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Front Cover - *Pteronymia alida cosanga* n. ssp., male feeding on Asteraceae flowers, Ecuador, near Cosanga. Photograph by Andrew Neild.

Inside Back Cover - *Pteronymia sao loreto* n. ssp., male recently emerged from pupa, Ecuador, Napo Wildlife Center. Photograph by Keith Willmott.

Back Cover - *Brevioleria arzialia loronia* n. ssp., male, Ecuador, Napo Wildlife Center. Photograph by Keith Willmott.

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A new species and thirty-eight new subspecies of equatorial Ithomiini (Lepidoptera, Nymphalidae, Danainae)

Keith R. Willmott¹, Gerardo Lamas², Jason P. W. Hall³, Fabio Vitale⁴, Pierre Boyer⁵,
Jean-Claude Petit⁶, Jamie Radford⁷ and Marianne Elias⁸

1. McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA; kwillmott@flmnh.ufl.edu; 2. Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; 3. Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; 4. Museo di Storia Naturale del Salento Calimera, Lecce, Italy; 5. Le Puy-Sainte-Réparate, France; 6. DUCY, France; 7. Cambridge, United Kingdom; 8. Institut de Systématique, Évolution, Biodiversité, CNRS MNHN Sorbonne Université, EPHE, Université des Antilles, Paris, France.

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Abstract: Neotropical ithomiine butterflies provide some of the most outstanding examples of Müllerian mimicry in nature, and the nearly 400 species of this tribe exhibit remarkable geographic color pattern variation. Here, we describe the following new ithomiine taxa from Ecuador and adjacent countries: *Scada reckia ruiza* Lamas & Willmott, **n. ssp.**, *Methona grandior batesi* Lamas & Willmott, **n. ssp.**, *Elzunia bomplandii golondrina* Willmott, Lamas & Hall, **n. ssp.**, *Ithomia agnosia zumba* Lamas & Willmott, **n. ssp.**, *Ithomia arduinna ardua* Lamas, Vitale & Boyer, **n. ssp.**, *Ithomia hymettia petitia* Lamas & Willmott, **n. ssp.**, *Ithomia iphianassa occidentissa* Lamas & Willmott, **n. ssp.**, *Hyalyris antea lalimba* Lamas & Willmott, **n. ssp.**, *Hyalyris praxilla leuca* Willmott & Lamas, **n. ssp.**, *Hyalyris praxilla abscondita* Lamas, Radford & Willmott, **n. ssp.**, *Hyalyris oca equatoria* Willmott & Lamas, **n. ssp.**, *Hyalyris oca aurea* Lamas & Willmott, **n. ssp.**, *Hypothyris cantobrica zamorita* Willmott, Boyer & Vitale, **n. ssp.**, *Napeogenes glycera mirador* Lamas, Willmott & Radford, **n. ssp.**, *Hyposcada illinissa morona* Lamas & Willmott, **n. ssp.**, *Hyposcada kena unki* Lamas, Willmott & Boyer, **n. ssp.**, *Hyposcada taliata laetitia* Lamas & Willmott, **n. ssp.**, *Ollantaya olerioides baeza* Willmott & Lamas, **n. ssp.**, *Oleria tremona benigna* Lamas & Willmott, **n. ssp.**, *Oleria radina bonita* Willmott & Lamas, **n. ssp.**, *Oleria tigilla raya* Lamas & Willmott, **n. ssp.**, *Oleria onega astigara* Willmott & Lamas, **n. ssp.**, *Episcada clausina bomboiza* Willmott & Lamas, **n. ssp.**, *Episcada hymenaea mirifica* Lamas & Willmott, **n. ssp.**, *Episcada polita pichincha* Willmott & Lamas, **n. ssp.**, *Episcada arcadia* Lamas & Willmott, **n. sp.**, *Episcada arcadia navarro* Lamas & Willmott, **n. ssp.**, *Pteronymia alida luctuosa* Willmott & Lamas, **n. ssp.**, *Pteronymia alida cosanga* Willmott & Lamas, **n. ssp.**, *Pteronymia alida francisca* Willmott & Lamas, **n. ssp.**, *Pteronymia inania bethana* Willmott & Lamas, **n. ssp.**, *Pteronymia hara olerina* Willmott & Lamas, **n. ssp.**, *Pteronymia sao loreto* Lamas & Willmott, **n. ssp.**, *Brevioleria arzialia lorida* Lamas & Willmott, **n. ssp.**, *Hypoleria alema pastaza* Willmott & Lamas, **n. ssp.**, *Hypomenitis hermana serafina* Willmott & Lamas, **n. ssp.**, *Hypomenitis hermana chamba* Willmott & Lamas, **n. ssp.**, *Hypomenitis oneidodes guarumales* Boyer, Petit & Willmott, **n. ssp.**, *Hypomenitis oneidodes nicolasi* Willmott & Lamas, **n. ssp.** These new taxa have remained undescribed until now for a variety of reasons, including incorrect application of existing names, confusion with described taxa due to Müllerian mimicry, and the discovery of new taxa through field work. One new species is described based on unusually marked differences in the genitalia of both sexes in comparison with congeners, discovered during the course of this study. For descriptions of new subspecies, we use morphological, molecular, distributional and ecological data to support our taxonomic hypotheses, figuring both sexes and the male genitalia for the majority of new taxa, providing 91 new DNA barcodes, and including notes on biology and distribution, with maps showing the distributions of neighboring and similar taxa. Nevertheless, future revision will be needed in a number of cases, when molecular data become more taxonomically comprehensive. We also designate a lectotype for *Ithomia agarista* C. Felder & R. Felder, 1862, synonymize *Hypoleria chrysodonia elegans* Winhard, 2021 and *Hypoleria chrysodonia pallida* Winhard, 2021 with *Ithomia orolina* var. *chrysodonia* Bates, 1862 (**n. syn.**), and treat *Episcada clausina flava* Winhard, 2021 as a subspecies of *Episcada polita* Weymer, 1899: *Episcada polita flava* **n. stat.**

Key words: Amazon, Andes, clearwing butterflies, cloudforest, Colombia, DNA barcode, Ecuador, morphology, Neotropical region, Peru, rainforest, Solanaceae, systematics, taxonomy.

Resumen: Las mariposas Neotropicales de la tribu Ithomiini ofrecen algunos de los ejemplos más extraordinarios del mimetismo Mülleriano en la naturaleza, y las casi 400 especies de esta tribu exhiben una muy notable variación geográfica en los patrones de coloración de sus alas. Aquí, describimos los siguientes nuevos taxones de Ithomiini del Ecuador y los países vecinos: *Scada reckia ruiza* Lamas & Willmott, **n. ssp.**, *Methona grandior batesi* Lamas & Willmott, **n. ssp.**, *Elzunia bomplandii golondrina* Willmott, Lamas & Hall, **n. ssp.**, *Ithomia agnosia zumba* Lamas & Willmott, **n. ssp.**, *Ithomia arduinna ardua* Lamas, Vitale & Boyer, **n.**

ssp., *Ithomia hymettia petitia* Lamas & Willmott, **n. ssp.**, *Ithomia iphianassa occidentissa* Lamas & Willmott, **n. ssp.**, *Hyalyris antea lalimba* Lamas & Willmott, **n. ssp.**, *Hyalyris praxilla leuca* Willmott & Lamas, **n. ssp.**, *Hyalyris praxilla abscondita* Lamas, Radford & Willmott, **n. ssp.**, *Hyalyris oca equatoria* Willmott & Lamas, **n. ssp.**, *Hyalyris oca aurea* Lamas & Willmott, **n. ssp.**, *Hypothyris cantobrica zamorita* Willmott, Boyer & Vitale, **n. ssp.**, *Napeogenes glycera mirador* Lamas, Willmott & Radford, **n. ssp.**, *Hyposcada illinissa morona* Lamas & Willmott, **n. ssp.**, *Hyposcada kena unki* Lamas, Willmott & Boyer, **n. ssp.**, *Hyposcada taliata laetititia* Lamas & Willmott, **n. ssp.**, *Ollantaya olerioides baeza* Willmott & Lamas, **n. ssp.**, *Oleria tremona benigna* Lamas & Willmott, **n. ssp.**, *Oleria radina bonita* Willmott & Lamas, **n. ssp.**, *Oleria tigilla raya* Lamas & Willmott, **n. ssp.**, *Oleria onega astigara* Willmott & Lamas, **n. ssp.**, *Episcada clausina bomboiza* Willmott & Lamas, **n. ssp.**, *Episcada hymenaea mirifica* Lamas & Willmott, **n. ssp.**, *Episcada polita pichincha* Willmott & Lamas, **n. ssp.**, *Episcada arcadia* Lamas & Willmott, **n. sp.**, *Episcada arcadia navarro* Lamas & Willmott, **n. ssp.**, *Pteronymia alida luctuosa* Willmott & Lamas, **n. ssp.**, *Pteronymia alida cosanga* Willmott & Lamas, **n. ssp.**, *Pteronymia alida francisca* Willmott & Lamas, **n. ssp.**, *Pteronymia inania bethana* Willmott & Lamas, **n. ssp.**, *Pteronymia hara olerina* Willmott & Lamas, **n. ssp.**, *Pteronymia sao loreto* Lamas & Willmott, **n. ssp.**, *Brevioleria arzialia loronia* Lamas & Willmott, **n. ssp.**, *Hypoleria alema pastaza* Willmott & Lamas, **n. ssp.**, *Hypomenitis hermana serafina* Willmott & Lamas, **n. ssp.**, *Hypomenitis hermana chamba* Willmott & Lamas, **n. ssp.**, *Hypomenitis oneidodes guarumales* Boyer, Petit & Willmott, **n. ssp.**, *Hypomenitis oneidodes nicolasi* Willmott & Lamas, **n. ssp.** Estos nuevos taxones han permanecido sin descripción científica hasta ahora por varios motivos, incluyendo la aplicación incorrecta de nombres existentes, la confusión con taxones descritos debida al mimetismo Müllleriano y el descubrimiento de nuevos taxones a través del trabajo de campo. Se describe una nueva especie basada en diferencias inusualmente marcadas en los genitales de ambos sexos en comparación con las especies congénéricas, descubiertas durante el curso de este estudio. Para las descripciones de nuevas subespecies, utilizamos datos morfológicos, moleculares, de distribución y ecológicos para sostener nuestras hipótesis taxonómicas, con ilustraciones de ambos sexos y los genitales de los machos para la mayoría de los nuevos taxones, proporcionando 91 nuevos códigos de barra de ADN e incluyendo notas sobre la biología y distribución, con mapas que muestran la distribución de taxones similares y vecinos. No obstante, serán necesarias revisiones futuras en varios casos, cuando los datos moleculares estén disponibles para más taxones. También, designamos un lectotipo para *Ithomia agarista* C. Felder & R. Felder, 1862, sinonimizamos *Hypoleria chrysodonia elegans* Winhard, 2021 e *Hypoleria chrysodonia pallida* Winhard, 2021 con *Ithomia orolina* var. *chrysodonia* Bates, 1862 (**n. syn.**), y tratamos *Episcada clausina flava* Winhard, 2021 como una subespecie de *Episcada polita* Weymer, 1899: *Episcada polita flava* **n. stat.**

Palabras clave: Amazon, Andes, bosque nublado, bosque tropical, código de barra ADN, Colombia, Ecuador, mariposas de alas transparentes, morfología, Perú, región Neotropical, Solanaceae, sistemática, taxonomía.

INTRODUCTION

The Neotropical butterfly tribe Ithomiini displays some of the most outstanding examples of intraspecific diversity in wing color patterns. This variation can be local (e.g., Hill *et al.*, 2012) as well as geographic (e.g., Brown, 1977a, 1979, 1980). Since all adult ithomiines are believed to be unpalatable (Brown, 1984; Chai & Srygley, 1990; McClure *et al.*, 2019) and involved in Müllerian mimicry (Beccaloni, 1997; Chazot *et al.*, 2014a), the few known hybrid zones between subspecies are typically narrow; the sharp, congruent shifts in color patterns across co-mimetic species from one region of the Amazon to the next were compared by Henry Walter Bates to “the touch of an enchanter’s wand” (H. W. Bates, quoted in Müller (1879: xxix)). As in better known mimetic butterflies such as *Heliconius* Kluk, 1780 (Nymphalidae, Heliconiinae), narrow hybrid zones are regarded as an outcome of strong purifying natural selection against unfamiliar hybrid phenotypes (Mallet & Barton, 1989). The phenotypic stability and discrete distributions of many ithomiine subspecies inspired their choice as one of several model groups of butterflies to identify areas of endemism, potentially marking the locations of putative Pleistocene rainforest refugia suggested to have been involved in the evolution of the Neotropical lowland biota (Brown, 1977a, 1979, 1982, 1987; but see Dasmahapatra *et al.*, 2010). Studies of ithomiine communities have also shown that the

benefits of Müllerian mimicry in sharing the cost of educating naïve predators (Müller, 1879; Sherratt, 2008) have led to convergence in color pattern, microhabitat and elevational range (Elias *et al.*, 2008; Chazot *et al.*, 2014a). Finally, because mimicry provides a clear means to quantify species interactions within communities, ithomiines have also been used as models for research on spatial variation in indices of taxonomic, evolutionary and ecological diversity (Chazot *et al.*, 2016b; Doré *et al.*, submitted). As such, an improved understanding of ithomiine geographic color pattern variation has potential implications for research into speciation, community ecology, macroecology, biogeography and conservation.

The marked geographic shifts in color pattern within ithomiine species mentioned above resulted in many taxa that are now regarded as subspecies being treated as distinct species by early taxonomists. Revisions to Ithomiini species-level taxonomy by Fox (1940, 1956, 1960, 1967), Fox & Real (1971), Brown (1977b, 1980) and Lamas (1979, 1980, 1986, 2004) greatly improved our understanding of relationships among ithomiine taxa and spatial patterns of taxonomic diversity. Nevertheless, the species or subspecies status of many allopatric ithomiine taxa, both described and undescribed, could benefit from more detailed ecological and molecular study. Bates (1862: 500) recognized the difficulties in classifying allopatric ithomiine taxa more than 150 years ago, stating that “many of these local [Amazonian ithomiine] species have the

appearance of being geographical varieties; I could not help suspecting them to be such when I met with them in nature, the differences between the forms of one and those of another locality relating in many cases simply to the colours and colour-patterns of the wings. The marks of distinction, however, are in the majority so well defined, so ordinarily common to all the individuals concerned, and there is so generally an absence of connecting links, that they are held on all hands to be good and true species.”

There is thus still significant work to do in clarifying the species-level taxonomy of the Ithomiini. The tribe now contains nearly 400 species and nearly 1950 subspecies, with a significant number of the latter still undescribed (Lamas, 2004; Lamas & Willmott, unpublished data). The majority of undescribed taxa are in the most diverse subtribes, namely the Napeogenina, Oleriina, Dircennina, and Godyridina, which have been the focus of recent research by Lamas and Willmott (e.g., Willmott & Lamas, 2006, 2007, 2008), with taxonomic revisions in progress for *Hyalyris* Boisduval, 1870, *Hyposcada* Bates, 1862, *Oleria* Hübner, 1816, *Episcada* Godman & Salvin, 1879, *Pteronymia* Butler & Druce, 1872, *Velamysta* Haensch, 1909, *Veladyris* Fox, 1945, and *Hypomenitis* Fox, 1945. Although revisions are the ideal solution for descriptions of new taxa, Willmott *et al.* (2020) argued that there was a more immediate need for names for currently undescribed ithomiines that feature regularly in broader phylogenetic, ecological and evolutionary research (e.g., Willmott & Mallet, 2004; Mallarino *et al.*, 2005; Jiggins *et al.*, 2006; Willmott & Freitas, 2006; Brehm *et al.*, 2007; Elias *et al.*, 2007, 2008; De-Silva *et al.*, 2010, 2015, 2017; Willmott *et al.*, 2011, 2017; Chazot *et al.*, 2014a,b, 2016a,b, 2017, 2018, 2019), as well as in sequence records in GenBank and in numerous other webpages. Furthermore, as a result of long-term research by the authors in Ecuador and Peru, a considerable amount of distributional, ecological, morphological and molecular data are now available to enable confident taxonomic decisions to be made in most cases. Publication of such data should facilitate studies of related taxa and hopefully result in new data becoming available, which will ultimately result in more robust taxonomic revisions. Willmott *et al.* (2020) thus described 12 new species and three subspecies from Ecuador and adjacent countries, and here we continue this study by focusing at the subspecies level.

MATERIALS AND METHODS

The authors and colleagues have been conducting field work throughout Ecuador and Peru for many years to collect butterfly material for taxonomic study and document distribution and behavior. Field methods are described in more detail in Willmott *et al.* (2020), but, briefly, involved collection of adults using long-handled nets as well as single rope techniques, with intensive sampling of ithomiine leks and Asteraceae flowers that are sources of pyrrolizidine alkaloids; and several field trips concentrated on rearing immature stages.

More than 107,000 ithomiine specimens, in more than 50 public and private collections in the Americas and Europe, were studied to locate types, study variation and record distribution data. The following collection acronyms are used (for institutions

we use the acronym preferred by its own researchers, and for private collections we use a consistent acronym formed from the first two letters of the given name and surname of the collection curator): **AMNH**: American Museum of Natural History, New York, NY, USA; **ANNE**: Andrew Neild collection, St Albans, UK; **BMB**: Booth Museum of Natural History, Brighton, UK; **BME**: Bohart Museum of Entomology, University of California, Davis, CA, USA; **CAS**: California Academy of Sciences, San Francisco, CA, USA; **DATR**: David Trembath collection, Surrey, UK; **DZUP**: Coleção Entomológica Padre Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil; **EUIEB**: Edinburgh University Institute of Evolutionary Biology, Edinburgh, UK; **FAVI**: Fabio Vitale Collection, now part of ZSM, Munich, Germany; **FLMNH**: McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Gainesville, FL, USA; **FRPI**: Francisco Piñas collection, Quito, Ecuador; **GETE**: Gerrit ten Broek collection, Amsterdam, Netherlands; **HAWA**: Haydon Warren-Gash collection, Pressac, France; **HERENCIA**: Corporación Herencia Natural y Cultural collection, Florencia, Colombia; **IAVH**: Instituto Alexander von Humboldt, Villa de Leyva, Colombia; **INABIO**: Instituto Nacional de Biodiversidad, Quito, Ecuador; **JARA**: James Radford collection, Cambridge, UK; **JELE**: Jean F. Le Crom collection, Bogotá, Colombia; **JEPE**: Jean-Claude Petit collection, Ducy, France; **MNHN**: Muséum national d’Histoire Naturelle, Paris, France; **MfN**: Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt Universität, Berlin, Germany; **MNRJ**: Museu Nacional, Rio de Janeiro, Brazil (collection destroyed by fire in 2018); **MUSM**: Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; **MZSP**: Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; **MZUJ**: Muzeum Zoologiczne Uniwersytetu Jagiellońskiego, Kraków, Poland; **NHMUK**: Natural History Museum, London, UK; **OLMI**: Olaf H. H. Mielke collection, Curitiba, Brazil; **OUM**: Oxford University Museum, Oxford, UK; **PIBO**: Pierre Boyer collection, Le Puy, France; **PUCE**: Museo de Entomología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador; **RYHI**: Ryan Hill collection, University of the Pacific, CA, USA; **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; **ZSM**: Zoologische Staatssammlung München, Munich, Germany. Specimen label data are presented in the following format: **Country**: *State/Province/Department*: locality, [latitude, longitude], elevation, (collector), date of collection, number of specimens and sex, [specimen voucher number and notes], (collection). Localities from labels without latitude and longitude data were georeferenced in Google Earth, using a variety of methods to place them, including gazetteers, notes on the itineraries of collectors, published entomological collection gazetteers (e.g., Brown, 1941; Brown, 1979) and recent publications. Locality maps were prepared in ArcMap 10.6.1 using GIS data layers freely available via the internet.

As described in Willmott *et al.* (2020), during ongoing

research on the phylogenetics and systematics of Ithomiini we dissected males and females, where available, for all species in the genera under revision as listed above, the great majority of species in other genera not revised by Fox (1940, 1956, 1960, 1967) and Fox & Real (1971), and representatives from revised genera, representing approximately 300 ithomiine species. Morphological study methods were as described by Willmott *et al.* (2020). The terminology for genitalic and abdominal structures follows Scoble (1992), and nomenclature for venation follows Comstock & Needham (1898). We illustrate the male genitalia for all new taxa where it was readily possible to make dissections, and the wing venation, androconia, and female genitalia of the new species *Episcada arcadia* **n. sp.** We refer to the hair-like scales at the dorsal costal edge of the hindwing as androconial scales, following Schulz *et al.* (1988) and subsequent authors, since they have all the characteristics of typical androconial scales, despite also being present in females of a couple of species of *Methona* Doubleday, [1847]. Illustrated aspects of the abdomen and genitalia in this paper vary among genera depending on characters that are most informative for diagnosing species in each case. We use the abbreviations DFW, VFW, DHW and VHW for dorsal and ventral forewing and hindwing, and (W&H) for (Willmott & Hall, unpublished data). Descriptions include FW length of the holotype, as well as other specimens where available.

To help inform taxonomic decisions, we attempted to sequence the DNA ‘barcode’ region (Hebert *et al.*, 2003) for as many Ecuadorian ithomiine taxa as possible, in addition to related taxa from throughout the Neotropics (Chazot *et al.*, 2019). DNA extraction, PCR techniques and sequencing were as described by Willmott *et al.* (2020). Where necessary, fragments were assembled into composite sequences and all new sequences were combined with sequences of relevant taxa available from GenBank and aligned using BioEdit v. 7.1.3 (Hall, 1999). The initial resulting matrix contained 2712 sequences, from which we selected a set of 575 exemplar sequences relevant to the new taxa described here, representing 186 species and 290 taxa, including 91 new sequences representing 40 species and 57 taxa (Appendix 1). The final aligned sequences were of length 633 bp. To examine relationships among taxa we split the matrix into 8 smaller matrices containing a single genus or several related genera, and conducted a neighbor-joining (NJ) analysis using MEGA 7.0.18 (Kumar *et al.*, 2016), with the Kimura 2-parameter substitution model, partial deletion of sites with missing data, and other default settings. Because NJ analyses of DNA barcode data recover topologically similar trees (at least for well-supported nodes within species groups) to those generated using other approaches, such as Bayesian analyses (e.g., Benmesbah *et al.*, 2018; Willmott *et al.*, 2020), we did not consider it necessary to perform other kinds of analyses. New sequences are deposited in GenBank (Appendix 1).

