	damp, shady primary forest understorey on steep slope beside trail	1	under leaf	16/02 2002	18/02 2002						1		died	didn't eat
Likely	KRW-296	RA	egg	3	18/02/2002	damp, shady primary forest understorey on steep slope beside trail	1	under leaf with 2 other eggs								?		kept by RA	fate not recorded
voucher	KRW-330 (6N-U)	KW	4/5	1	04/12/2006	shady understorey near stream	1	under leaf					04/12 2006	17/12 2006	08/01 2007	adult	female	voucher	
Likely	KRW-335 (6F-J,L,M)	ME	2	1	05/12/2006	shady understorey near stream	-	under leaf			06/12 2006	08/12 2006	25/12 2006			4		died	parasitised Diptera
Likely	KRW-335 (6F-J,L,M)	ME	2	1	05/12/2006	shady understorey near stream	-	under leaf				08/12 2006				3		died	
Likely	KRW-335 (6F-J,L,M)	ME	3	1	05/12/2006	shady understorey near stream	-	under leaf				11/12 2006	28/12 2006			4		died	