We considered data from morphology, DNA sequences, distribution and ecology to support our taxonomic hypotheses. Descriptions of new subspecies should justify why the taxon is associated with the nominate subspecies and how it differs from conspecific taxa. Ideally, there should exist morphological characters, and/or evidence from molecular data, and ecological information (e.g., habitat, elevational range) that support a

close relationship with the nominate subspecies, or at least other named taxa with which it is regarded as conspecific. Furthermore, the new subspecies should be diagnosable by one or more characters that are consistently present over a defined geographic region. Following Willmott (2003) and Braby *et al.* (2012), such characters should be those that vary within species but not between closely related sympatric species; in the Ithomiini, characters suggestive of subspecies status typically include the color patterns of the wings and body, while variation in characters such as wing shape and venation, androconial scales and genitalic morphology support species status. In a few cases we describe subspecies that are known from only one locality or a small area, where there is reason to regard the population as geographically isolated from neighboring populations, and thus we can infer that it likely has a discrete range (e.g., *Napeogenes glycera mirador* **n. ssp.**). In other cases, the new subspecies may show a mimetic wing pattern observed in more common co-mimics that are known to occur within a specific region, and it is thus reasonable to assume likewise for the new taxon (e.g., *Hypomenitis oneidodes guarumales* **n. ssp.**). Finally, some new subspecies occur outside the known range of named subspecies and we regarded their wing color patterns as sufficiently distinct, in comparison with longer series of conspecifics that showed little variation, to merit description (e.g., *Elzunia bomplandii golondrina* **n. ssp.**, *Hyaliris oca aurea* **n. ssp.**, *Hypomenitis hermana chamba* **n. ssp.**). In a number of cases there will likely need to be future revision of the species level classification, and hopefully additional faunistic studies such as this will provide the new data needed for the many still poorly documented ithomiine taxa. The generic classification follows Chazot *et al.* (2019), which contains the most taxonomically comprehensive phylogeny for Ithomiini to date. Although some changes to the generic classification will be needed, we have decided not to adopt yet the recent generic changes proposed by Zhang *et al.* (2021), pending a more exhaustive evaluation of alternative taxonomic solutions.

RESULTS AND DISCUSSION

Scada reckia ruiza Lamas & Willmott, **new subspecies**

Figs. 1A,B, 10A-C, 31A

Scada reckia n. ssp.: Lamas (2004: 175, no. 60j)

Diagnosis and identification: This subspecies is distinguished from all other *S. reckia* (Hübner, 1808) subspecies by the increased translucency of the black FW postdiscal band and less intense yellow markings. The FW postdiscal yellow patch fades distally without a clear edge, in contrast to other *S. reckia* subspecies. The geographically closest taxon is *S. reckia ethica* (Hewitson, [1861]) (Fig. 1C), which occurs from SE Ecuador to NE Peru in wet forest, and which also has more prominent white dorsal marginal spots, especially in the DHW, and a translucent black line on the HW along the discocellular veins and veins Cu₁ and M₃. In fact, *S. reckia ruiza* **n. ssp.** most closely resembles the sympatric *Scada kusa* (Hewitson, 1872), which differs most obviously by the more opaque black FW postdiscal band, the black translucent to opaque scales at the base of cell Cu₂-Cu₁, and the more prominent white DFW marginal spots.

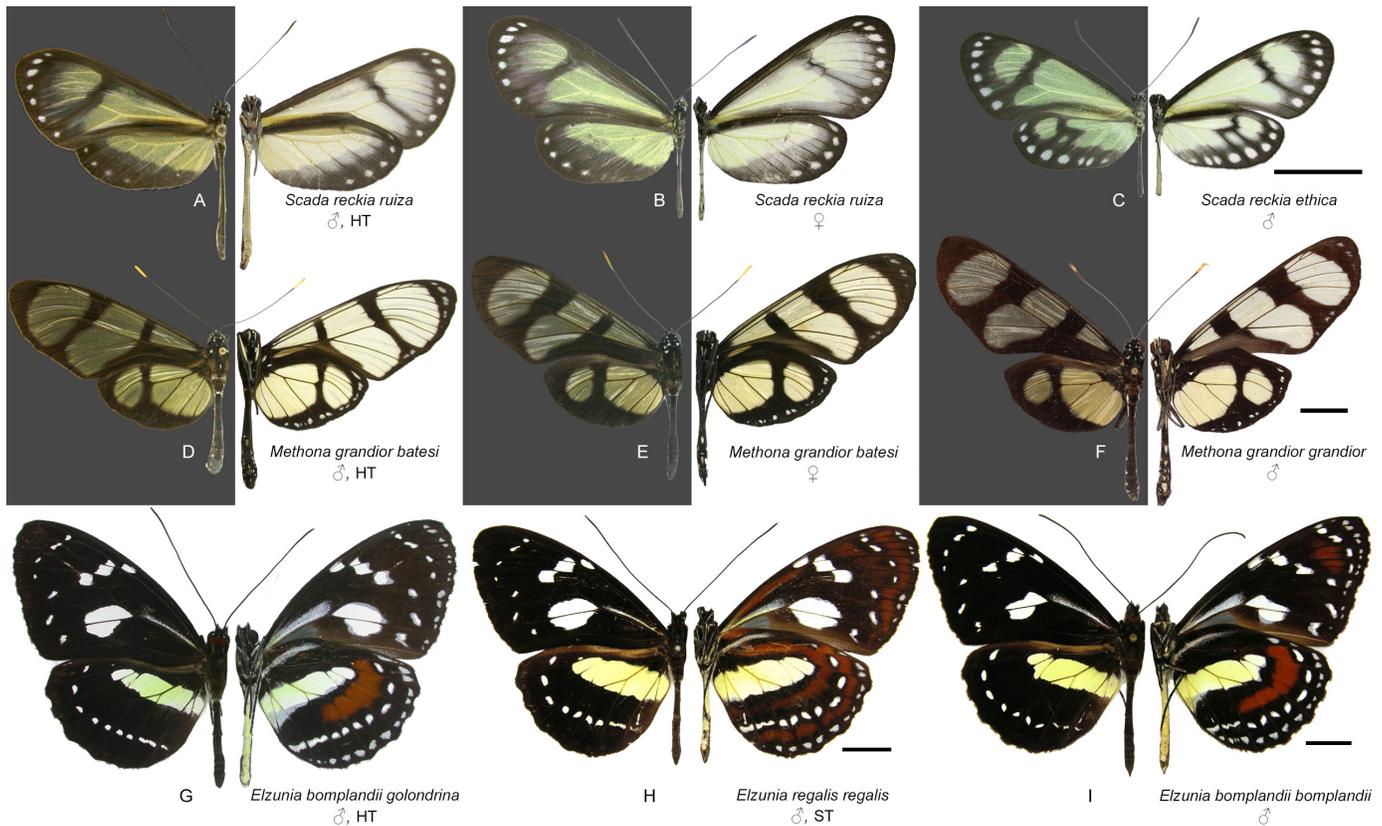


Fig. 1. Adults of new and similar *Scada*, *Methona* and *Elzunia* taxa, all from Ecuador unless otherwise stated. See text for wing lengths of new taxa, other scale bars are 1 cm. **A.** *Scada reckia ruiza* n. ssp., holotype ♂, Peru, Amazonas, 20 km N Pedro Ruiz (MUSM). **B.** *Scada reckia ruiza* n. ssp., ♀, Zamora-Chinchipe, km 22 Zumba-Loja rd. (FLMNH). **C.** *Scada reckia ethica*, ♂, Morona-Santiago, Río Shangaimé (FLMNH). **D.** *Methona grandior batesi* n. ssp., holotype ♂, Peru, Madre de Dios, Pakitza (MUSM). **E.** *Methona grandior batesi* n. ssp., ♀, Orellana, Yuturi, Río Manduro trail (FLMNH). **F.** *Methona grandior grandior*, ♂, French Guiana, East Berbice-Corentyne, Jaguar Camp (FLMNH). **G.** *Elzunia bomplandii golondrina* n. ssp., holotype ♂, Carchi, Santa Rosa (FLMNH; LEP-00102). **H.** *Elzunia regalis regalis*, ♂, Colombia, “Bogotá” (NHMUK, syntype of *Tithorea regalis* Stichel). **I.** *Elzunia bomplandii bomplandii*, ♂, Colombia, Boyacá, Minas de Muzo (NHMUK).

Description: MALE (Fig. 1A, 10A-C): Forewing length 24 mm (mean 22.7 mm, n=4). *Wings:* as illustrated (Figs. 1A), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes bare; antennae black, except for white scales ventrally near base; labial palpi black laterally, white ventrally; top of head black with central white stripe, frons white, with central black stripe. *Thorax:* dorsal surface brown with pale yellow forming a central stripe, and along sides and posterior edge, ventral surface yellowish white, with dark brown where legs fold; forelegs, mid- and hindlegs brown with white laterally. *Abdomen:* dorsal surface brown, ventral surface yellowish white. *Genitalia* (Fig. 10A-C): notable features include lobed upper valva posterior projection (Fig. 10A), broadly flaring uncus in dorsal view (Fig. 10B), and relatively short inner valva projection not extending past edge of valva (Fig. 10C).

FEMALE: (Fig. 1B): Forewing length 25 mm (n=1). *Wings:* as illustrated (Fig. 1B), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: PERU: Amazonas: 20 km N Pedro Ruiz [Gallo], [5°54'S, 77°58'W], 1200 m, (Lamas, G.), 15 Dec 1975, (MUSM).

PARATYPES (24♂, 11♀): **Ecuador:** Zamora-Chinchipe: E of Zumba, km 2.6 El Pite-Río Mayo rd., [4°51'58"S, 79°54'0"W], 1000 m, (Willmott, K. R., J. C. R., J. I. R.), 25 Jun 2014, 1♂, (INABIO), 26 Jun 2014, 1♀ [FLMNH-MGCL-280506], (FLMNH); km 18 Zumba-Los Sungas rd., Quebrada Huanchunangui, [4°55'11"S, 79°9'54"W], 1100 m, (Willmott, K. R.), 11 Oct 2010, 1♂ [FLMNH-MGCL-146754], 1♂ [FLMNH-MGCL-146769], 1♂ [FLMNH-MGCL-146787], 1♀ [FLMNH-MGCL-146781], (FLMNH), 2♂, 1♀ (INABIO), (Willmott, K. R., J. C. R., J. I. R.), 23 Jun 2013, 1♂ [FLMNH-MGCL-157885], (FLMNH); km 2 Zumba-San Andrés rd., [4°51'18"S, 79°8'48"W], 1400 m, (Willmott, K. R., J. C. R., J. I. R.), 23 Jun 2014, 1♂ [FLMNH-MGCL-280507],

(FLMNH); km 22 Zumba-Loja rd., [4°46'10"S, 79°76'W], 1100 m, (Willmott, K. R., Hall, J. P. W.), 21-23 Jul 1993, 1♂, 1♀ [Genitalic dissection SCADA-7], (FLMNH); km 22 Zumba-Loja rd., [4°46'10"S, 79°76'W], 1140 m, (Willmott, K. R.), 10 Oct 2010, 1♂ [FLMNH-MGCL-146673], (FLMNH), 1♂, (INABIO); km 4.3 San Andrés-Jimbura rd., [4°47'59"S, 79°18'18"W], 2020 m, (Willmott, K. R.), 13 Oct 2010, 1♂ [FLMNH-MGCL-146743], (FLMNH); Río Numbala, 850 m, (Abbé Gaujon), Aug 1885, 1♀, (NHMUK); Río Palanda, km 35 Zumba-Loja rd., [4°37'53"S, 79°8'16"W], 1100 m, (Willmott, K. R., Hall, J. P. W.), 20 Jul 1993, 1♂ [Genitalic dissection SCADA-6], (FLMNH), 27 Sep 1997, 1♂, (FLMNH); Zumba-Loja rd., Palanda, [4°40'S, 79°8'W], 1100 m, (Beccaloni, G. W.), 1 Sep 1992, 1♂, (NHMUK). **Peru:** Amazonas: same data as HT, 3♂, 1♀, (MUSM); Pedro Ruiz [Gallo], [5°57'S, 77°59'W], 1000 m, (Lamas, G.), 16 Dec 1975, 1♂, (MUSM); Buenos Aires, opp. Bagua Grande, [5°41'S, 78°24'W], 1300 m, (Hocking, P.), 3 Sep 1975, 1♀, (MUSM); 18 Sep 1979, 1♀, (MUSM); 0-5 km E La Peca, [5°37'S, 78°26'W], 1100-1400 m, (Lamas, G.), 23 Sep 1999, 1♂, (MUSM); Bagua Grande, Cumba, [5°56'S, 78°40'W], 500 m, (Pintado, J.), 2012, 2♂, 1♀, (MUSM); **Cajamarca:** Río Chinchipe, [5°31'S, 78°33'W], 1800 m, (Pratt, A. & E.), Sep 1912, 1♀ [PT *zeroca*], (NHMUK); Cochalán, W of Tamborapa, [5°28'S, 78°59'W], 600m, (Lamas, G.), 17 Mar 1985, 2♂, 1♀, (MUSM).

Other records: Ecuador: Zamora-Chinchipe: km 2.5 Zumba-San Andrés rd., [4°51'18"S, 79°3'47"W], 1370 m, (Willmott, K. R.), 12 Oct 2010, (W&H).

Etymology: The name is derived from the type locality and is treated as a feminine noun in apposition.

Taxonomy and variation: This taxon is treated as a subspecies of *S. reckia* since both genitalic characters and DNA sequence data (Fig. 19) support a close relationship between it and other taxa currently treated as subspecies of that species (Lamas,



Fig. 2. Adults of new and similar *Ithomia* taxa, all from Ecuador unless otherwise stated. See text for wing lengths of new taxa, other scale bars are 1 cm. **A.** *Ithomia agnosia zumba* n. ssp., holotype ♂, Peru, Amazonas, Pedro Ruiz (MUSM). **B.** *Ithomia agnosia zumba* n. ssp., ♀, Zamora-Chinchi, km 35 Zumba-Loja rd. (FLMNH). **C.** *Ithomia agnosia agnosia*, ♂, Zamora-Chinchi, Quebrada Chorillos (FLMNH). **D.** *Ithomia arduinna ardua* n. ssp., holotype ♂, Morona-Santiago, Cunza (FLMNH). **E.** *Ithomia arduinna ardua* n. ssp., ♀, Morona-Santiago, environs of Méndez (FLMNH). **F.** *Ithomia arduinna arduinna*, ♂, Peru, Madre de Dios, Pakitza (USNM). **G.** *Ithomia hymettia petitia* n. ssp., ♂, Colombia, Valle del Cauca, Buga (PIBO). **H.** *Ithomia hymettia petitia* n. ssp., holotype ♀, Imbabura, above Getsemani (JEPE). **I.** *Ithomia hymettia hymettia*, ♂, Colombia (MNHN). **J.** *Ithomia iphianassa occidentissa* n. ssp., holotype ♂, Pichincha, Centinela ridge (FLMNH). **K.** *Ithomia iphianassa occidentissa* n. ssp., ♀, Pichincha, old Quito-Sto. Domingo rd., Río Pilatón (FLMNH). **L.** *Ithomia iphianassa ethilla*, ♂, Esmeraldas, km 10 San Lorenzo-Lita rd., Estación Experimental 'La Chiquita' (FLMNH).

2004). Fox (1967) identified three species groups in *Scada* Kirby, 1871 based on genitalic characters, and the flaring uncus in dorsal view and lack of a pointed dorsal posterior process on the valva place *S. reckia ruiza* n. ssp. in the 'ethica-group', in which Fox (1967) placed *S. reckia*, among other taxa. Lamas (2004) substantially revised Fox's (1967) classification, reducing the 15 species recognized by the latter author to 5, and treating all of the species in Fox's 'ethica-group', and some from his 'zemira-group', as subspecies of *S. reckia*. Barcode data (Fig. 19) placed *S. reckia ruiza* in a clade containing most of the central and west Amazonian subspecies of *S. reckia* (*sensu* Lamas, 2004), including its geographical neighbor *S. reckia ethica* (Fig. 1C). However, *S. r. reckia* from eastern Brazil formed a clade with *S. kusa*, *S. zemira* (Hewitson, 1856) and *S. reckia ortygia* (Druce, 1876), and the relationships

between this clade, the Amazonian *S. reckia* clade containing *S. reckia ruiza*, and *Scada zibia* (Hewitson, 1856), were not strongly resolved. Thus, future work might show that *S. reckia* as currently conceived is better treated as several species and that the taxonomy needs revision (see also Freitas *et al.*, 2020).

Distribution and natural history: This new subspecies occurs in the upper valley of the Río Marañón and its tributaries in extreme northeastern Peru and adjacent southeastern Ecuador (Fig. 31A), being replaced in wetter forest to the east by *S. reckia ethica*. Both sexes of *S. reckia ruiza* n. ssp. can be found flying from 0.5-2 m above the ground in the shady understorey of dry forest remnants in stream valleys, and in secondary growth along forest edges, from 1000-2020 m. The new subspecies flies with and is presumably co-mimetic of the dry forest endemic species *Scada kusa*.



Fig. 3. Adults of new and similar *Hyalyris* taxa, all from Ecuador unless otherwise stated. See text for wing lengths of new taxa, other scale bars are 1 cm. **A.** *Hyalyris antea lalimba* n. ssp., holotype ♂, Peru, Amazonas, Pedro Ruiz (MUSM). **B.** *Hyalyris antea lalimba* n. ssp., ♀, Peru, Amazonas, Chachapoyas (NHMUK). **C.** *Hyalyris latilimbata*, ♂, Loja, Tambo Negro (FLMNH). **D.** *Hyalyris praxilla leuca* n. ssp., holotype ♂, Zamora-Chinchi, Río Palanda, km 35 Zumba-Loja rd. (FLMNH). **E.** *Hyalyris praxilla leuca* n. ssp., ♀, Zamora-Chinchi, Quebrada Limones (FLMNH). **F.** *Hyalyris mestra mestra*, ♀, Zamora-Chinchi, Quebrada de Chorillos (FLMNH). **G.** *Hyalyris praxilla abscondita* n. ssp., holotype ♂, Peru, Amazonas, PV3 (Alfonso Ugarte) (MUSM). **H.** *Hyalyris praxilla abscondita* n. ssp., ♀, Peru, Amazonas, PV3 (Alfonso Ugarte) (MUSM). **I.** *Hyalyris praxilla praxilla*, ♂, Morona-Santiago, km. 9.5 Chigüinda-Gualaquiza rd., river (FLMNH-MGCL-113480). **J.** *Hyalyris ocna equatoria* n. ssp., holotype ♂, Pastaza, Shell (FLMNH). **K.** *Hyalyris ocna equatoria* n. ssp., ♀, Sucumbíos, Río Palmar, trail above S. bank (FLMNH). **L.** *Hyalyris ocna ocna*, ♂, Colombia, Tolima, Río Chili (NHMUK). **M.** *Hyalyris ocna aurea* n. ssp., holotype ♂, Peru, Amazonas, PV3 (Alfonso Ugarte) (MUSM). **N.** *Hyalyris ocna aurea* n. ssp., ♀, Zamora-Chinchi, Chinapintza (FLMNH). **O.** *Hyalyris antea amarilla*, ♀, Zamora-Chinchi, Quebrada de Chorillos (FLMNH).

Methona grandior batesi Lamas & Willmott, new subspecies
Figs. 1D,E, 10D-H, 31B

Methona grandior grandior: Forbes (1944) (in part)
Methona grandior n. ssp.: Lamas (2004: 175, no. 52c)
Methona grandior ssp.: Elias et al. (2007: supplementary information)
Methona grandior: Elias et al. (2008: S1); Chazot et al. (2014b)

Diagnosis and identification: This new subspecies is distinguished from the nominate subspecies (Fig. 1F), from the central Amazon to Guianas, by the even black HW postdiscal cell band that is not narrower in the middle, and on the FW by the reduced black markings. Most notably these reduced markings include the apical black area, the anterior portion of the black

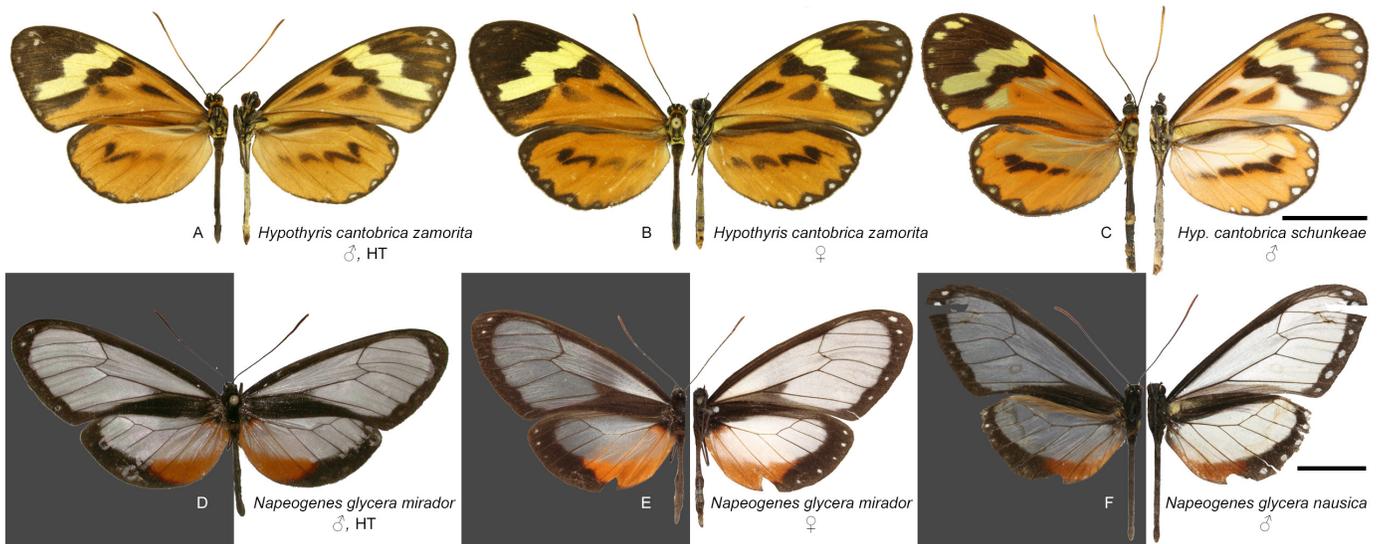


Fig. 4. Adults of new and similar *Hypothyris* and *Napeogenes* taxa, all from Ecuador unless otherwise stated. See text for wing lengths of new taxa, other scale bars are 1 cm. **A.** *Hypothyris cantobrica zamorita* n. ssp., holotype ♂, Morona-Santiago, Cunza (FLMNH). **B.** *Hypothyris cantobrica zamorita* n. ssp., ♀, Morona-Santiago, Cunza (FLMNH). **C.** *Hypothyris cantobrica schunkeae*, ♂, Peru, Huánuco, Tingo María (FLMNH). **D.** *Napeogenes glycera mirador* n. ssp., holotype ♂, Peru, Amazonas, Alfonso Ugarte (MUSM). **E.** *Napeogenes glycera mirador* n. ssp., ♀, Morona-Santiago, Cónдор Mirador (FLMNH). **F.** *Napeogenes glycera nausica*, ♂, Morona-Santiago, km 25 Macas-Nueve de Octubre rd. (PIBO).

postdiscal band distal of the discal cell, and the black bar in the discal cell. *Methona grandior incana* (Forbes, 1944) in the adjacent east Andean foothills has even broader black markings than the nominate subspecies, and the HW translucent areas whitish rather than yellowish. *Methona grandior batesi* n. ssp. is sympatric with the very similar taxa *M. curvifascia* Weymer, 1883 and *M. confusa* Butler, 1873, and can be distinguished as follows. On the VHW, males of *M. grandior batesi* differ from those of *M. confusa* by having a shorter yellow-brown bar at the base of the costa, and an entirely black cell M_1 -Rs that lacks pale yellow translucent scales. *Methona curvifascia* males have two thin, parallel white lines in the black costal area anterior of the discal cell and the terminal abdominal tergites end in two posteriorly directed points, resembling ‘claws’ in lateral view. Females of *M. grandior batesi* differ from those of *M. curvifascia* in having elongate, hair-like scales at the DHW costa, and from *M. confusa* by the black rather than pale translucent yellow VHW cell M_1 -Rs.

Description: MALE (Fig. 1D, 10D-H): Forewing length 53 mm (mean 49 mm, n=2). *Wings:* as illustrated (Fig. 1D), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes bare; antennae dark brown with yellow club; labial palpi white with black latero-ventral edge; top of head black with four white spots, frons black. *Thorax:* dorsal surface dark brown with two central white dashes, ventral surface black with six white spots, forelegs brown with prominent white tarsus, mid- and hindlegs dark brown except ventral femur yellowish white. *Abdomen:* dorsal surface dark brown laterally with yellowish white stripe in anterior half, terminal five segments with white central spot, ventral surface dark brown with central white spots on terminal segments. *Genitalia* (Fig. 10D-H): notable features include terminal tergite extended into broad lateral lobes (Fig. 10D,E).

FEMALE: (Fig. 1E): Forewing mean length 45 mm (n=2). *Wings:* as illustrated (Fig. 1E), DHW with hair-like androconial scales, as in male, but scales distal of discal cell underlying hair-like androconial scales similar to those in surrounding cells, not differentiated as denser, darker androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: PERU: Madre de Dios: Parque Manu, Pakitza,

[11°53'S,70°58'W], 400 m, (Lamas, G.), 17 Oct 1990, (MUSM).

PARATYPES (45♂, 39♀): **Brazil:** Acre: Rio Juruá, Porto Walter, 1♀ (MZSP). **Colombia:** Amazonas: [Rio] Amaca-yacú, [3°48'S,70°19'W], (Richter, L.), 1♂, (AMNH); [Rio] Loreto-yacú, [3°49'S,70°26'W], (Richter, L.), 1♂, (AMNH); **Ecuador:** Napo: Rio Napo, (Sarkady), 1879, 1♀, (MNHN); Archidona, [0°55'S,77°48'W], 1♀ (MfN); **Orellana:** Rio Tiputini, via Auca, Estación Científica Yasuní, [0°40'27"S,76°23'49"W], 220-250 m, (Willmott, K. R., Hall, J. P. W.), 16-18 Aug 1999, 1♂ [Genitalic dissection KW-15-209], (FLMNH); Laguna Añangu, Napo Wildlife Center, Napo trail, [0°30'35"S,76°26'13"W], 250 m, (Elias, M.), 13 Dec 2005, 1♂ [FLMNH-MGCL-ECD-52], (FLMNH); Rio Manduro, Rio Napo, Yarina, [0°28'14"S,76°50'W], 300 m, (Gallice, G.), 25 Sep 2010, 1♂ [YL1174], (FLMNH); Rio Napo, Boca del Rio Añangu, [0°31'43"S,76°23'41"W], 220-300 m, (Willmott, K. R.), 11 Dec 2005, 1♂ [FLMNH-MGCL-ECD-55], (FLMNH), 12 Nov 2005, 1♂ [FLMNH-MGCL-ECD-53], (INABIO); Rio Napo, Rio Yuturi, Rio Manduro trail, [0°33'29"S,76°2'39"W], 250 m, (Willmott, K. R.), 20 Nov 2003, 2♀, (FLMNH); Rio Napo, Sacha Lodge, [0°28'14"S,76°27'33"W], 240 m, (Gallice, G.), 10 Oct 2010, 1♀ [SL1461], (FLMNH); Rio Tiputini, Estación Científica Yasuní, camino torre, [0°40'46"S,76°24'W], 240 m, (Willmott, K. R., J. C. R., J. I. R.), 7 Jul 2014 [FLMNH-MGCL-195768], (FLMNH); Rio Tiputini, Tiputini Biodiversity Station, [0°42'12"S,76°0'30"W], 200-250 m, (Gallice, G.), 9 Dec 2010, 1♂ [TB3273], (INABIO); Rio Tiputini, via Auca, Estación Científica Yasuní, [0°40'27"S,76°23'49"W], 220-250 m, (Gallice, G.), 16 Nov 2010, 1♂ [YN2471], (FLMNH); **Pastaza:** Rio Pastaza, Kapawi village, [2°32'16"S,76°50'10"W], (Willmott, K. R., Hall, J. P. W.), 23 Jul 2009, 1♂ [FLMNH-MGCL-144785], (FLMNH). **Peru:** Amazonas: Huambo, [6°34'S,77°23'W], 1600 m, (Stolzmann, J.), 1880, 1♂, (NHMUK); lower Rio Nieva, [4°36'S,77°52'W], (Bassler, H.), 1♂ [PT *Thyridia grandior*], (CU); Rio Santiago, [4°24'S,77°38'W], (Bassler, H.), 1♂, [PT *Thyridia grandior*], (AMNH); **Cuzco:** Rio Urubamba, (Bassler, H.), 1♂, [PT *Thyridia grandior*], (AMNH); **Huánuco:** Rio Monzón, [9°19'S,76°00'W], 1000 m, (Schunke, J. M.), 28 May 1975, 1♂, (MUSM); **Junín:** Chanchamayo, [11°4'S,75°19'W], 1♂, (MUSM); **Loreto:** Pebas, [3°19'S,71°51'W], 120 m, (Mathan, M. de), 1880, 3♂, 1♀, (NHMUK), Nov 1906, 1♂, (NHMUK); Rio Cachiyacu, [5°50'S,76°33'W], 200 m, (Stuart), 1893, 1♀, (NHMUK); Rio Ucayali, [4°28'S,73°31'W], 1913, 1♂, (NHMUK); Rio Abujao, [8°28'S,74°11'W], (Bassler, H.), 1♀, (AMNH); Rio Cushabatay, [7°11'S,75°16'W], (Bassler, H.), 1♂, 1♀ [PTs *Thyridia grandior*], (AMNH); [Rio] Huallaga, (Vráz, E.), 1894, 1♂, (MfN); Castaña, [0°48.22'S,75°14.40'W], 150 m, (Lamas, G.), 29 Oct 1991, 1♀, (MUSM); Arcadia, [0°59.37'S,75°18.55'W], 150 m, (Lamas, G.), 4 Nov 1993 (Lamas, G.), 1♀, (MUSM); Yurimaguas, [5°54'S, 76°06'W], 180 m, (Büche, M.), Apr 1993, 1♂, (MUSM); Rio Marañón, José Olaya, [4°34'S,73°45'W], 120 m, (Büche, M.),

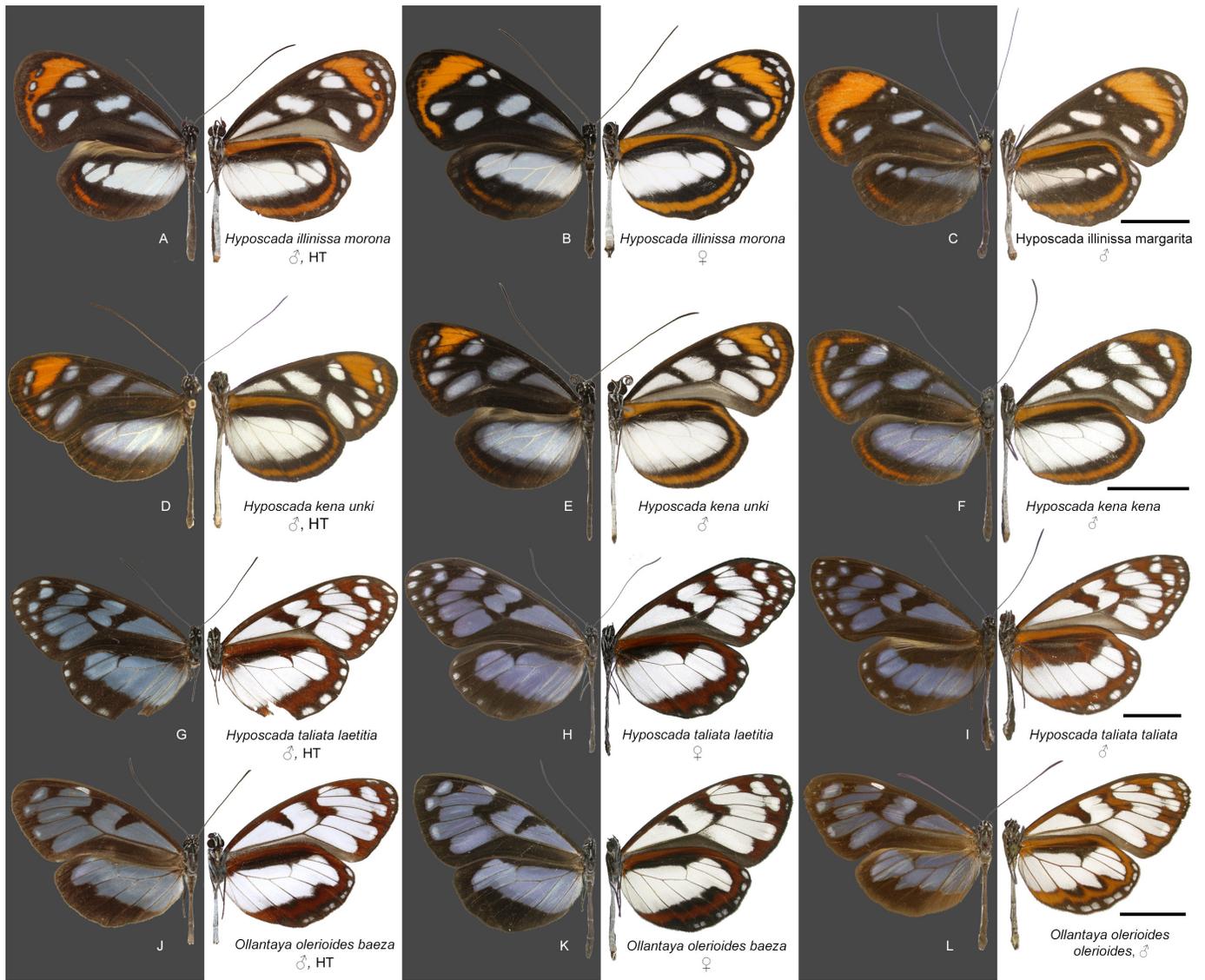


Fig. 5. Adults of new and similar Oleriina taxa, all from Ecuador unless otherwise stated. See text for wing lengths of new taxa, other scale bars are 1 cm. **A.** *Hyposcada illinissa morona* n. ssp., holotype ♂, Morona-Santiago, km 3 Puerto Morona-San José de Morona (FLMNH). **B.** *Hyposcada illinissa morona* n. ssp., ♀, Morona-Santiago, km 3 Puerto Morona-San José de Morona (FLMNH). **C.** *Hyposcada illinissa margarita*, ♂, Peru, San Martín, San Antonio de Cumbasa (NHMUK). **D.** *Hyposcada kena unki* n. ssp., holotype ♂, Peru, Amazonas, Cerro Unki (MUSM). **E.** *Hyposcada kena unki* n. ssp., ♂, Morona-Santiago, Río Kusuimi (FLMNH). **F.** *Hyposcada kena kena*, ♂, Napo, Apuya (FLMNH). **G.** *Hyposcada taliata laetitia* n. ssp., holotype ♂, Morona-Santiago, km 14 Limón-Gualaceo rd. (FLMNH). **H.** *Hyposcada taliata laetitia* n. ssp., ♀, Morona-Santiago, Río Abanico (FLMNH). **I.** *Hyposcada taliata taliata*, ♂, Peru, Pasco, Cushi (NHMUK). **J.** *Ollantaya olerioides baeza* n. ssp., holotype ♂, Morona-Santiago, Río Abanico (FLMNH). **K.** *Ollantaya olerioides baeza* n. ssp., ♀, Morona-Santiago, Río Abanico (FLMNH). **L.** *Ollantaya olerioides olerioides*, ♂, Bolivia, Cochabamba, Yunga del Espíritu Santo (NHMUK).

Mar 1993, 1♂, (MUSM); Río Ampiyacu, [3°19'S,71°51'W], 120 m, (Lequerica, H.), 1♂, (MUSM); Cerros de Orellana, Lupunay, 120 m, (Hocking, P.), 15 Aug 1988, 1♂, (MUSM); Río Sucusari, Explornapo-ACEER, [3°14'S,72°55'W], 140 m, (Grados, J.), 10 Sep 1995, 1♂, 1♀, (MUSM), 17 Sep 1995, 1♀, (MUSM), (Lamas, G.), 18 Sep 1995, 1♀, (MUSM), (Harvey, D.), 19 Sep 1995, 1♀, (MUSM), (Caldas, A.), 7 Sep 1995, 1♀, (MUSM); Zona Reservada de Sierra del Divisor, Río Tapiche, 4.5 km SSE Ana María, [7°3'22.71"S, 74°6'51.56"W], 190 m, (Espinoza, C.), 20-22 Feb 2009, 2♂, 1♀, (MUSM); 24.5 km SW Constitución, Río Yaquirana, [6°56'59.87"S,73°51'19.89"W], 288 m, (Espinoza, C.), 14-18 Mar 2009, 1♀, (MUSM); 32 km E Monte Alegre, Río Tapiche, [6°28'31"S,74°04'32"W], 139 m, (García, A.), 14-15 Feb 2008, 1♀, (MUSM); Zona Reservada Allpahuayo-Mishana, Yarinal 02, [3°57'S,73°26'W], 170 m, (Ramírez, J. J.), 8 Mar 2002, 1♂, (MUSM); Yarinal 1, [3°57'S,73°25'W], 170 m, (Ramírez, J. J.), 31 Jul 2001, 1♀, (MUSM); km 28 Iquitos-Nauta, [3°59'S,73°26'W], 180 m, (Ramírez, J. J.), 20 Jan 2003, 2♂, (MUSM); Agua Blanca, [3°56'S,73°28'W], 140m, (Ramírez, J. J.), 7 Sep 2003, 1♂, (MUSM),

10 Jan 2004, 1♂, (MUSM), 13 Jan 2005, 1♂, 1♀, (MUSM); Río Putumayo, El Estrecho, [2°28'S,72°42'W], 130 m, (Büche, M.), Feb 1994, 2♀, (MUSM); Río Putumayo, Soplin Vargas, [0°23'S,74°40'W], 200 m, (Lequerica, H.), Dec 2010, 1♀, (MUSM); Río Pucacuro, Coconilla, [2°42'S,75°06'W], 160 m, (Ramírez, J. J.), 20 Jul 2003, 1♀ (MUSM); Río Samiria, Estación Biológica Pithecia, [5°11'S,74°42'W], 180 m, (Pacheco, V.), 3 Nov 1979, 1♀, (MUSM); *Madre de Dios*: Puerto Maldonado, [12°36'S,69°11'W], 300 m, 1♀, (ZSM); Parque Manu, Pakitza, [11°55'48"S,71°15'18"W], 340-400 m, 1♂, (USNM), [11°53'S,70°58'W], 350 m, (Pogue, M. G.), 20 Sep 1988, 1♂, 1♀ [*in copula*], (MUSM), 17 Sep 1988, 1♀, (MUSM), 400 m, (Lamas, G.), 8-14 Sep 1989, 1♀, (MUSM), 400m, (Robbins, R.), 7 Oct 1990, 1♂, (MUSM), (Lamas, G.), 10 Oct 1990, 1♀, (MUSM), 15 Oct 1990, 1♀, (MUSM), (Macdonald, J.), 4 Nov 1990, 1♀, (MUSM), 7 Nov 1990, 1♂, (MUSM), 11 Nov 1990, 1♂, 1♀, (MUSM), (Rowe, W.), 4 Nov 1990, 2♀, (MUSM), 11 Nov 1990, 1♂, (MUSM); *Pasco*: Río Pachitea, [8°45'S,74°32'W], (Tessmann, G.), 2♂, 1♀, (MfN); Alto Yurinaqui, Eneñas, [10°45'S,75°13'W], 1400 m, (Hocking, P.), 1 Nov 1965, 1♂, (MUSM);

entre Quebrada Shamantari y Puerto Davis, [ca. 09°59'S, 74°40'W], (Grados, J., Carrasco, J.), 15 Nov 1994, 1♂, (MUSM); *San Martín*: 'Chambireyacu' [=Río Chambirayacu], [5°54'S, 76°24'W], 120 m, (Mathan, M. de), Jun-Aug 1885, 1♂, 1♀, (NHMUK); Yacusisa, [6°46'S, 76°49'W], 500-600 m, (Calderón, A.), 19 Dec 2007, 1♀, (MUSM), 10 Feb 2008, 1♀, (MUSM).

Other records: **Bolivia:** No data, 1♀, (MfN). **Brazil:** *Acre:* Alto Rio Juruá, 1♂, 1♀ (MNRJ), 1♀ [PT *Thyridia grandior*], (AMNH). **Colombia:** *Amazonas:* Leticia, 1♂, (AMNH); *Caquetá:* Barrio Bellavista, (Sañudo, C., Muñoz, F.), 20 Sep 2007, 1 specimen, (HERENCIA). **Ecuador:** *Orellana:* Laguna Añangu, Napo Wildlife Center, Napo trail, [0°30'35"S, 76°26'13"W], 250 m, (Willmott, K. R.), 18 Oct 2005, 1♂, (W&H); *Pastaza:* Puyo-Macas rd., Arutum, [1°46'48"S, 77°50'24"W], 800-900 m, (Eoff, K.), Jul 2012, (photograph live specimen) (Eoff, K., email and photo to KRW 17 Oct 2013).

Etymology: This subspecies is named after Henry Walter Bates (1825-1892) for his seminal contributions to mimicry theory. It is a masculine noun in the genitive case.

Taxonomy and variation: In addition to diagnostic wing pattern and morphological traits discussed above under Diagnosis, the male genitalia of *M. grandior batesi* n. ssp. are similar to those of *M. g. grandior* in having elongated lateral lobes on the terminal tergite (Fig. 10D,E) and saccus similar in length to the vinculum (Fig. 10F), both characters noted as diagnostic for the species in Forbes's (1944) description. Forbes (1944: 714) noted that "on coloring there are three distinct races, but two of them intergrade and will not be separately named at present", referring to *M. g. grandior* and *M. grandior batesi*. We have examined more than 30 individuals of the nominate subspecies and more than 80 of the new subspecies and conclude that the differences are sufficiently discrete and confined to relatively large geographic regions that the unnamed phenotype warrants taxonomic recognition. *Methona grandior incana* and *M. grandior batesi* occur in very close geographic proximity and we have examined five specimens, from Ecuador (Río Anzu and "Río Napo"), that are phenotypically intermediate between these two taxa.

Distribution and natural history: This new subspecies occurs in rain forest from 100-1450 m in the western Amazon, from eastern Colombia through Ecuador to southeastern Peru and western Brazil (and possibly northwestern Bolivia) (Fig. 31B). In eastern Ecuador, however, in the provinces of Pastaza, Tungurahua, Morona-Santiago and Zamora-Chinchi, it is replaced above 1000 m by *M. grandior incana*. In Ecuador and Peru, both sexes of *M. grandior batesi* n. ssp. have been encountered as uncommon, solitary individuals flying from the late morning until 15:30 hrs, from 1-3 m above the ground, in tall primary forest with relatively open understorey. We observed one individual feeding on a flowering tree in the canopy, at approximately 30 m above the ground, at 07:00 hrs.

Elzunia bomplandii golondrina Willmott, Lamas & Hall, **new subspecies**

Figs. 1G, 10I-K, 31C

Elzunia humboldt n. ssp.: Lamas (2004: 172, no. 18j)

Diagnosis and identification: The taxa previously treated as subspecies of *Elzunia humboldt* (Latreille, [1809]) by Lamas (2004) were recently split into three species by Le Crom *et al.* (2018), on the basis of wing pattern, genitalia and distribution data, which provides evidence for sympatry between some taxa

in central Colombia. These three species include *E. humboldt*, whose taxa lack a pale discal band on the DHW, *E. regalis* (Stichel, 1903), whose taxa have a pale DHW discal band and reddish markings on the VHW between the white postdiscal band and marginal spots (Fig. 1H), and *E. bomplandii* (Guérin-Méneville, [1844]), whose taxa have a pale discal DHW band and lack reddish markings on the VHW between the white postdiscal spots and marginal spots (Fig. 1I, 31C). This new subspecies has a wing pattern that is characteristic of the last group, and is perhaps most similar to *E. b. bomplandii* (Fig. 1I). It may be distinguished from all the subspecies in the last group by the following combination of characters: white DFW postdiscal spots in cells 2A-Cu₂ and Cu₂-Cu₁ relatively broad, with the latter more than half the width of the former; DHW pale discal band not uniformly yellow, but becoming white anteriorly and posteriorly; DHW white postdiscal spots small, rounded, and forming a straight line; VFW lacking any reddish markings; VHW with reddish brown markings confined to a curving postdiscal band between veins Cu₂ and Rs.

Description: MALE (Fig. 1G, 10I-K): Forewing length 43 mm (mean 44 mm, n=4). *Wings:* as illustrated (Fig. 1G), tuft of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes with scattered short setae; antennae dark brown; labial palpi black with white outer dorsal edge and ventral inner edge, long black hairs ventrally; top of head black with scattered white central hairs, frons black with two white spots below antennae base. *Thorax:* dorsal surface black except for narrow white midline in anterior half, and long, dense reddish brown hairs at anterior edge/pronotum, tegula black edged with white, ventral surface white except black where legs fold, forelegs, mid- and hindlegs black dorsally and white ventrally. *Abdomen:* dorsal surface black, ventral surface white shading to pale yellow posteriorly. *Genitalia* (Fig. 10I-K): as illustrated, typical of the genus.

FEMALE: unknown.

Types: HOLOTYPE ♂: **ECUADOR:** *Carchi:* Reserva Las Golondrinas, N of La Carolina, Santa Rosa, [0°49'38"N, 78°7'42"W], 1700 m, (Willmott, K. R., Hall, J. P. W.), 29 Nov 1996, [Genitalic dissection KW-19-11], (FLMNH, to be deposited in INABIO).

PARATYPES (5♂): **Ecuador:** *Carchi:* Reserva Forestal Golondrinas, [0°49'29"N, 78°7'48"W], 1650 m, 28 Jan 2005, 1♂, (MZUJ); Reserva Forestal Golondrinas, [0°49'29"N, 78°7'48"W], 1700 m, (Wojtusiak, J., Pyrcz, T.), 23 Jun 1999, 1♂, (MZUJ); Reserva Las Golondrinas, N of La Carolina, Santa Rosa, [0°49'38"N, 78°7'42"W], 1700 m, (Willmott, K. R., Hall, J. P. W.), 29 Nov 1996, 3♂, (FLMNH).

Other records: Same data as HT except 4,5 Sep 1996 (W&H).

Etymology: This subspecies name is derived from the Spanish word 'golondrina', meaning a swallow, and the root of the name Reserva Las Golondrinas, the type and indeed only known locality for this subspecies. It is treated as a feminine noun in apposition.

Taxonomy and variation: Fox (1956) recognized seven species of *Elzunia* Bryk, 1937 in his revision of the genus, whereas Lamas (2004) reduced this number to two, namely the smaller *Elzunia pavonii* (Butler, 1873), found across a wide elevational range in southern Ecuador and northern Peru, but mostly occurring in dry forest, and the larger *Elzunia humboldt*, confined to a narrow elevational range in cloud forest in Colombia and Ecuador. DNA sequence data group *E. bomplandii golondrina* n. ssp. with east Ecuadorian *E. humboldt* (Fig. 19), but unfortunately no sequences are yet available from *E. bomplandii* as treated by Le Crom *et al.* (2018). We have also not found consistent genitalic characters to infer relationships



Fig. 6. Adults of new and similar Oleriina taxa, all from Ecuador unless otherwise stated. See text for wing lengths of new taxa, other scale bars are 1 cm. **A.** *Oleria tremona benigna* n. ssp., holotype ♂, Zamora-Chinchipe, Quebrada Las Dantas (FLMNH). **B.** *Oleria tremona benigna* n. ssp., ♀, Zamora-Chinchipe, San Francisco, casa de Arcoiris (FLMNH). **C.** *Oleria tremona tremona*, ♂, Napo, Cordillera de los Guacamayos, Baeza-Tena rd. (NHMUK). **D.** *Oleria radina bonita* n. ssp., holotype ♂, Sucumbíos, Río Sucio (FLMNH). **E.** *Oleria radina bonita* n. ssp., ♀, Sucumbíos, Quebrada El Garrapatal (FLMNH). **F.** *Oleria radina radina*, ♂, Colombia, Cundinamarca, “Bogotá” (MfN; dissection BERL-10). **G.** *Oleria tigilla raya* n. ssp., holotype ♂, Peru, Pasco, Río Raya (MUSM). **H.** *Oleria tigilla raya* n. ssp., ♀, Peru (NHMUK). **I.** *Oleria tigilla tigilla*, ♂, Napo, Jatun Sacha (NHMUK). **J.** *Oleria onega astigara* n. ssp., holotype ♂, Napo, Apuya (FLMNH). **K.** *Oleria onega astigara* n. ssp., ♀, Sucumbíos, Pañacocha (FLMNH). **L.** *Oleria onega janarilla*, ♂, Sucumbíos, El Recodo (FLMNH). **M.** *Oleria agarista*, lectotype ♂ of *Ithomia agarista*, [Peru], “Río Negro” (NHMUK) (labels at right of specimen). **N.** *Oleria ilderina lerida*, ♂, Sucumbíos, El Recodo (FLMNH).

among montane *Elzunia* taxa, so the treatment of this taxon as a subspecies of *E. bomplandii* is based on wing pattern characters as discussed above under Diagnosis. However, despite its similarity to *E. b. bomplandii*, which occurs in the Colombian Cordillera Oriental, *E. bomplandii golondrina* is geographically closest to *E. humboldt carlosi* Le Crom & Llorente, 2018 (which has no DHW discal band) and *E. r. regalis* from west

Colombia, and its sister taxon is thus difficult to determine. Incorporation of additional molecular data will therefore likely help further revise the taxonomy of this difficult group. The new subspecies is also similar in dorsal (but not ventral) wing pattern to *E. pavonii*, which is sister to all wet montane forest *Elzunia* sequenced to date (Fig. 19).

Distribution and natural history: This new subspecies is known only from the type locality in northwestern Ecuador (Fig. 31C), where solitary males were found flying 2-4 m above the ground inside primary cloud forest near a river.

Ithomia agnosia zumba Lamas & Willmott, **new subspecies**
Figs. 2A,B, 11A-C, 31D

Ithomia agnosia n. ssp.: Lamas (2004: 181, 133e)

Diagnosis and identification: This subspecies is distinguished from the geographically closest subspecies, the nominate (Fig. 2C), by the much less intense white and more translucent pale FW postdiscal band. White scales within this band are confined to the costa and the base of veins M_2 and M_1 , instead of filling the cells between these veins.

Description: MALE (Fig. 2A, 11A-C): Forewing length 24 mm (mean 23.3 mm, n=3). *Wings:* as illustrated (Fig. 2A), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes bare; antennae black; labial palpi white except for broad black stripe ventro-laterally; top of head black with central white stripe, frons white, with central black stripe. *Thorax:* dorsal surface dark brown with scattered white scales laterally and forming central stripe, ventral surface yellow except for reddish brown where legs fold, forelegs, mid- and hindlegs with mixed brown and white scales, pronotum reddish orange. *Abdomen:* dorsal surface dark brown, ventral surface white. *Genitalia* (Fig. 11A-C): notable features include broad, elongate patch of cornuti near tip of aedeagus and squarish upper valva projections in lateral view (Fig. 11A).

FEMALE: (Fig. 2B): Forewing length 21 mm (n=1). *Wings:* as illustrated (Fig. 2B), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **PERU:** *Amazonas:* Pedro Ruiz [Gallo], [5°57'S, 77°59'W], 900 m, (Lamas, G.), 900 m, 16 Dec 1975, (MUSM).

PARATYPES (15♂, 17♀): **Ecuador:** *Zamora-Chinipe:* km 30 Zumba-Chito rd., [4°56'42"S, 79°4'20"W], 750 m, (Willmott, K. R., J. C. R., J. I. R.), 14 Jun 2013, 1♀ [FLMNH-MGCL-157863], (FLMNH); km 8 Zumba-Chito rd., [4°53'28"S, 79°6'54"W], 1150 m, (Willmott, K. R., J. C. R., J. I. R.), 1 Jun 2013, 1♂ [FLMNH-MGCL-157862], (FLMNH), 1♂, (INABIO); Progreso, c. km 10 Zumba-Valladolid rd., [4°50'2"S, 79°6'6"W], 1400 m, (Padrón, S., Aldaz, R.), 15 May 2008, 1♀ [FLMNH-MGCL-119040], (FLMNH); Río Palanda, km 35 Zumba-Loja rd., [4°37'53"S, 79°8'16"W], 1100 m, (Willmott, K. R., Hall, J. P. W.), 20 Jul 1993, 2♂ [Genitalic dissection ITHOM-3], 1♀, (FLMNH). **Peru:** *Amazonas:* same data as HT, 1♂, 1♀, (MUSM); opp. Bagua Grande, Buenos Aires, [5°41'S, 78°24'W], 1300 m, (Hocking, P.), 3 Sep 1975, 1♂, (MUSM); Muyo, near Aramango, [5°25'S, 78°27'W], 250 m, (Lamas, G.), 12 Dec 1975, 1♀, (MUSM); *Cajamarca:* Charape, [5°25'S, 78°59'W], (Pratt), Jun 1912, 3♂, 3♀, (NHMUK); San Ignacio, [5°09'S, 79°00'W], 1100-1300 m, (Lamas, G.), 7 Feb 1978, 2♂, 2♀, (MUSM); 5 km W Jaén, [5°42'S, 78°50'W], 800 m, (Lamas, G.), 10-11 Feb 1975, 2♂, 3♀, (MUSM); La Florida, [6°52'S, 79°08'W], 950 m, (Zanini, L.), 6 May 1967, 1♂, (MUSM); between Jaén and La Corona, [5°43'S, 78°52'W], 1300m, (Lamas, G.), 16 March 1985, 1♂, (MUSM); Charape, [5°25'S, 78°59'W], 1200m, (Lamas, G.), 10 Nov 1985, 1♀, (MUSM); W of Tamborapa, Cochalán, [5°28'S, 78°59'W], 600 m, (Lamas, G.), 19 Mar 1985, 2♀, (MUSM); Puerto Quiracas, Río Chinchipe, km 103 Jaén-San Ignacio, [5°11'S, 78°54'W], 500 m, (Lamas, G.), 15 Nov 1985, 1♀, (MUSM); Contumazá, Bosque de Cachil, [7°24'S, 78°47'W], 2430 m, (Grados, J.), 20 Oct 2014, 1♂, (MUSM).

Etymology: The name is derived from that of the town of Zumba, in the vicinity of which most Ecuadorian specimens

were collected, and it is treated as a feminine noun in apposition.

Taxonomy and variation: This taxon is placed as a subspecies of *I. agnosia* Hewitson, [1855] because, aside from the differences in the FW postdiscal band described above, it shows no differences in terms of male genitalia, wing shape, venation, androconial scales and pattern of dark scaling, which are characters that serve to distinguish other congeners. Furthermore, DNA barcodes showed no consistent differences between individuals of *I. agnosia zumba* n. ssp. and the nominate subspecies from southern Ecuador (Zamora valley) (Fig. 20).

Distribution and natural history: This subspecies occurs in extreme southeastern Ecuador and northeastern Peru in the upper tributaries of the Río Marañón (Fig. 31D). In Ecuador it is rather local, occurring near streams in secondary growth near relatively moist forest, from 750-1400 m, whereas in Peru it has been recorded from 500-2430 m.

Ithomia arduinna ardua Lamas, Vitale & Boyer, **new subspecies**
Figs. 2D,E, 11D-E, 31E

Ithomia arduinna n. ssp.: Lamas (2004: 181, no. 135b)

Napeogenes sylphis: Piñas (2004: 35, fig. 193), misidentification

Diagnosis and identification: This subspecies is distinguished from the nominate subspecies (Fig. 2F) as follows. On the FW, *I. a. ardua* n. ssp. has a narrower black apical border, particularly in cell M_1-R_5 ; the white postdiscal band is broader and more even in both shape and translucency; there is white scaling in the discal cell opposite the base of cell Cu_2-Cu_1 , and more extensive white in cell Cu_2-Cu_1 ; and the black discal bar is more evenly tapering, with a less pronounced step at its distal edge at the base of cell Cu_2-Cu_1 . On the VHW, the black scaling on the raised area at the costa containing the androconial scales is more extensive, whereas this raised area is ringed with orange scaling in the nominate subspecies. Also on the HW, there is more extensive white translucent scaling, extending into cells M_3-M_1 .

Description: MALE (Fig. 2D, 11D-E): Forewing length 24 mm (n=1). *Wings:* as illustrated (Fig. 2D), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head, thorax, abdomen:* same as *Ithomia agnosia zumba* n. ssp. *Genitalia* (Fig. 11D-E): notable features include elongate patch of sparse, large cornuti near tip of aedeagus and upturned posterior valva tip (Fig. 11D).

FEMALE: (Fig. 2E): Forewing length 22 mm (n=1). *Wings:* as illustrated (Fig. 2E), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **ECUADOR:** *Morona-Santiago:* [c. 26 km S] Méndez, 'Cunza' [=Río Cumtsa], [2°51'56"S, 78°20'38"W], 800-1200 m, (Aldaz, E.), Sep-Oct 2003, [Genitalic dissection KW-15-210], (FLMNH, to be deposited in INABIO).

PARATYPES (5♂, 7♀): **Ecuador:** *Morona-Santiago:* [c. 26 km S] Méndez, 'Cunza' [=Río Cumtsa], [2°51'56"S, 78°20'38"W], 1000 m, (E. Aldaz), Sep-

Fig. 7 (p. 13, facing page). Adults of new and similar *Episcada* taxa, all from Ecuador unless otherwise stated. See text for wing lengths of new taxa, other scale bars are 1 cm. **A.** *Episcada clausina bomboiza* n. ssp., holotype ♂, Morona-Santiago, Bomboiza (FLMNH). **B.** *Episcada clausina bomboiza* n. ssp., ♀, Morona-Santiago, Bomboiza (FLMNH). **C.** *Episcada clausina clausina*, ♂, Bolivia, Santa Cruz, Prov. del Sara (NHMUK). **D.** *Episcada hymenaea mirifica* n. ssp., holotype ♂, Peru, Cuzco, Quebrada Quitacalzón (MUSM).

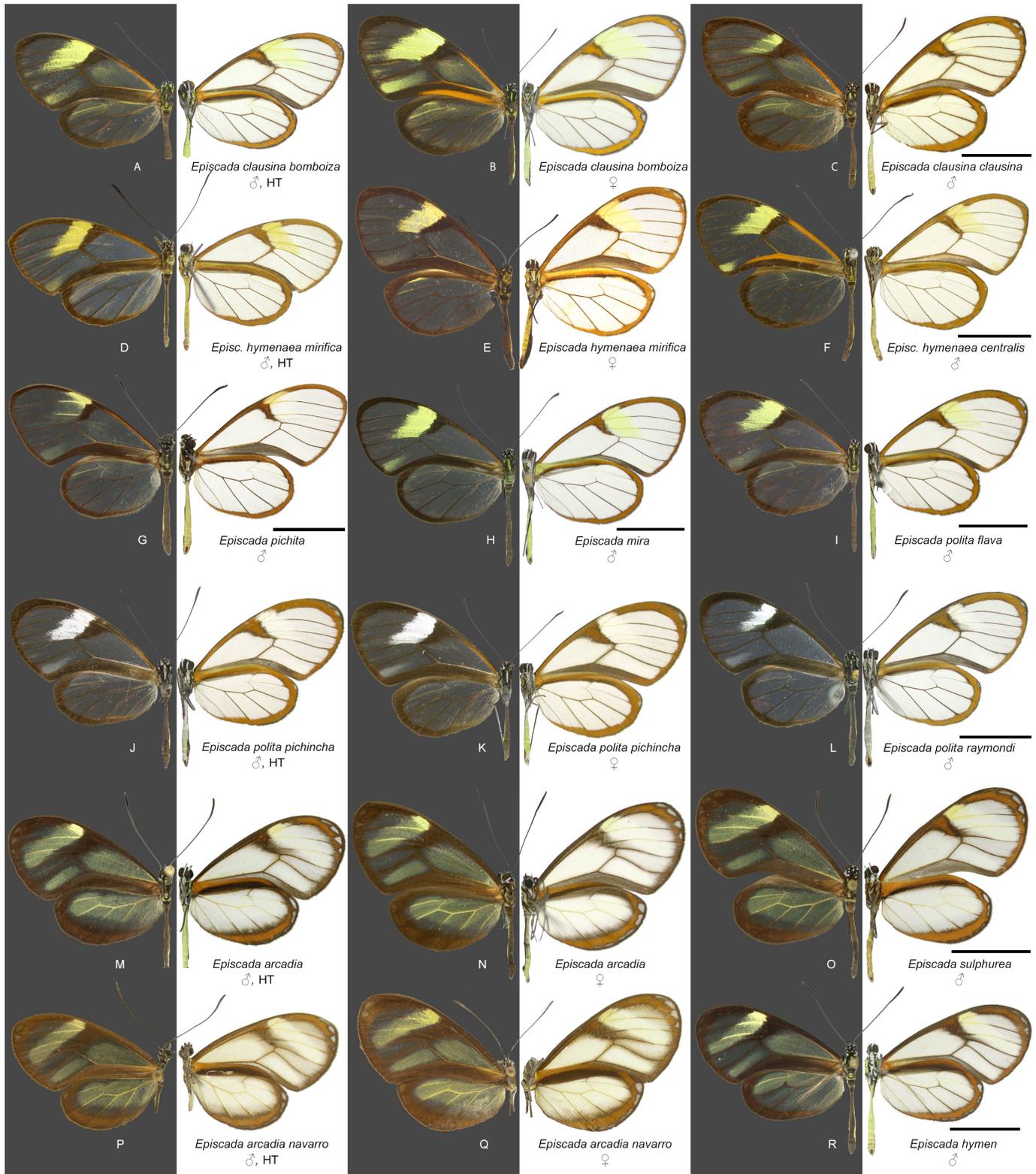


Fig. 7 (continued). E. *Episcada hymenaea mirifica* n. ssp., ♀, Tungurahua, Río Blanco (FLMNH). F. *Episcada hymenaea centralis*, ♂, Brazil, Mato Grosso, Buriti (NHMUK). G. *Episcada pichita*, ♂, Napo, Sumaco (FLMNH). H. *Episcada mira*, ♂, Zamora-Chinchipe, Chinapintza (FLMNH). I. *Episcada polita flava* n. comb., ♂, Tungurahua, Río Zuñac (FLMNH). J. *Episcada polita pichincha* n. ssp., holotype ♂, Carchi, Reserva Las Golondrinas, Santa Rosa (FLMNH). K. *Episcada polita pichincha* n. ssp., ♀, Carchi, Reserva Las Golondrinas, Santa Rosa (FLMNH). L. *Episcada polita raymondi*, ♂, Venezuela, Distrito Federal, Colonia Tovar rd to Chichiriviche (ANNE). M. *Episcada arcadia* n. sp., holotype ♂, Orellana, Boca del Río Añangu (FLMNH). N. *Episcada arcadia* n. sp., ♀, Napo, Jatun Sacha (NHMUK). O. *Episcada sulphurea*, ♂, Peru, Madre de Dios, 15 km downstream Shintuya (FLMNH; KW-21-27). P. *Episcada arcadia navarro* n. ssp., holotype ♂, Peru, San Martín, Navarro (MUSM). Q. *Episcada arcadia navarro* n. ssp., ♀, Peru, San Martín, Navarro (MUSM). R. *Episcada hymen*, ♂, Peru, Madre de Dios, Los Amigos Biological Station (FLMNH; KW-21-26).

Oct 2003, 1♂, 1♀, (FAVI); environs de Méndez, [2°42'57"S,78°19'4"W], 550 m, (Boyer, P.), 5 Mar 1998, 1♂, 3♀, (PIBO); km 115 route de Morona, [2°59'S,77°48'29"W], 400-500 m, (Boyer, P.), 23 Nov 2002, 1♂, (PIBO); km 16 Méndez-Limón rd., [2°47'36"S,78°20'34"W], 850 m, (Boyer, P.), 10 Dec 1997, 2♀, (PIBO); km 30 Méndez-Limón rd., Río Yungantza, [2°52'13"S,78°21'56"W], 650 m, (Willmott, K. R.), 4 Nov 2010, 1♀ [FLMNH-MGCL-146776], (FLMNH); nr. Sueúa, Río Miriumi, [2°24'48"S,78°13'54"W], 900 m, (Trembath, D. A.), 31 Oct 1996, 1♂ [1500m'; No. 15821], (DATR). **Peru:** Amazonas: km 44 Sarameriza-Chiriaco, Cerro Unki, [4°37'S,77°40'W], 790 m, (Mallet, J., Eeley, H.), 10 Jun 1986, 1♂, (MUSM).

Etymology: The subspecies name is derived from the feminine Latin adjective 'ardua', meaning difficult, hard, tiresome, in recognition of the effort needed to find this elusive taxon in the field.

Taxonomy and variation: This taxon is treated as a subspecies of *I. arduinna* d'Almeida, 1952 (Fig. 2F) because the two taxa share a white translucent postdiscal band on the FW that is continuous from the costa to the margin in cell Cu_1-M_3 , in contrast to most other congeners in which the band terminates in cell M_3-M_2 . The shape of the raised area at the costa containing the androconial scales is similar to *I. arduinna*, as is the HW shape, which is relatively rounded and more strongly angled at the costa distal of the androconial scale pouch than the otherwise similar *Ithomia salapia ardea* Hewitson, 1855. The latter taxon further differs in having an evenly curved inner edge to the dark apical area on the FW, whereas *I. arduinna arduinna* and the female, at least, of *I. arduinna ardua n. ssp.*, have the inner edge more sharply angled at vein M_1 , with this being a distinctive feature of the species. Furthermore, the genitalia of *I. a. ardua* are similar to those of the nominate subspecies in having an upturned, pointed process at the distal tip of the valva, a long line of sparse, spine-like cornuti, and relatively broad inner basal lobes on the valva in ventral view. DNA sequence data suggest that the sister species of *I. arduinna* is the west Amazonian *Ithomia amarilla* Haensch, 1903 (Jiggins *et al.*, 2006; Fig. 20); we do not know of any evidence of sympatry between these species, but they have been collected within c. 20 km of one another in Ecuador and the male genitalia are quite distinct, with *I. amarilla* lacking the upturned process on the valva and having narrow, finger-like projections from the basal part of the valva in ventral view.

Distribution and natural history: *Ithomia arduinna ardua n. ssp.* occurs in lowland foothill rain forest from approximately 400-1000 m, although precise elevational data are lacking. The subspecies is known only from northern Peru (Amazonas) to southern Ecuador (Fig. 31E), where it has been found only in the valleys of the Río Zamora and Río Upano, and the upper Río Santiago. The taxon appears to be rare and local in the field; we found a single female flying at 10:50 hrs 1 m above the ground, on a steep slope, in the understorey of undisturbed forest approximately 10 m from the edge of the forest and a pasture, and individuals of both sexes in a patch of forest near the main road from Méndez to Guarumales.

Ithomia hymettia petitia Lamas & Willmott, **new subspecies**
Figs. 2G,H, 11G-H, 31F

Diagnosis and identification: The male of *I. hymettia petitia n. ssp.* differs from the nominate subspecies (Fig. 2I) in having translucent grayish rather than smoky brown wings, slightly broader black margins and FW discocellular bar, with a resulting smaller translucent space in FW cell R_5-R_4 , translucent whitish scaling in the postdiscal area in FW cells M_3-R_5 and in the HW discal cell, and an entirely black DFW anal margin without an orange stripe posterior of the cubital vein. The female also differs in all of these respects, in particular in having much more intense white scaling on the FW.

Description: MALE (Fig. 2G, 11G-H): Forewing length 27 mm (n=1). *Wings:* as illustrated (Fig. 2G), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes bare; antennae black; labial palpi white except for broad black stripe ventro-laterally; top of head black with central white stripe, frons white, with central black stripe. *Thorax:* dorsal surface dark brown with scattered white scales laterally and forming central stripe, ventral surface yellow except for black where legs fold, forelegs, mid- and hindlegs black dorsally and white ventrally, pronotum black. *Abdomen:* dorsal surface black, ventral surface pale yellow. *Genitalia* (Fig. 11G-H): notable features include oval patch of cornuti in middle of aedeagus and protruding lower valva projection in lateral view (Fig. 11G); vertical saccus is presumed an artifact.

FEMALE: (Fig. 2H): Forewing length 27 mm (n=1). *Wings:* as illustrated (Fig. 2H), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♀: **ECUADOR:** Imbabura: above Getsemani, [0°47'55"N,78°21'18"W], 1200 m, (Petit, J.-C.), 20 Nov 2004, (JEPE).

PARATYPES (4♂, 6♀): **Colombia:** *Quindío:* Pijao, [4°19'55"N,75°41'58"W], 1900 m, (Warren-Gash, H.), 29 May 2007, 1♂, (HAWA); *Valle del Cauca:* Buga, [3°54'N,76°18'W], Oct 1990, 2♂, 1♀, (PIBO); Cali, [3°27'N,76°31'W], 1000 m, 2♀ [ex coll. P. Kieffer], (PIBO); Saladito, [3°29'N,76°37'W], 1900 m, (Warren-Gash, H.), 3 Jun 2007, 2♀, (HAWA); Yanacunas, [3°26'4"N,76°37'34"W], 1700 m, (Warren-Gash, H.), 1 Oct 2006, 1♀, (HAWA); *Cauca:* Tambito, [2°30'57"N,77°0'46"W], 1000 m, (Pyrz, T. W.), 22 Sep 1996, 1♂, (MZUJ).

Other data: **Colombia:** *Risaralda:* c. 15 km SE Pereira, Otún Quimbaya Sanctuary, [4°44'2"N,75°35'11"W], 1800 m, (Garwood, K.), Oct 2012, 1♀, (photograph of live specimen) (Garwood, K., email and photograph to KRW 13 Nov 2012).

Etymology: This subspecies is named after Jean-Claude Petit, who collected the holotype and only known Ecuadorian specimen, in recognition of his remarkable contributions to the knowledge of Ecuadorian butterflies, in particular through his research in Parque Nacional Sangay and Reserva Ecológica Cotacachi-Cayapas. It is treated as a Latinized masculine noun in the genitive case.

Taxonomy and variation: Males of both subspecies of *I. hymettia* (Staudinger, 1885) share with *Ithomia lagusa* Hewitson, [1856], a taxon formerly considered conspecific (Lamas, 2004), a hindwing venation that differs from other *Ithomia* Hübner, 1816 in looking like that of *Napeogenes* Bates, 1862, with the HW discocellular veins 3d and 2d forming an almost straight line, without a medial recurrent vein (Mr)

Fig. 8 (p. 15, facing page). Adults of new and similar *Pteronymia* taxa, all from Ecuador unless otherwise stated. See text for wing lengths of new taxa, other scale bars are 1 cm. **A.** *Pteronymia alida luctuosa n. ssp.*, holotype ♂, Carchi, Reserva Las Golondrinas, Santa Rosa (FLMNH). **B.** *Pteronymia alida luctuosa n. ssp.*, ♀, Carchi, Reserva Las Golondrinas, Santa Rosa (FLMNH). **C.** *Pteronymia alida zabina*, ♀, "New Granada" (NHMUK).

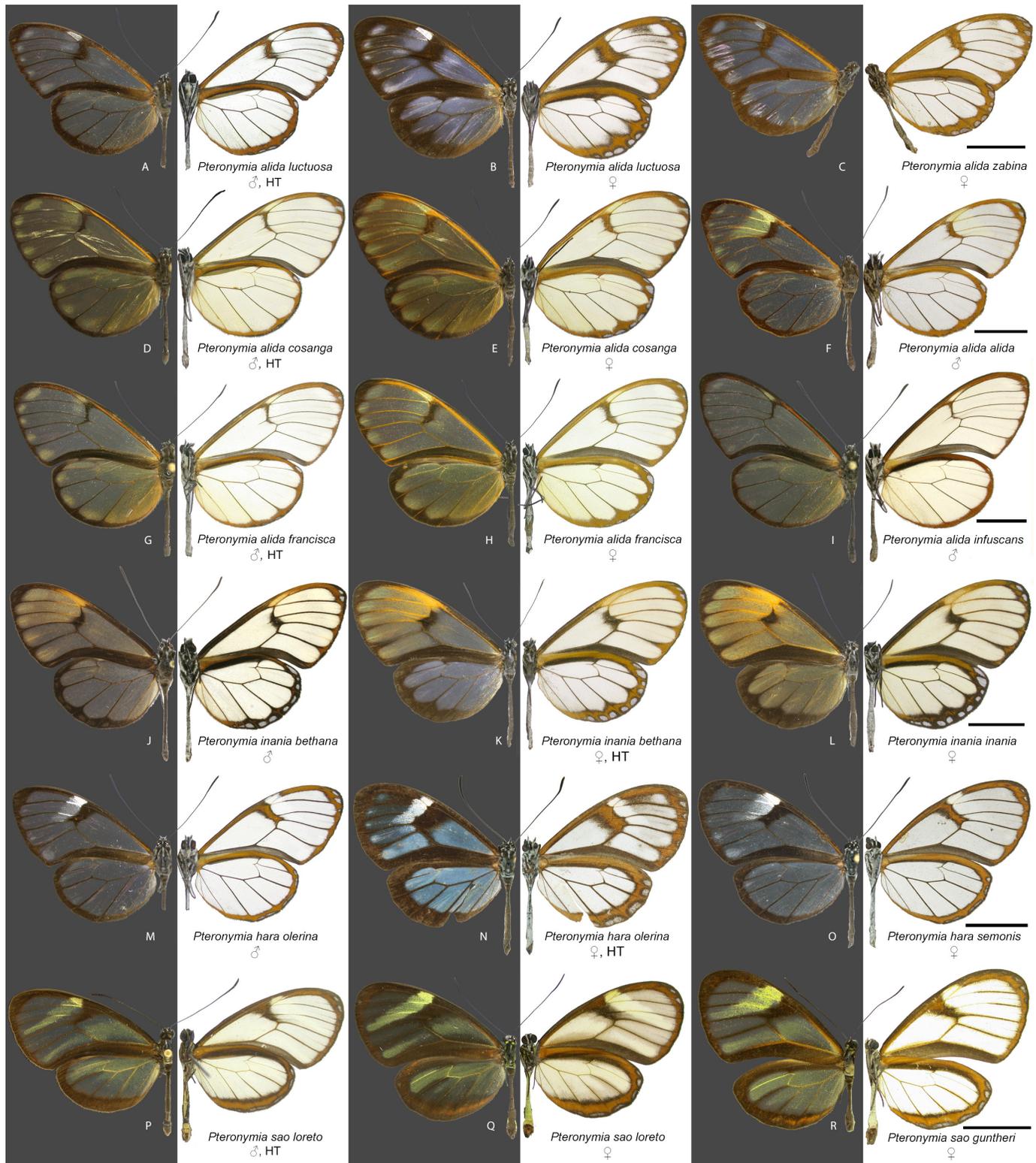


Fig. 8 (continued). **D.** *Pteronymia alida cosanga* n. ssp., holotype ♂, Sucumbíos, Quebrada El Garrapatal (FLMNH). **E.** *Pteronymia alida cosanga* n. ssp., ♀, Sucumbíos, Quebrada El Garrapatal (FLMNH). **F.** *Pteronymia alida alida*, ♂, Venezuela, Mérida, Pedregosa (NHMUK). **G.** *Pteronymia alida francisca*, holotype ♂, Zamora-Chinchipe, San Francisco, casa de Arcoiris (FLMNH). **H.** *Pteronymia alida francisca*, n. ssp., ♀, Zamora-Chinchipe, San Francisco, casa de Arcoiris (FLMNH). **I.** *Pteronymia alida infuscans*, ♂, Peru, Pasco, Palcamayo (GETE). **J.** *Pteronymia inania bethana* n. ssp., ♂, Morona-Santiago, km. 9.5 Chigüinda-Gualaquiza rd., hillside (FLMNH). **K.** *Pteronymia inania bethana* n. ssp., holotype ♀, Zamora-Chinchipe, Chinapintza (FLMNH). **L.** *Pteronymia inania inania*, ♀, Morona-Santiago, Río Abanico (FLMNH). **M.** *Pteronymia hara olerina* n. ssp., ♂, Carchi, Lita, ridge east of Río Baboso (FLMNH). **N.** *Pteronymia hara olerina* n. ssp., holotype ♀, Carchi, Reserva Las Golondrinas, Santa Rosa (FLMNH). **O.** *Pteronymia hara semonis*, ♀, Imbabura, Los Cedros, ridge on trail from road (FLMNH). **P.** *Pteronymia sao loreto* n. ssp., holotype ♂, Peru, Loreto, Castaña (MUSM). **Q.** *Pteronymia sao loreto* n. ssp., ♀, Sucumbíos, Laguna de Pañacocha (NHMUK). **R.** *Pteronymia sao guntheri*, ♀, Peru, Madre de Dios, Cuzco Amazónico (FLMNH).

intruding into the HW discal cell. The two species appear to be broadly sympatric in Colombia, but with *I. hymettia* occurring at higher elevations. This new taxon is associated with *I. hymettia* rather than *I. lagusa* since it shares with the former species a FW discal cell lacking a dark bar and the base of FW R₅-R₄ being translucent rather than opaque. Furthermore, both subspecies of *I. hymettia* seem to occur at slightly higher elevations, approximately 1000-1900 m rather than 600-1600 m. We have not been able to obtain DNA barcodes for *I. lagusa* or *I. h. hymettia*, nor dissect the latter, but the male genitalia of *I. hymettia petitia* n. ssp. differ strongly from those of *I. lagusa* in having a much longer, more sinuous aedeagus with a patch of cornuti located far from the tip of the aedeagus, straighter valva in dorsal view, and a more prominent ventral projection of the valva in lateral view. Based on distribution data, and differences in morphology and DNA sequences, *I. hymettia*, *I. lagusa* and *I. adelinda* Hewitson, 1868 (containing east Andean taxa formerly considered subspecies of *I. lagusa* by Lamas (2004)) are now treated as distinct species (Mallarino *et al.*, 2005; Elias *et al.*, 2009; Chazot *et al.*, 2019).

Among co-occurring species, the female of *I. hymettia* is perhaps most similar to that of *I. avella* Hewitson, 1854, but similarly appearing subspecies of the latter species have a dark bar in the FW discal cell, while *I. terra* Hewitson, [1853] is smaller and, at least in the western Andes, has dark scaling around the base of HW veins Cu₁ and M₃. Within *I. hymettia petitia* there is some variation in the intensity of the white FW band, especially in the female, which increases from western Colombia to northwestern Ecuador. At present, too few specimens are known to determine whether this variation is clinal or represents stable populations.

Distribution and natural history: This is a rare taxon in collections and it inhabits cloud forest habitats from 1000-1900 m, from the Colombian Cordillera Occidental to northwestern Ecuador (Fig. 31F). The taxon may also occur in the Colombian Cordillera Central, but more specimens with reliable, precise data are needed to define its distribution and that of the nominate subspecies in that region.

Ithomia iphianassa occidentissa Lamas & Willmott, new subspecies

Figs. 2J,K, 11I-K, 32A

Ithomia iphianassa n. ssp.: Lamas (2004: 181, no. 145g)

Ithomia cleora: Piñas (2004: 42, fig. 273, 275, 276, 282, 283, 284), misidentification

Ithomia iphianassa ssp. nov.: Mallarino *et al.* (2005: Table 1)

Diagnosis and identification: This subspecies is distinguished from the neighboring *I. iphianassa ethilla* Neustetter, 1929 (Fig. 2L), which replaces it to the north (Fig. 32A), in the discal cells of both wings being predominantly yellow, whereas *I. iphianassa ethilla* has the HW discal cell and basal half of the FW discal cell orange or tinged with orange throughout, and

in having a narrower black DHW border. *Ithomia iphianassa ethilla* often has a strong black spot on the HW discocellulars, which is only very rarely observed in *I. iphianassa occidentissa* n. ssp., and when present is indistinct. *Ithomia iphianassa ethilla* also typically has a broader and longer orange band within the DHW marginal black area, and has more extensive black scaling on the forewing. *Ithomia iphianassa alienassa* Haensch, 1905 and *I. iphianassa phanassa* Herrich-Schäffer, 1865, from Colombia, are the most similar other subspecies; in comparison with *I. iphianassa occidentissa*, the former, from the Cauca valley, has narrower black margins and markings throughout both wings, while the latter, from the Colombian Cordillera Oriental, has a continuous orange DHW marginal band, among other differences.

Description: MALE (Fig. 2J, 11I-K): Forewing length 26 mm (mean 25.8 mm, n=4). *Wings:* as illustrated (Fig. 2J), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes bare; antennae black basally changing gradually throughout middle to yellow orange club; labial palpi white except for broad black stripe ventro-laterally; top of head black with central yellow stripe, frons yellow, with central black stripe. *Thorax:* dorsal surface dark brown with scattered yellow scales laterally and forming central stripe, ventral surface yellow except for reddish brown where legs fold, forelegs, mid- and hindlegs with mixed brown and white scales, pronotum reddish orange. *Abdomen:* dorsal surface dark brown, ventral surface yellow. *Genitalia* (Fig. 11I-K): notable features include sparse triangular 'teeth' near tip of aedeagus, broad patch of cornuti near tip of aedeagus (Fig. 11I) and narrow 'finger'-like projections from basal portion of valva (Fig. 11K).

FEMALE: (Fig. 2K): Forewing mean length 25.6 mm (n=5). *Wings:* as illustrated (Fig. 2K), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **ECUADOR:** *Pichincha:* nr. Patricia Pilar, Centinela ridge, [0°36'12"S,79°18'36"W], 600 m, (Willmott, K. R.), 12 Aug 1996, [Genitalic dissection KW-15-211], (FLMNH, to be deposited in INABIO).

PARATYPES (101♂, 132♀): **Ecuador:** *Pichincha:* [12 km E] Santo Domingo [de los Colorados], [Hotel] Tinalandia, [0°18'S,79°4'W], 650 m, (Vénédictoff, N.), 10 Jul 1973, 1♂ [FLMNH-MGCL-253644], (FLMNH), 14 Mar 1972, 1♀ [FLMNH-MGCL-253651], (FLMNH), 24 Aug 1973, 1♀ [FLMNH-MGCL-253650], (FLMNH), 25 Aug 1973, 1♂ [FLMNH-MGCL-253645], 1♂ [FLMNH-MGCL-253646], (FLMNH), 4 May 1972, 1♀ [FLMNH-MGCL-253649], (FLMNH); [Alluriquín], Río Toachi, [0°19'6"S,78°57'13"W], 1000 m, (de Lafebre, R.), Jan 1969, 1♂ [FLMNH-MGCL-253667], 1♀ [FLMNH-MGCL-253669], (FLMNH); [Alluriquín], Río Toachi, [0°19'6"S,78°57'13"W], 1100 m, (de Lafebre, R.), Aug 1969, 1♂ [FLMNH-MGCL-253671], 1♂ [FLMNH-MGCL-253672], 1♂ [FLMNH-MGCL-253673], 1♂ [FLMNH-MGCL-253674], 1♂ [FLMNH-MGCL-253679], 1♂ [FLMNH-MGCL-253680], 1♀ [FLMNH-MGCL-253675], 1♀ [FLMNH-MGCL-253676], 1♀ [FLMNH-MGCL-253677], 1♀ [FLMNH-MGCL-253678], (FLMNH), Jan 1969, 1♂ [FLMNH-MGCL-253668], (FLMNH); [Alluriquín], Río Toachi, [0°19'6"S,78°57'13"W], 1200 m, (de Lafebre, R.), Apr 1969, 1♀ [FLMNH-MGCL-253683], (FLMNH); [Alluriquín], Río Toachi, [0°19'6"S,78°57'13"W], 650 m, (Velástegui, S. E.), 30 Jul 1973, 1♂, 1 Jul 1973, 1♀ (MUSM); [Alluriquín], Río Toachi, [0°19'6"S,78°57'13"W], 700-1000 m, (de Lafebre, R.), Jun 1968, 1♀ [FLMNH-MGCL-253684], (FLMNH); [Alluriquín], Río Toachi, [0°19'6"S,78°57'13"W], 880 m, (de Lafebre, R.), Jan 1969, 1♂ [FLMNH-MGCL-253670], (FLMNH); [c. 10 km N Pedro Vicente Maldonado], Celica, [0°10'N,79°5'W], (Boyer, P.), (PIBO); [Salto de] Napac, [0°20'6"S,78°53'24"W], 1000 m, (Sullivan, J. B.), 3 Dec 1975, 1♀ [FLMNH-MGCL-253662], (FLMNH); 12 km E Santo Domingo de los Colorados, [Hotel] Tinalandia, [0°18'S,79°4'W], 750-850 m, (Austin, G. & A.), 10 May 1988, 1♀ [FLMNH-MGCL-253642], (FLMNH), 13 May

Fig. 9 (p. 17, facing page). Adults of new and similar Godyridina taxa, all from Ecuador unless otherwise stated. See text for wing lengths of new taxa, other scale bars are 1 cm. **A.** *Brevioleria arzalia loronia* n. ssp., holotype ♂, Peru, Loreto, Arcadia (MUSM). **B.** *Brevioleria arzalia loronia* n. ssp., ♀, Orellana, Napo Wildlife Center, Napo trail (FLMNH). **C.** *Brevioleria aelia oncidia*, ♂, Peru, Loreto, Pebas (NHMUK, syntype *Ithomia tenera* Srnka). **D.** *Hypoleria alema pastaza* n. ssp., holotype ♂, Pastaza, Shell (FLMNH).



Fig. 9 (continued). E. *Hypoleria alema pastaza* n. ssp., ♀, Pastaza, Hacienda Moravia (FLMNH). F. *Hypoleria alema ina*, ♂, Zamora-Chinchipe, Quebrada de Chorillos (FLMNH). G. *Hypomenitis hermana serafina* n. ssp., holotype ♂, Zamora-Chinchipe, San Francisco, casa de Arcoiris (FLMNH). H. *Hypomenitis hermana serafina* n. ssp., ♀, Zamora-Chinchipe, San Francisco, casa de Arcoiris (FLMNH). I. *Hypomenitis hermana hermana*, ♂, Tungurahua, environs of Ambato (NHMUK). J. *Hypomenitis hermana chamba* n. ssp., holotype ♂, Zamora-Chinchipe, km 4.3 San Andrés-Jimbura rd. (FLMNH). K. *Hypomenitis hermana joiceyi*, ♀, Sucumbios, Quebrada El Garrapatal (FLMNH). L. *Hypomenitis hermana joiceyi*, ♂, Sucumbios, Quebrada El Garrapatal (FLMNH). M. *Hypomenitis oneidodes guarumales* n. ssp., holotype ♂, Morona-Santiago, Guarumales/Hidropaute (PIBO). N. *Hypomenitis oneidodes guarumales* n. ssp., ♀, Morona-Santiago, Guarumales/Hidropaute (NHMUK). O. *Hypomenitis oneidodes oneidodes*, ♂, Napo, Estación Científica Yanayacu (FLMNH). P. *Hypomenitis oneidodes nicolasi* n. ssp., holotype ♂, Zamora-Chinchipe, San Francisco, casa de Arcoiris (FLMNH). Q. *Hypomenitis oneidodes nicolasi* n. ssp., ♀, Zamora-Chinchipe, San Francisco, casa de Arcoiris (NHMUK). R. *Hypomenitis oneidodes oneidodes*, ♀, Ecuador (NHMUK, holotype *Hypomenitis oneidodes* Kaye).

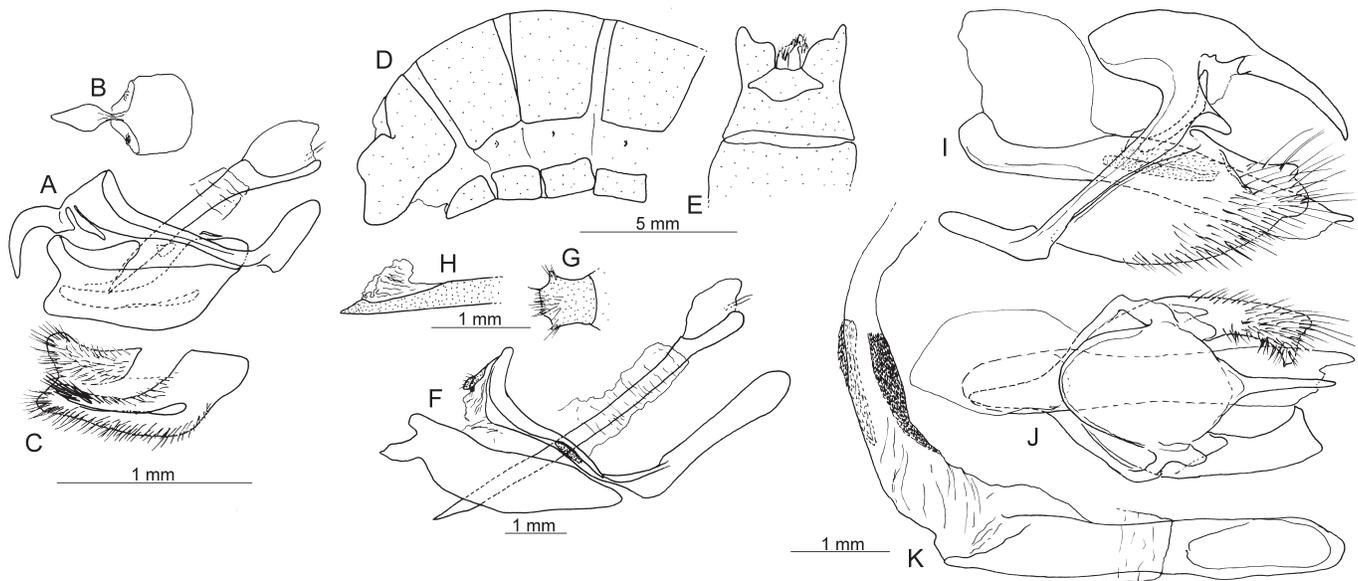


Fig. 10. Views of abdomens and male genitalia of new *Scada*, *Methona* and *Elzunia* taxa; shading representing sclerotization is variable, and setae are variously omitted for clarity. **A-C.** *Scada reckia ruiza* n. ssp., Ecuador, Zamora-Chinchi, Río Palanda (SCADA-6): **A**, lateral; **B**, dorsal tegumen and uncus; **C**, inside left valva. **D-H.** *Methona grandior batesi* n. ssp., Ecuador, Orellana, Estación Científica Yasuni (KW-15-209): **D**, lateral abdomen; **E**, dorsal posterior tip abdomen; **F**, lateral; **G**, dorsal uncus; **H**, lateral aedeagus. **I-K.** *Elzunia bomplandii golondrina* n. ssp., holotype (KW-19-11): **I**, lateral; **J**, dorsal; **K**, dorsal aedeagus, vesica everted.

1988, 1♀ [FLMNH-MGCL-253643], (FLMNH), 9 May 1988, 1♀ [FLMNH-MGCL-253640], 1♀ [FLMNH-MGCL-253641], (FLMNH); Hotel Tinalandia, Río Tanti, [0°20'S,79°0'30"W], 750-800 m, (Willmott, K. R., Hall, J. P. W.), 2-4 Jul 1991, 2♂, 2♀, (FLMNH), 29 Jun 1993, 1♂, 2♀, (FLMNH); km 20 Pacto-Guayabillas rd., [0°11'36"N,78°51'30"W], 800 m, (Aldaz, R.), 1♀ [FLMNH-MGCL-150774], (FLMNH); old Quito-Sto. Domingo rd., Río Pilatón, [0°18'52"S,78°55'41"W], 900 m, (Willmott, K. R., Hall, J. P. W.), 30 Jun 1993, 1♀, (FLMNH); Pisotanti, [0°17'S,79°4'W], 620 m, (Velástegui, S. E.), 22 Aug 1973, 1♀, 8 Feb 1988, 1♀, (MUSM); Río Mindo, Mindo, [0°4'20"S,78°45'W], 1000 m, (Willmott, K. R.), 10 Jul 1998, 1♀ [FLMNH-MGCL-143959], (FLMNH); Río Palenque, [0°36'12"S,79°18'36"W], 200 m, (Pliske, T.E.), 2 Apr 1973, 1♂ [FLMNH-MGCL-253748], 1♂ [FLMNH-MGCL-253749], 1♂ [FLMNH-MGCL-253750], 1♀ [FLMNH-MGCL-253754], 1♀ [FLMNH-MGCL-253755], (FLMNH), 30 Mar 1973, 1♀ [FLMNH-MGCL-253756], (FLMNH), 31 Mar 1973, 1♂ [FLMNH-MGCL-253757], (FLMNH); Río Palenque, [0°36'12"S,79°18'36"W], 220 m, (Vénédictoff, N.), 10 May 1976, 1♂ [FLMNH-MGCL-253687], 1♀ [FLMNH-MGCL-253692], (FLMNH); Río Palenque, [0°36'12"S,79°18'36"W], 400 m, (Dodson, C.), Sep 1973, 1♂ [FLMNH-MGCL-253689], 1♂ [FLMNH-MGCL-253690], 1♂ [FLMNH-MGCL-253691], 1♂ [FLMNH-MGCL-253697], 1♂ [FLMNH-MGCL-253698], 1♂ [FLMNH-MGCL-253699], 1♂ [FLMNH-MGCL-253700], 1♂ [FLMNH-MGCL-253701], 1♂ [FLMNH-MGCL-253702], 1♂ [FLMNH-MGCL-253703], 1♂ [FLMNH-MGCL-253711], 1♂ [FLMNH-MGCL-253712], 1♂ [FLMNH-MGCL-253713], 1♂ [FLMNH-MGCL-253714], 1♂ [FLMNH-MGCL-253715], 1♂ [FLMNH-MGCL-253716], 1♂ [FLMNH-MGCL-253717], 1♂ [FLMNH-MGCL-253723], 1♂ [FLMNH-MGCL-253724], 1♂ [FLMNH-MGCL-253725], 1♂ [FLMNH-MGCL-253726], 1♂ [FLMNH-MGCL-253727], 1♂ [FLMNH-MGCL-253728], 1♂ [FLMNH-MGCL-253729], 1♂ [FLMNH-MGCL-253734], 1♂ [FLMNH-MGCL-253735], 1♂ [FLMNH-MGCL-253736], 1♂ [FLMNH-MGCL-253737], 1♂ [FLMNH-MGCL-253738], 1♂ [FLMNH-MGCL-253739], 1♂ [FLMNH-MGCL-253741], 1♂ [FLMNH-MGCL-253742], 1♂ [FLMNH-MGCL-253743], 1♀ [FLMNH-MGCL-253693], 1♀ [FLMNH-MGCL-253694], 1♀ [FLMNH-MGCL-253695], 1♀ [FLMNH-MGCL-253696], 1♀ [FLMNH-MGCL-253704], 1♀ [FLMNH-MGCL-253705], 1♀ [FLMNH-MGCL-253706], 1♀ [FLMNH-MGCL-253707], 1♀ [FLMNH-MGCL-253708], 1♀ [FLMNH-MGCL-253709], 1♀ [FLMNH-MGCL-253710], 1♀ [FLMNH-MGCL-253718], 1♀ [FLMNH-MGCL-253719], 1♀ [FLMNH-MGCL-253720], 1♀ [FLMNH-MGCL-253721], 1♀ [FLMNH-MGCL-253722], 1♀ [FLMNH-MGCL-253730], 1♀ [FLMNH-MGCL-253731], 1♀ [FLMNH-MGCL-253732], 1♀ [FLMNH-MGCL-253733], (FLMNH), Sep 1973,

1♂ [FLMNH-MGCL-253688], (FLMNH), (Dodson, T.), 1♂ [FLMNH-MGCL-253740], 1♂ [FLMNH-MGCL-253744], 1♂ [FLMNH-MGCL-253745], 1♂ [FLMNH-MGCL-253747], 1♀ [FLMNH-MGCL-253751], 1♀ [FLMNH-MGCL-253752], 1♀ [FLMNH-MGCL-253753], (FLMNH), 1972, 1♂ [FLMNH-MGCL-253746], (FLMNH), (Pliske, T. E.), 13 Apr 1972, 1♂ [FLMNH-MGCL-253761], 1♂ [FLMNH-MGCL-253762], (FLMNH), 18 Apr 1972, 1♂ [FLMNH-MGCL-253759], (FLMNH), Apr 1972, 1♂ [FLMNH-MGCL-253760], (FLMNH), (Simon, M. J.), 10 Jul 1972, 1♂ [FLMNH-MGCL-253758], 1♀ [FLMNH-MGCL-253763], (FLMNH); Río Palenque, nr. Patricia Pilar, Estación Río Palenque, [0°36'12"S,79°18'36"W], 180 m, (Sullivan, J. B.), 2 Dec 1975, 1♀ [FLMNH-MGCL-253765], 1♀ [FLMNH-MGCL-253766], 1♀ [FLMNH-MGCL-253767], (FLMNH); Río Toachi, Alluriquín, [0°19'S,78°59'45"W], (Boyer, P.), (PIBO); Río Toachi, Alluriquín, [0°19'S,78°59'45"W], 620 m, (Velástegui, S. E.), 27 Jul 1973, 1♂, 2♀, (MUSM); San Pablo, [0°19'S,79°6'W], 1100 m, (de Lafebre, R.), Jun 1970, 1♂ [FLMNH-MGCL-253681], 1♂ [FLMNH-MGCL-253682], 1♀ [FLMNH-MGCL-253685], 1♀ [FLMNH-MGCL-253686], (FLMNH); Santo Domingo de los Colorados, [0°15'S,79°9'W], 900 m, (Goodfellow, W.), Oct 1898, 1♂, 2♀, (NHMUK), (Spillmann, W.), May 1928, 1♀, (NHMUK); Santo Domingo, [0°15'S,79°9'W], 1000 m, (de Lafebre, R.), Jan 1969, 1♂ [FLMNH-MGCL-253654], (FLMNH); Santo Domingo, [0°15'S,79°9'W], 350 m, (Jenkins, D. W.), 16 Oct 1976, 1♂ [FLMNH-MGCL-253605], 1♂ [FLMNH-MGCL-253606], 1♂ [FLMNH-MGCL-253607], 1♂ [FLMNH-MGCL-253608], 1♂ [FLMNH-MGCL-253609], 1♂ [FLMNH-MGCL-253610], 1♂ [FLMNH-MGCL-253611], 1♂ [FLMNH-MGCL-253619], 1♂ [FLMNH-MGCL-253620], 1♂ [FLMNH-MGCL-253621], 1♂ [FLMNH-MGCL-253622], 1♂ [FLMNH-MGCL-253623], 1♂ [FLMNH-MGCL-253624], 1♂ [FLMNH-MGCL-253625], 1♂ [FLMNH-MGCL-253631], 1♂ [FLMNH-MGCL-253632], 1♂ [FLMNH-MGCL-253633], 1♂ [FLMNH-MGCL-253634], 1♀ [FLMNH-MGCL-253612], 1♀ [FLMNH-MGCL-253613], 1♀ [FLMNH-MGCL-253614], 1♀ [FLMNH-MGCL-253615], 1♀ [FLMNH-MGCL-253616], 1♀ [FLMNH-MGCL-253617], 1♀ [FLMNH-MGCL-253618], 1♀ [FLMNH-MGCL-253626], 1♀ [FLMNH-MGCL-253627], 1♀ [FLMNH-MGCL-253628], 1♀ [FLMNH-MGCL-253629], 1♀ [FLMNH-MGCL-253630], 1♀ [FLMNH-MGCL-253635], 1♀ [FLMNH-MGCL-253636], 1♀ [FLMNH-MGCL-253637], 1♀ [FLMNH-MGCL-253638], 1♀ [FLMNH-MGCL-253639], (FLMNH); Santo Domingo, [0°15'S,79°9'W], 900 m, (de Lafebre, R.), Jan 1969, 1♂ [FLMNH-MGCL-253648], 1♂ [FLMNH-MGCL-253655], 1♂ [FLMNH-MGCL-253656], 1♂ [FLMNH-MGCL-253657], 1♂ [FLMNH-MGCL-253658], 1♂ [FLMNH-MGCL-253659], 1♂ [FLMNH-MGCL-253664], 1♀ [FLMNH-MGCL-253653], 1♀ [FLMNH-

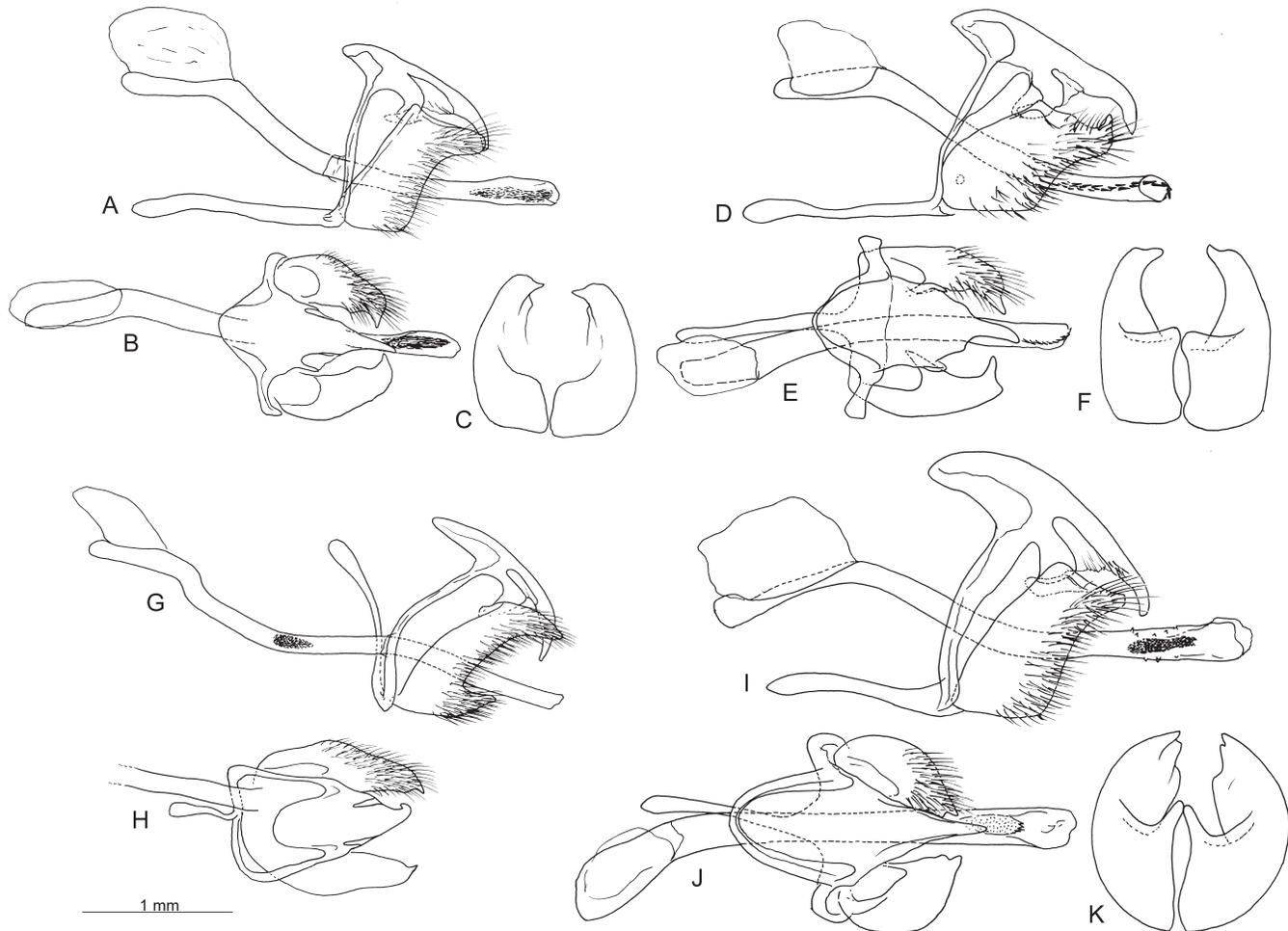


Fig. 11. Views of male genitalia of new *Ithomia* taxa; setae are variously omitted for clarity. **A-C.** *Ithomia agnosia zumba* n. ssp., Ecuador, Zamora-Chinchipec, Río Palanda (ITHOM-3): **A**, lateral; **B**, dorsal; **C**, ventral valvae. **D-E.** *Ithomia arduinna ardua* n. ssp., holotype (KW-15-210): **D**, lateral; **E**, dorsal; **F**, ventral valvae. **G-H.** *Ithomia hymettia petitia* n. ssp., Colombia, Valle del Cauca, Buga (PIBO): **G**, lateral; **H**, dorsal. **I-K.** *Ithomia iphianassa occidentissima* n. ssp., holotype (KW-15-211): **I**, lateral; **J**, dorsal; **K**, ventral valvae.

MGCL-253660], 1♀ [FLMNH-MGCL-253661], (FLMNH), Jul 1968, 1♂ [FLMNH-MGCL-253665], 1♂ [FLMNH-MGCL-253666], (FLMNH), Jan 1969, 1♂ [FLMNH-MGCL-253647], 1♂ [FLMNH-MGCL-253663], 1♀ [FLMNH-MGCL-253652], (FLMNH); Toachi Grande, [0°19'S, 78°57'W], 1100 m, (Velástegui, S. E.), 30 Jul 1973, 1♂, (MUSM); nr. Patricia Pilar, Centinela ridge, [0°36'12"S, 79°18'36"W], 600 m, (Willmott, K. R.), 12 Aug 1996, 1♀, (FLMNH), 1♀, (MUSM); *Guayas*: Milagro, [2°7'S, 79°36'W], (Thomas, R. H.), 1929, 1♂, (OUM); *Not located*: 'Ecuador', 2♀, (NHMUK).

Other specimens examined (not paratypes): Ecuador: *Loja*: 'San Pedro de Vilcabamba, Río Uchima' - (error), (de Lafébre, R.), Jul 1970, 1♀ [FLMNH-MGCL-253769], 1♀ [FLMNH-MGCL-253770], (FLMNH), Jul 1970, 1♂ [FLMNH-MGCL-253764], 1♀ [FLMNH-MGCL-253768], (FLMNH); *Napo*: 'km 30 Tena-Puyo rd., Satzayacu' - (error), (de Lafébre, R.), Nov 1967, 1♀ [FLMNH-MGCL-253775], 1♀ [FLMNH-MGCL-253776], (FLMNH); *Tungurahua*: 'Río Blanco' - (error), (de Lafébre, R.), Jun 1968, 1♀ [FLMNH-MGCL-253774], (FLMNH), Nov 1968, 1♂ [FLMNH-MGCL-253771], (FLMNH); 'Río Pastaza', (de Lafébre, R.), Dec 1968, 1♂ [FLMNH-MGCL-253772], (FLMNH), Nov 1967, 1♂ [FLMNH-MGCL-253773], (FLMNH); **Country unknown:** *Not located*: no data, 1♂ [FLMNH-MGCL-253777], (FLMNH), 1♂ [FLMNH-MGCL-253778], 1♂ [FLMNH-MGCL-253779], 1♂ [FLMNH-MGCL-253780], 1♂ [FLMNH-MGCL-253781], 1♂ [FLMNH-MGCL-253782], 1♂ [FLMNH-MGCL-253788], 1♂ [FLMNH-MGCL-253789], 1♂ [FLMNH-MGCL-253790], 1♂ [FLMNH-MGCL-253791], 1♂ [FLMNH-MGCL-253792], 1♂ [FLMNH-MGCL-253796], 1♂ [FLMNH-MGCL-253797], 1♂ [FLMNH-MGCL-253798], 1♂ [FLMNH-MGCL-253799], 1♂ [FLMNH-MGCL-253800], 1♂ [FLMNH-MGCL-253801], 1♂ [FLMNH-MGCL-253806], 1♂ [FLMNH-MGCL-253807], 1♂ [FLMNH-

MGCL-253808], 1♂ [FLMNH-MGCL-253809], 1♂ [FLMNH-MGCL-253810], 1♂ [FLMNH-MGCL-253813], 1♂ [FLMNH-MGCL-253814], 1♂ [FLMNH-MGCL-253815], 1♂ [FLMNH-MGCL-253816], 1♂ [FLMNH-MGCL-253817], 1♂ [FLMNH-MGCL-253818], 1♂ [FLMNH-MGCL-253819], 1♂ [FLMNH-MGCL-253820], 1♂ [FLMNH-MGCL-253821], 1♂ [FLMNH-MGCL-253822], 1♂ [FLMNH-MGCL-253823], 1♂ [FLMNH-MGCL-253824], 1♂ [FLMNH-MGCL-253825], 1♂ [FLMNH-MGCL-253826], 1♂ [FLMNH-MGCL-253827], 1♂ [FLMNH-MGCL-253828], 1♂ [FLMNH-MGCL-253829], 1♂ [FLMNH-MGCL-253830], 1♂ [FLMNH-MGCL-253831], 1♂ [FLMNH-MGCL-253832], 1♂ [FLMNH-MGCL-253833], 1♂ [FLMNH-MGCL-253834], 1♂ [FLMNH-MGCL-253835], 1♂ [FLMNH-MGCL-253836], 1♂ [FLMNH-MGCL-253837], 1♀ [FLMNH-MGCL-253783], 1♀ [FLMNH-MGCL-253784], 1♀ [FLMNH-MGCL-253785], 1♀ [FLMNH-MGCL-253786], 1♀ [FLMNH-MGCL-253787], 1♀ [FLMNH-MGCL-253793], 1♀ [FLMNH-MGCL-253794], 1♀ [FLMNH-MGCL-253795], 1♀ [FLMNH-MGCL-253802], 1♀ [FLMNH-MGCL-253803], 1♀ [FLMNH-MGCL-253804], 1♀ [FLMNH-MGCL-253805], 1♀ [FLMNH-MGCL-253811], 1♀ [FLMNH-MGCL-253812], (FLMNH).

Other records: **Ecuador:** *Esmeraldas*: Estación Científica Bilsa, [0°21'33"N, 79°42'2"W], 600 m, (Alex Young), Jul 1999, (collection unknown) (Young, A., undergraduate research project University of Leeds); *Pichincha*: [Pedro Vicente] Maldonado, [0°4'53"N, 79°2'57"W], 1100 m, (Piñas, F.), 13 Jul 1991, 1♀ [FDPR-8523], (FRPI); 12 km E Santo Domingo de los Colorados, [Hotel] Tinalandia, [0°18'S, 79°4'W], 800 m, (Piñas, F.), 13 Dec 2002, 1♀ [FDPR-8532], (FRPI), 23 Jul 2000, 1♀ [FDPR-8546], (FRPI), 25 Jul 2000, 1♀ [FDPR-8550], (FRPI), 25 Sep 1999, 1♀ [FDPR-8528], (FRPI), 7 Oct 2001, 1♀ [FDPR-8548], (FRPI), 8 Sep 1991, 1♀ [FDPR-8555], (FRPI), 8 Sep 2001, 1♀

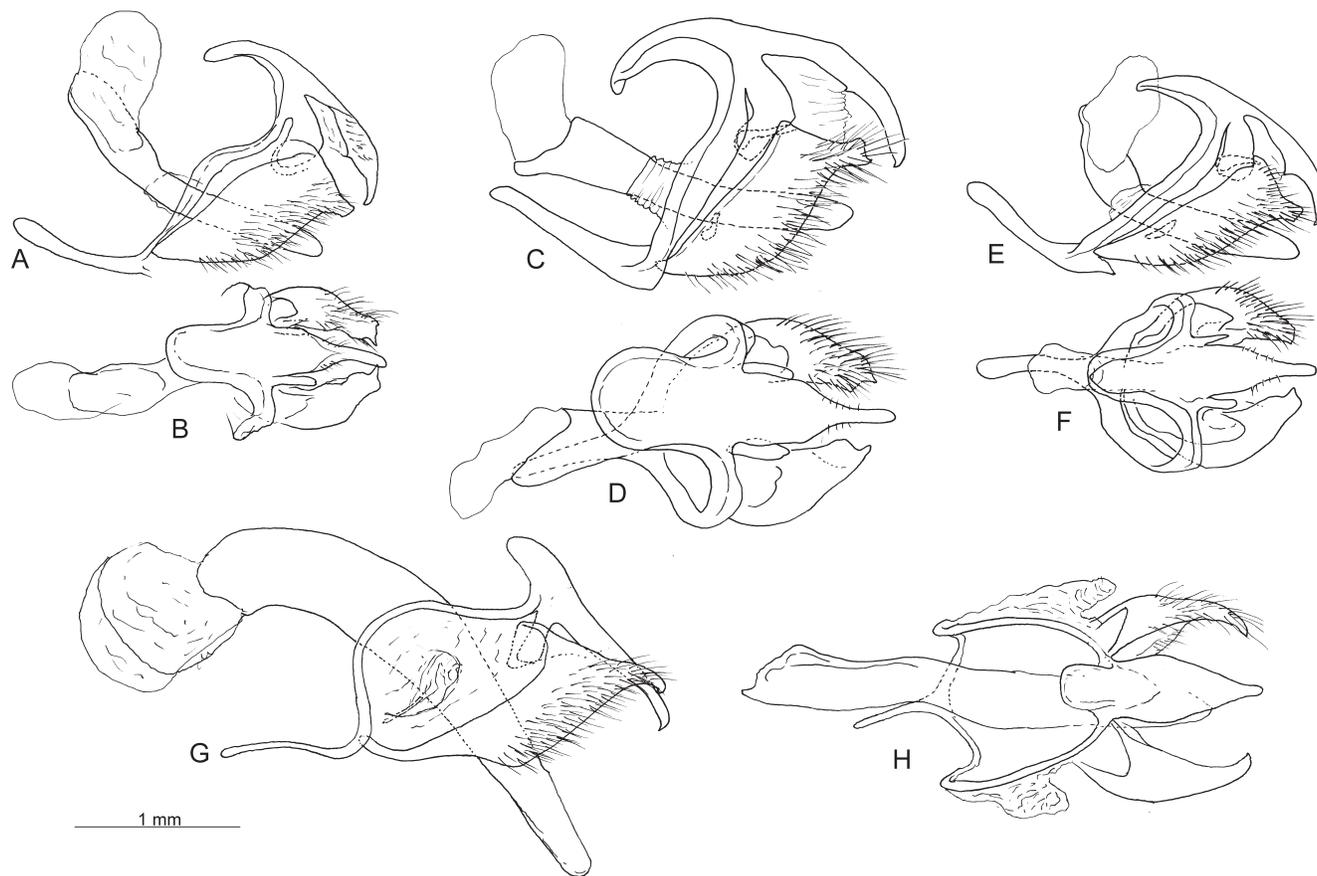


Fig. 12. Views of male genitalia of new *Hyaliris* and *Hypothyris* taxa; setae are variously omitted for clarity. **A-B.** *Hyaliris antea lalimba* n. ssp., Ecuador, Zamora-Chinchipec, E of Zumba (KW-21-01): **A**, lateral; **B**, dorsal. **C-D.** *Hyaliris praxilla leuca* n. ssp., holotype (HYALYRIS-9): **C**, lateral; **D**, dorsal. **E-F.** *Hyaliris ocna equatoria* n. ssp., holotype (HYALYRIS-11): **E**, lateral; **F**, dorsal. **G-H.** *Hypothyris cantobrica zamorita* n. ssp., holotype (KW-21-02): **G**, lateral; **H**, dorsal.

[FDPR-8533], 1♀ [FDPR-8534], 1♀ [FDPR-8535], 1♀ [FDPR-8538], (FRPI), 9 Sep 2001, 1♀ [FDPR-8513], 1♀ [FDPR-8524], 1♀ [FDPR-8529], 1♀ [FDPR-8530], 1♀ [FDPR-8531], 1♀ [FDPR-8536], 1♀ [FDPR-8544], 1♀ [FDPR-8545], 1♀ [FDPR-8547], 1♀ [FDPR-8549], (FRPI); Hotel Tinalandia, Río Tanti, [0°20'S, 79°0'30"W], 750-800 m, (Willmott, K. R., Hall, J. P. W.), 8-14 May 1994, (W&H); nr. La Unión del Toachi, Otongachi Reserve, [0°18'49"S, 78°57'15"W], 850 m, (Miller, J.), 1♂, 1♀, (photograph of live specimen) (Miller, J., by email 7 Jun 2010); Patricia del Pilar, [0°36'12"S, 79°18'36"W], 400 m, (Piñas, F.), 18 Aug 2001, 1♀ [FDPR-8551], (FRPI); Quito-Sto. Domingo old rd., Hacienda Santa Isabel, [0°18'48"S, 78°56'W], 900 m, (Willmott, K. R., Hall, J. P. W.), Jun, (W&H); Río Mindo, Mindo, [0°42'0"S, 78°45'W], 1200-1300 m, (Winhard W.), 15 Aug 1992, 1 specimen [INABIO-TABDP-20589], (INABIO); Río Palenque, nr. Patricia Pilar, Centro Científico Palenque, [0°36'12"S, 79°18'36"W], 200 m, (collection unknown) (Dodson, T., unpublished list at Centro Científico Río Palenque); Río Toachi, Alluriquín, [0°19'S, 78°59'45"W], 1000 m, (Piñas, F.), 13 Jun 1998, 1♀ [FDPR-8515], 1♀ [FDPR-8522], (FRPI); Río Toachi, Alluriquín, [0°19'S, 78°59'45"W], 900 m, (Piñas, F.), 4 Aug 2001, 1♀ [FDPR-8537], (FRPI); Taguaza, [0°18'S, 79°2'W], 1750 m, (Lafebre R.), Apr 1978, 1♀ [INABIO-TABDP-20885], (INABIO); *Manabí*: Montecristi, [1°3'32"S, 80°40'46"W], 158 m, (Piñas, F.), 16 Jun 1994, 1♀ [FDPR-8514], 1♀ [FDPR-8516], 1♀ [FDPR-8525], (FRPI); *Cotopaxi*: nr. Guayacán, Latacunga-Quevedo rd., San Marcos, [0°50'S, 79°10'W], 500 m, (Willmott, K. R.), 6 Aug 1996, (W&H); *El Oro*: Río Jubones, nr. Pasaje, Uzhcurrumi, [3°19'24"S, 79°35'42"W], 300 m, (Piñas, F.), 3 Jun 1995, 1♀ [FDPR-8542], (FRPI), 4 Mar 1995, 1♀ [FDPR-8521], (FRPI); Río Jubones, nr. Pasaje, Uzhcurrumi, [3°19'24"S, 79°35'42"W], 400 m, (Piñas, F.), 14 May 1994, 1♀ [FDPR-8517], 1♀ [FDPR-8552], (FRPI), 3 Jun 1995, 1♀ [FDPR-8541], (FRPI), 7 Apr 1995, 1♀ [FDPR-8518], 1♀ [FDPR-8526], (FRPI), 8 Jul 1994, 1♀ [FDPR-8527], 1♀ [FDPR-8543], 1♀ [FDPR-8554], (FRPI), Apr 1994, 1♀ [FDPR-8519], 1♀ [FDPR-8520], 1♀ [FDPR-8539], 1♀ [FDPR-8540], 1♀ [FDPR-8553], (FRPI).

Etymology: The species name is loosely based on the Latin adjective 'occidentalis', meaning western, in reference to its occurrence in western Ecuador, modified to resemble other *I. iphianassa* subspecies names (Lamas, 2004).

Taxonomy and variation: This taxon is treated as a subspecies of *I. iphianassa* Doubleday, 1847 because of its similar yellow and orange coloration, rarely present but distinctive black HW discocellular spot, and similar male genitalia, in particular the aedeagus with small 'teeth' near the distal tip and base of the valva with narrow, finger-like projections in ventral view. DNA barcodes group the taxon with *I. iphianassa ethilla* (Fig. 20), as well as the allopatric Amazonian species *Ithomia salapia*, a close relationship known from previous studies (Mallarino et al., 2005). Although rather variable, like most *I. iphianassa* taxa, several characters observed in long series of specimens consistently distinguish *I. iphianassa occidentissa* n. ssp. from *I. iphianassa ethilla*, which replaces it in northern Ecuador, as discussed under the Diagnosis. The taxon is common in collections and the lack of a name probably reflects its similarity to *Ithomia cleora* Hewitson, 1855, under which name it is often misidentified. *Ithomia cleora* is endemic to moist forests from northwestern Ecuador to northwestern Peru and can be found flying together with *I. iphianassa occidentissa*. The two species are close relatives but not sister species (Mallarino et al., 2005; Elias et al., 2009), and *I. cleora*, also a very variable species, may

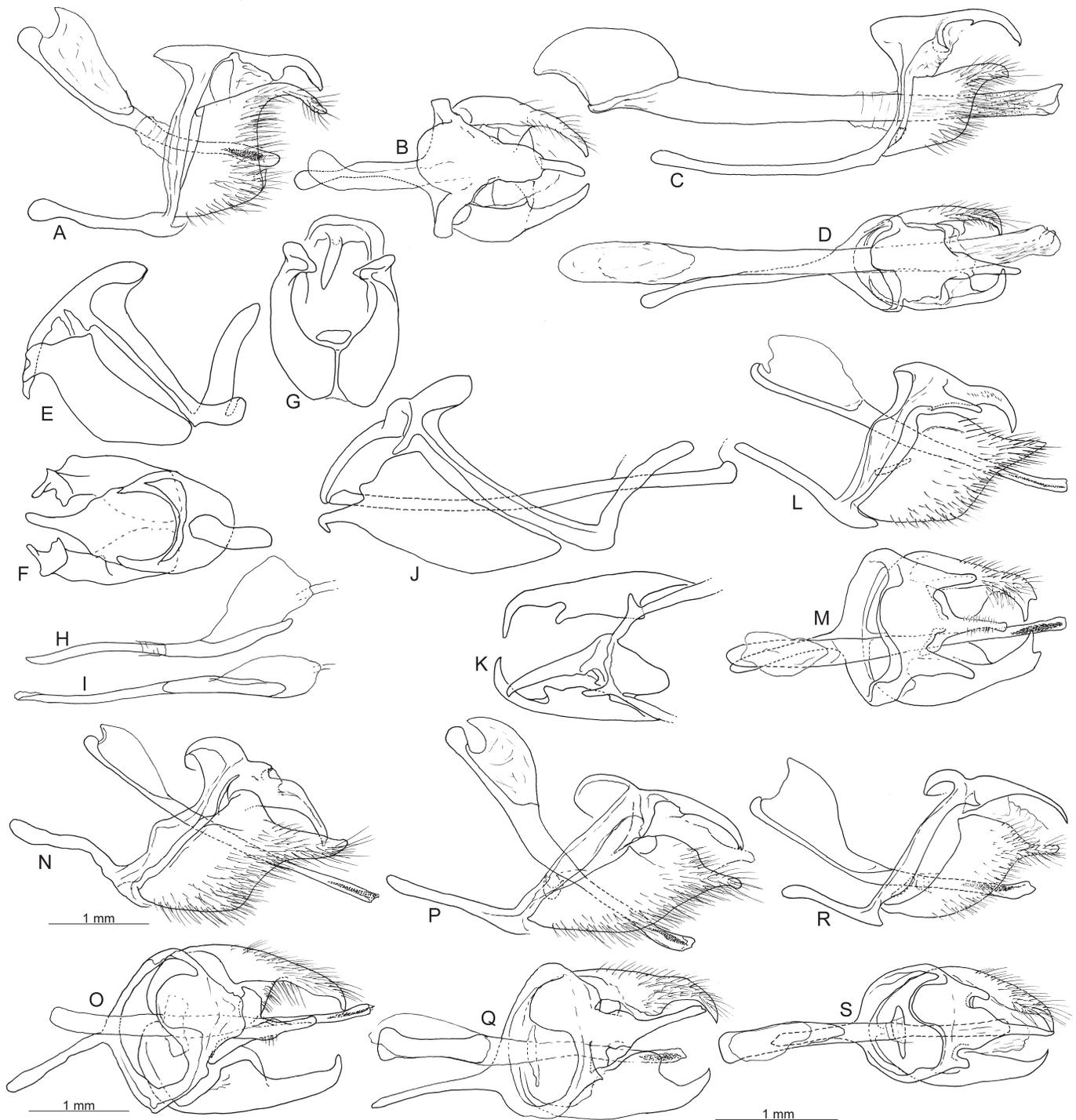


Fig. 13. Views of male genitalia of new Oleriina taxa; setae are variously omitted for clarity. **A-B.** *Hyposcada illinissa morona* n. ssp., holotype (KW-21-03): **A**, lateral; **B**, dorsal. **C-D.** *Hyposcada kena unki* n. ssp., Ecuador, Morona-Santiago, Río Kusuimi (KW-21-04): **C**, lateral; **D**, dorsal. **E-I.** *Hyposcada taliata laetitia* n. ssp., holotype (OLERIA-39): **E**, lateral; **F**, dorsal; **G**, posterior; **H**, lateral aedeagus; **I**, dorsal aedeagus. **J-K.** *Ollantaya olerioides baeza* n. ssp., holotype (OLERIA-15): **J**, lateral; **K**, dorsal. **L-M.** *Oleria tremona benigna* n. ssp., holotype (OLERIA-24): **L**, lateral; **M**, dorsal. **N-O.** *Oleria radina bonita* n. ssp., holotype (KW-21-05): **N**, lateral; **O**, dorsal. **P-Q.** *Oleria tigilla raya* n. ssp., Ecuador, Zamora-Chinchi, Reserva Maycú (KW-21-06): **P**, lateral; **Q**, dorsal. **R-S.** *Oleria onega astigara* n. ssp., holotype (OLERIA-33): **R**, lateral; **S**, dorsal.

be most reliably distinguished by the translucent yellow scaling in FW cell Cu_2-Cu_1 not being aligned with the similar scaling in the distal part of the discal cell, whereas these yellow areas are often fused in *I. iphianassa occidentissa*. There are also subtle differences in wing shape (*I. cleora* has a more elongate HW)

and male genitalia (*I. iphianassa* has more elongate ventral inner projections from the valva in ventral view).

Distribution and natural history: This is a very common species in central western Ecuador, in the provinces of Pichincha and southern Esmeraldas, with scarcer records from Manabí

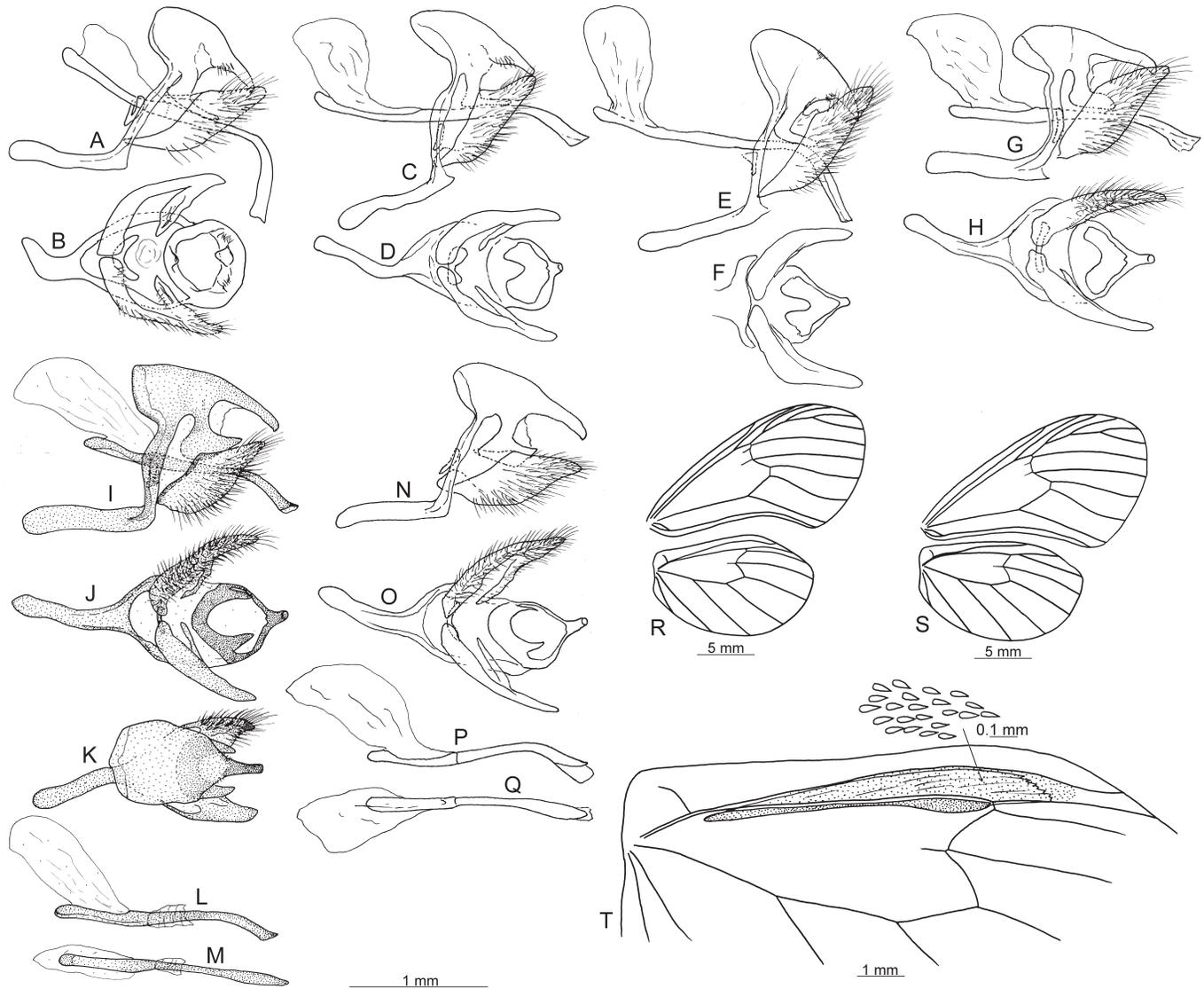


Fig. 14. Views of male genitalia (A-Q), male (R) and female (S) wing venation and male androconial scales (T) of new and similar *Episcada* taxa; shading representing sclerotization is variable, and setae are variously omitted for clarity. **A-B.** *Episcada clausina bomboiza* n. ssp., holotype (EPISCD-1): **A**, lateral; **B**, ventral. **C-D.** *Episcada hymenaea mirifica* n. ssp., Peru, Cuzco, 35 km W Pilcopata (KW-21-18): **C**, lateral; **D**, ventral. **E-F.** *Episcada polita pichincha* n. ssp., holotype (KW-21-07): **E**, lateral; **F**, ventral. **G-H.** *Episcada sulphurea*, Peru, Madre de Dios, Alto Río Madre de Dios (KW-21-27): **G**, lateral; **H**, ventral. **I-M.** *Episcada arcadia* n. sp., holotype (KW-21-25): **I**, lateral; **J**, dorsal; **K**, dorsal; **L**, lateral aedeagus; **M**, dorsal aedeagus. **N-O.** *Episcada arcadia navarro* n. ssp., holotype (MUSM): **N**, lateral; **O**, ventral; **P**, lateral aedeagus; **Q**, dorsal aedeagus. **R.** *Episcada arcadia* n. sp., male wing venation (FLMNH-ECD-76). **S.** *Episcada arcadia* n. sp., female wing venation (FLMNH-ECD-80). **T.** *Episcada arcadia* n. sp., male wing venation and androconial scales (FLMNH-ECD-76).

and as far south as El Oro (Fig. 32A). It occurs from 500-1000 m in rain forest habitats, particularly along forest edges and in secondary forest, flying with and closely resembling *I. cleora*.

Hyaliris antea lalimba Lamas & Willmott, **new subspecies**
Figs. 3A,B, 12A-B, 32B

Hyaliris antea n. ssp.: Lamas (2004: 177, no. 74j)

Diagnosis and identification: This subspecies is most similar to *H. antea amarilla* (Ecuador, Zamora-Chinchi to Peru, Cajamarca) (Fig. 3O) and *H. antea frater* (Salvin, 1869) (Peru, Pasco and Junín), which occur to the north and south of its distribution. It may be distinguished from both (and all other

H. antea subspecies) by the yellowish tinge to the forewing transparent areas, which are similar in color to the hindwing, and by the much broader black FW distal margin in the female, enclosing large white marginal spots.

Description: MALE (Fig. 3A, 12A-B): Forewing length 33 mm (mean 30.8 mm, n=2). *Wings:* as illustrated (Fig. 3A), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes brown, bare, with isolated white scales at base; antennae dark brown; labial palpi black with some white scaling along inside ventral edge and dorsally almost to tip; top of head with two white spots behind base of antennae and white spot in middle of head between bases of antennae, frons black with two white spots below bases of antennae. *Thorax:* dorsal surface dark brown with thin white medial stripe, ventral surface dark brown with broad white scaling on posterior half of mesothorax and slight white scaling posterior half of metathorax, forelegs, mid-

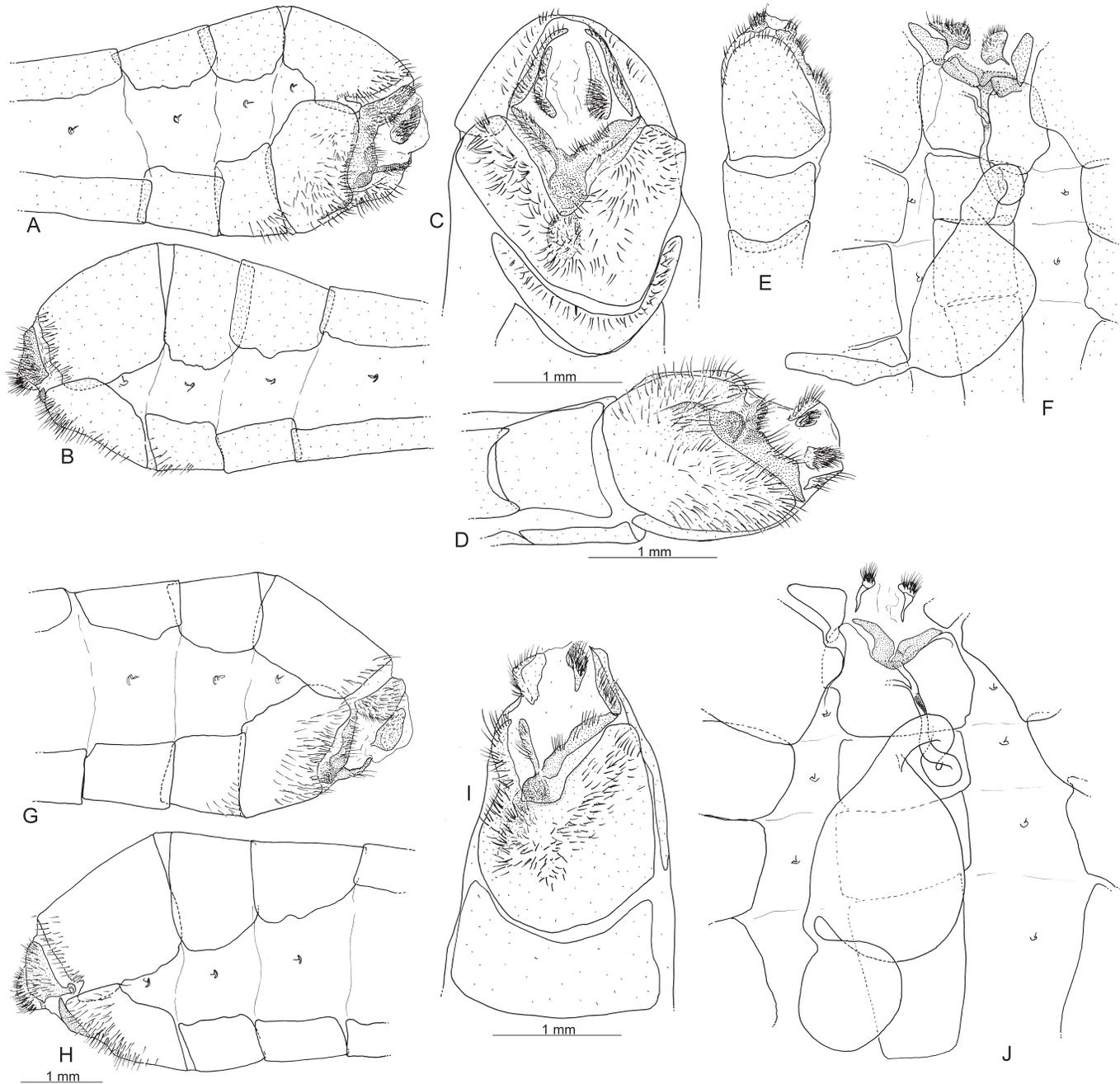


Fig. 15. Views of female abdomen and genitalia of new *Episcada* taxa; shading representing sclerotization is variable. **A-F.** *Episcada arcadia* n. sp., Ecuador, Río Napo, Boca del Río Añangu (KW-21-29): **A**, left lateral abdomen; **B**, right lateral abdomen; **C**, posterior abdomen tip; **D**, ventral abdomen tip; **E**, dorsal abdomen tip; **F**, dorsal genitalia. **G-J.** *Episcada arcadia navarro* n. ssp., paratype, Peru, San Martín, Navarro (MUSM): **G**, left lateral abdomen; **H**, right lateral abdomen; **I**, ventral abdomen tip; **J**, dorsal genitalia.

and hindlegs dark brown with white scaling ventrally. *Abdomen*: dorsal surface dark brown, ventral surface white. *Genitalia* (Fig. 12A-B): notable features include slightly bent aedeagus in lateral view (Fig. 12A) and single pointed valva posterior projection in dorsal view (Fig. 12B).

FEMALE: (Fig. 3B): Forewing mean length 30 mm (n=2). *Wings*: as illustrated (Fig. 3B), lacking DHW costal androconial scales. *Head, thorax, abdomen*: similar to male.

Types: HOLOTYPE ♂: **PERU**: Amazonas: Pedro Ruiz [Gallo], [5°57'S, 77°59'W], 900 m, (Lamas, G.), 16 Dec 1975, (MUSM).

PARATYPES (24♂, 33♀): **Ecuador**: Zamora-Chinchipec: E of Zumba, below El Pite, Río Mayo, [4°52'49"S, 79°5'30"W], 740 m, (Willmott, K. R., J. C. R., J. I. R.), 25 Jun 2014, 1♀ [FLMNH-MGCL-280585], 1♀ [FLMNH-MGCL-280586], 1♀ [FLMNH-MGCL-280587], (FLMNH); E of Zumba,

km 2.6 El Pite-Río Mayo rd., [4°51'58"S, 79°5'40"W], 1000 m, (Willmott, K. R., J. C. R., J. I. R.), 22 Jun 2014, 1♂ [FLMNH-MGCL-280578]; Genitalia dissection KW-21-01], 1♀ [FLMNH-MGCL-280579], (FLMNH), 25 Jun 2014, 1♂ [FLMNH-MGCL-280580], 1♂ [FLMNH-MGCL-280584], 1♀ [FLMNH-MGCL-280581], 1♀ [FLMNH-MGCL-280582], 1♀ [FLMNH-MGCL-280583], (FLMNH); km 18 Zumba-Los Sungas rd., Quebrada Huanchunangui, [4°55'11"S, 79°9'54"W], 1100 m, (Willmott, K. R.), 11 Oct 2010, 1♂ [FLMNH-MGCL-146706], 1♂ [FLMNH-MGCL-146814], 1♀ [FLMNH-MGCL-146697], 1♀ [FLMNH-MGCL-146704], 1♀ [FLMNH-MGCL-146725], 1♀ [FLMNH-MGCL-146738], 1♀ [FLMNH-MGCL-146771], 1♀ [FLMNH-MGCL-146772], 1♀ [FLMNH-MGCL-146783], 1♀ [FLMNH-MGCL-146840], (FLMNH), 3♀, (INABIO). **Peru**: Amazonas: Chachapoyas, [6°14'S, 77°53'W], 2345 m, (Mathan, M. de), 1889, 3♂, 1♀, (NHMUK); Buenos Aires, opp. Bagua Grande,

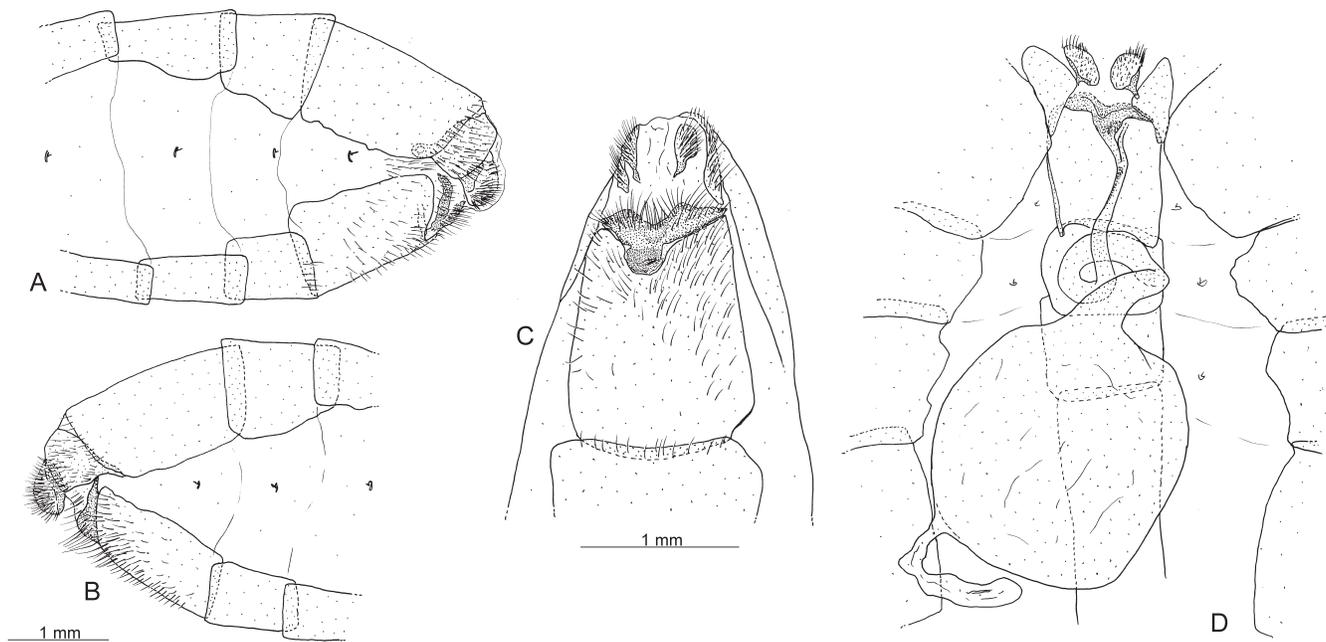


Fig. 16. Views of female abdomen and genitalia of *Episcada sulphurea*, Peru (MUSM); shading representing sclerotization is variable. **A**, left lateral abdomen; **B**, right lateral abdomen; **C**, ventral abdomen tip; **D**, dorsal genitalia.

[5°41'S, 78°24'W], 1300 m, (Hocking, P.), 3 Sep 1975, 4♂, 5♀, (MUSM); same data as HT, 6♂, 1♀, (MUSM); (Calderón, B.), Nov 2004, 1♂, (MUSM); 0-5 km E La Peca, [5°37'S, 78°26'W], 1100-1400 m, (Lamas, G.), 23 Sep 1999, 3♀, (MUSM); Quebrada Cuija, [5°54'S, 77°58'W], 1500 m, (Lamas, G.), 21 Nov 1996, 1♂, (MUSM); Chosgón, [5°56'S, 78°01'W], 1850 m, (Hocking, P.), 1-5 Sep, 2009, 1♂, (MUSM); San Antonio, [6°15'S, 77°55'W], 1950 m, (Campos, L. F.), 23 Nov 2009, 1♀, (MUSM); Cumba, Bagua Grande, [5°56'S, 78°40'W], 500 m, (Pintado, J.), 2012, 1♀, (MUSM); Catarata Gocta, [6°01'S, 77°53'W], ca. 1600 m, (Rosser, N.), 31 Oct 2014, 1♂, (MUSM); *Cajamarca*: 5 km W Jaén, [5°42'S, 78°50'W], 800 m, (Lamas, G.), 10-11 Feb 1975, 1♂, (MUSM); 2-8 km NE Hacienda Montesecco, [6°51'S, 79°06'W], 1200-1400 m, (Lamas, G.), 12-22 Nov 1978, 1♂, (MUSM); entre La Balsa y El Chaupe, [5°10'-12'S, 79°03'W], 1650-1850 m, (Grados, J.), 21 Jun 1995, 1♀, (MUSM); Naranja, [6°16'S, 78°51'W], 2300 m, (Lamas, G.), 6 Nov 1998, 1♀, (MUSM); San Luis de Lucma, Cutervo, [6°17'S, 78°38'W], 2200 m, (Pintado, J.), 2012, 1♀, (MUSM); *San Martín*: Mashuyacu, [6°31'S, 77°15'W], 1300 m, (Calderón, B.), Dec 2004, 1♂, (MUSM). *Not located*: 'Peru', 1♂, (MUSM).

Etymology: The name is derived from that of *Hyalyris latilimbata*, a species which is a close mimic of this subspecies, and it is treated as a feminine noun in apposition.

Taxonomy and variation: We treat this taxon as a subspecies of *H. antea* because it shares with the nominate subspecies similar male HW venation, with a short vein separating the base of veins M_1 and R_s (almost touching in the otherwise similar species *H. praxilla* (Hewitson, 1870) and *H. mestra* (Hopffer, 1874)), similar male genitalia (slightly angled aedeagus and single inward point at posterior tip of valva in dorsal view), and because DNA barcode data group it with other *H. antea* taxa, including the nominate subspecies (Fig. 21). In wing pattern, however, *Hyalyris antea lalimba* n. ssp. most closely resembles *H. latilimbata* (Weymer, 1890) (Fig. 3C), a species endemic to dry forests of northern Peru and southern Ecuador, which is a member of a different species group, being closely related to *H. coeno* (Doubleday, 1847), *H. mestra* and *H. praxilla* (Fox & Real, 1971; Chazot *et al.*, 2019; Fig. 21). The two species may be distinguished by numerous subtle characters; the male of *H.*

antea lalimba has HW venation (discocellular veins 3d and 2d aligned instead of angled) and shape (more elongate) as in other *H. antea* subspecies, and both sexes of *H. antea lalimba* lack or barely show a white spot in the VHW tornus in cell 3A-2A that is prominent in *H. latilimbata*, and have the white apical spot in FW cell M_1-R_5 smaller than that in R_5-R_4 (the opposite is found in *H. latilimbata*).

Specimens of this new taxon from southeastern Ecuador and northern Peru show a substantial amount of variation; in both sexes there is a black bar variably intruding in from the distal margin along vein Cu_1 , and in the female the forewing black distal margin ranges from being similar in width to the holotype, or even broader than in the figured female. Some females are similar to *H. antea amarilla*, but with yellow filling the HW transparent area and a very faint yellowish tinge in the FW transparent area. We interpret this variation to be due to intergradation with *H. antea amarilla*, which appears to replace *H. antea lalimba* at higher elevations in cloud forest. This apparent intergradation and a lack of obvious morphological differences supports placement of *H. antea lalimba* as a subspecies of *H. antea*, and their DNA barcodes show no divergence, at least between *H. antea lalimba* and specimens phenotypically similar to *H. antea amarilla* from adjacent higher elevations.

Distribution and natural history: This subspecies ranges from southeastern Ecuador in the valley of the Río Chinchipe to northern Peru, both in the valley of the Río Marañón, and the western slopes of the western Andes (Fig. 32B). In Ecuador, the subspecies occurs from 740-1100 m in remnant fragments of moist forest along rivers and streams, whereas in Peru it has been recorded from 500-2345 m. At the end of the wet season, we found both sexes flying from 1-2 m above the ground along shady trails and in forest understorey from 14:30 to 16:00

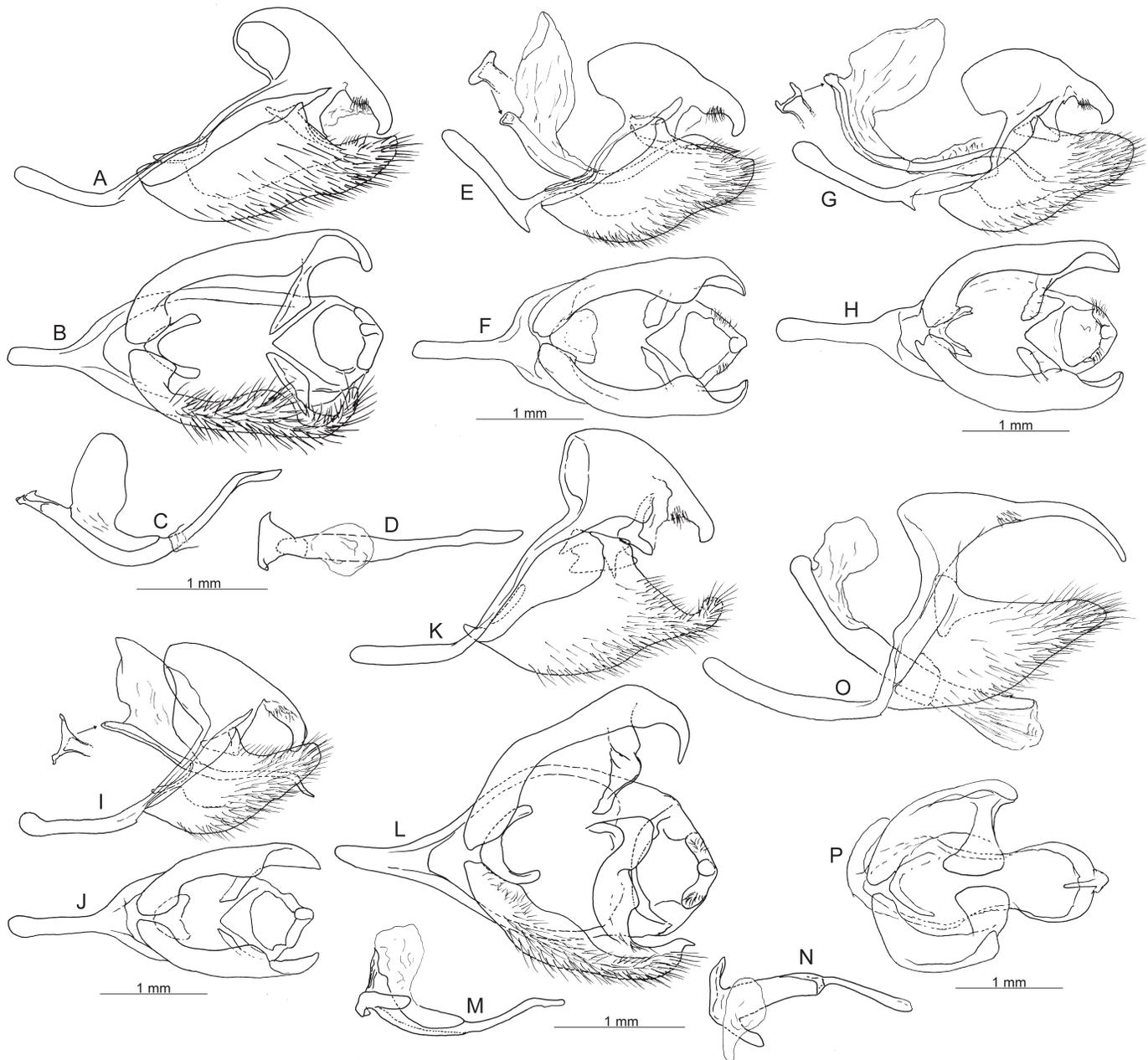


Fig. 17. Views of male genitalia of new *Pteronymia* taxa; setae are variously omitted for clarity. **A-D.** *Pteronymia alida luctuosa* n. ssp., holotype (PTERON-8): **A**, lateral; **B**, ventral; **C**, lateral aedeagus; **D**, dorsal aedeagus. **E-F.** *Pteronymia alida cosanga* n. ssp., holotype (KW-21-09): **E**, lateral (inset dorsal aedeagus tip); **F**, ventral. **G-H.** *Pteronymia alida francisca* n. ssp., holotype (KW-21-10): **G**, lateral (inset dorsal aedeagus tip); **H**, ventral. **I-J.** *Pteronymia inania bethana* n. ssp., Ecuador, Morona-Santiago, km. 9.5 Chigüinda-Gualaquiza rd. (KW-21-11): **I**, lateral (inset dorsal aedeagus tip); **J**, ventral. **K-N.** *Pteronymia hara olerina* n. ssp., Ecuador, Carchi, Lita ridge east of Río Baboso (PTERON-4): **K**, lateral; **L**, ventral; **M**, lateral aedeagus; **N**, dorsal aedeagus. **O-P.** *Pteronymia sao loreto* n. ssp., Ecuador, Sucumbíos, Laguna de Pañacocha (KW-21-12): **O**, lateral; **P**, ventral.

hrs, and a male was observed nectaring on purple Asteraceae flowers. In the middle of the dry season, we found both sexes congregating in numbers in a single, shaded understory site in a deep stream gully, along with other ithomiines which this subspecies presumably mimics, such as *H. latilimbata*, *Scada reckia ruiza* n. ssp. and *Scada kusa*. The subspecies is apparently replaced in higher elevation cloud forest by *H. antea amarilla*.

Hyalyris praxilla leuca Willmott & Lamas, new subspecies
Figs. 3D,E, 12C-D, 32C

Hyalyris praxilla n. ssp.: Lamas (2004: 177, no. 84b)

Hyalyris praxilla undescribed subsp.: Brehm et al. (2007: Table 2)

Diagnosis and identification: *Hyalyris praxilla leuca* n. ssp. is distinguished from the nominate subspecies (Fig. 3I) by the lack of any reddish orange in the HW tornus and anal margin. Both sexes are distinguished from very similar forms of *H. antea amarilla* with white HW translucence by being larger

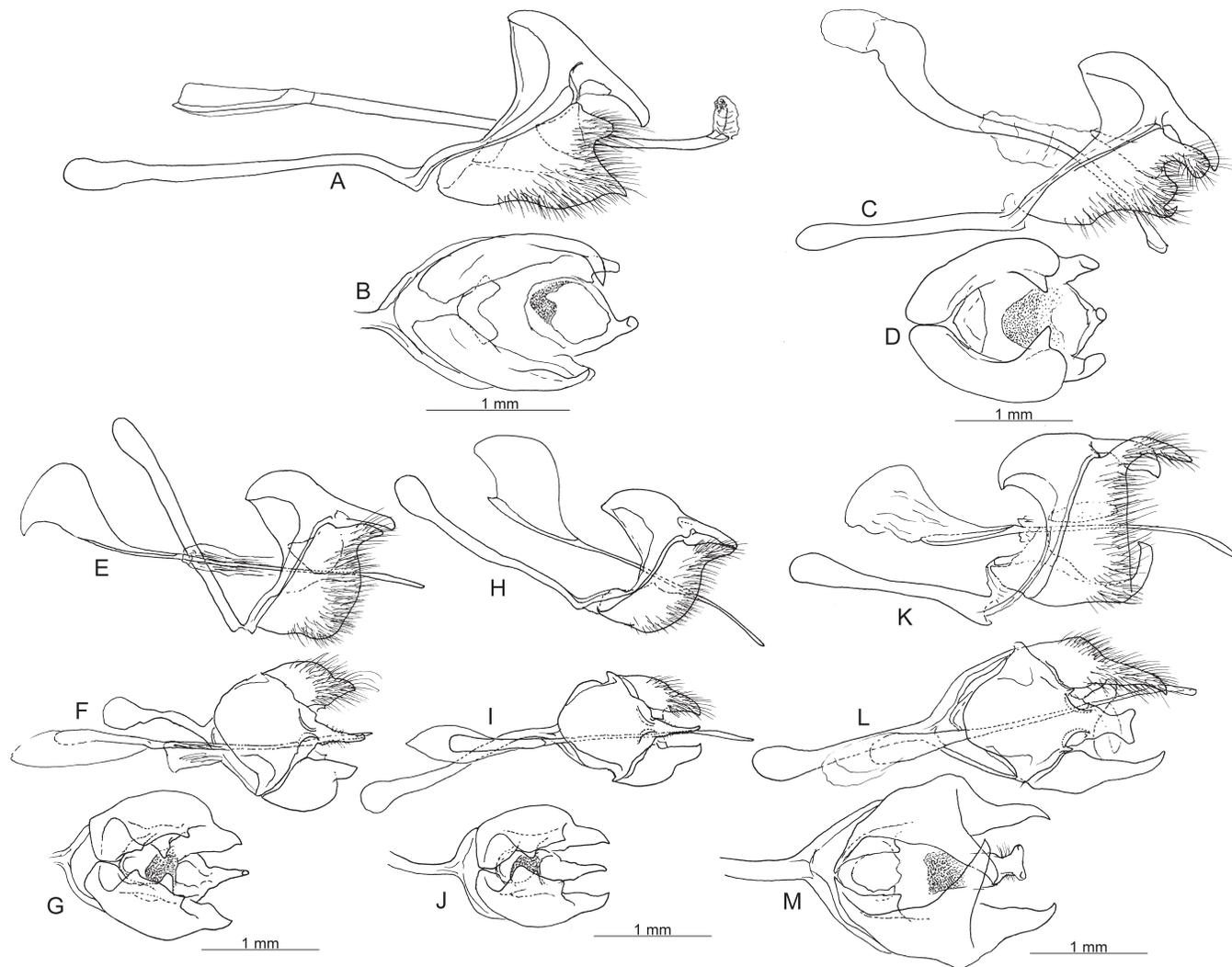


Fig. 18. Views of male genitalia of new Godyridina taxa; setae are variously omitted for clarity. **A-D.** *Brevioleria arzalia loronia* n. ssp., Ecuador, Pastaza, Río Pindo Grande (KW-21-13): **A**, lateral; **B**, ventral. **C-D.** *Hypoleria alema pastaza* n. ssp., holotype (KW-21-14): **C**, lateral; **D**, ventral. **E-G.** *Hypomenitis hermana serafina* n. ssp., holotype (KW-21-15): **E**, lateral; **F**, dorsal; **G**, ventral. **H-J.** *Hypomenitis hermana chamba* n. ssp., holotype (KW-21-16): **H**, lateral; **I**, dorsal; **J**, ventral. **K-M.** *Hypomenitis oneidodes nicolasi* n. ssp., holotype (KW-20-14): **K**, lateral; **L**, dorsal; **M**, ventral.

with more rounded rather than elongate wings. The male is further distinguished from *H. antea amarilla* by HW veins M_1 and Rs meeting at their bases, rather than having their bases separated by a short vein, and by the white marginal spots on the VHW being placed at the basal edge of the black border, rather than near its middle. The female is further distinguished from *H. antea amarilla* by having broader black wing margins.

Description: MALE (Fig. 3D, 12C-D): Forewing length 35 mm (mean 36 mm, $n=4$). *Wings:* as illustrated (Fig. 3D), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes brown, bare, with narrow fringe of white scales at base; antennae black; labial palpi as in *H. antea lalimba* n. ssp.; top of head with two white spots behind base of antennae, frons black. *Thorax:* dorsal surface black, ventral surface black with white spot in middle of mesothorax, slight white scaling on metathorax, forelegs, mid- and hindlegs black with scattered white scaling ventrally. *Abdomen:* dorsal surface black, ventral surface black with scattered white scales throughout. *Genitalia* (Fig. 12C-D): notable features include straight aedeagus in lateral view (Fig. 12C) and single pointed valva posterior projection at outer edge of valva in dorsal view (Fig. 12D).

FEMALE: (Fig. 3E): Forewing length 39 mm ($n=1$). *Wings:* as illustrated (Fig. 3E), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **ECUADOR:** *Zamora-Chinchipe:* Río Palanda, km 35 Zumba-Loja rd., [4°37'53"S,79°8'16"W], 1100 m, (Willmott, K. R., Hall, J. P. W.), 20 Jul 1993, [Genitalic dissection HYALYRIS-9], (FLMNH, to be deposited in INABIO).

PARATYPES (22♂, 14♀): **Ecuador:** *Zamora-Chinchipe:* 7 km SW Guayzimi, San José, [4°42'29"S,78°43'36"W], 1400 m, (Willmott, K. R., Hall, J. P. W.), 2 Aug 2009, 1♂ [FLMNH-MGCL-144728], (FLMNH); above San José, 7 km SW Guayzimi, Quebrada Guayzimi, [4°5'6"S,78°44'33"W], 1550 m, (Willmott, K. R., Hall, J. P. W.), 10,12 Aug 2009, 1♀ [FLMNH-MGCL-144729], (FLMNH); ancienne route Loja-Zamora km 40, 1500 m, (Boyer, P.), 17 May 2000, 1♀, (PIBO); Cordillera de Nanguipa, Santa Cruz de Nambija, [4°0'S,78°45'46"W], 1600-2000 m, (Boyer, P.), 30 Nov 1998, 2♂, 2♀, (PIBO); El Limón, Zamora, Quebrada Limones, [4°4'30"S,78°58'27"W], 1200 m, (Willmott, K. R.), 8 Feb 2002, 1♂, (NHMUK); El Limón, Zamora, Quebrada Limones, [4°4'30"S,78°58'27"W], 1200-1400 m, (Aldaz, R.), 19 Oct 2006, 1♂ [FLMNH-MGCL-111189], 1♀ [FLMNH-MGCL-111188], (FLMNH); km 7 Zamora-Loja old rd., Quebrada Chorillos, [4°1'55"S,79°0'12"W], (Elias, M., Toporov, S.), 14 Aug 2011, 1♂, (MNHN), 28 Aug 2011, 1♂, (MNHN);

km 7 Zamora-Loja old rd., Quebrada Chorrillos, [4°1'55"S,79°0'12"W], 1250 m, (Willmott, K. R., Hall, J. P. W.), 16 May 2000, 1♂, (FLMNH); 7-8 Nov 1996, 1♂, (FLMNH); nr. Romerillos, P. N. Podocarpus, Quebrada Las Dantas, [4°14'26"S,78°56'W], 1700 m, (Willmott, K. R.), 30 Oct 1997, 1♂, (FLMNH); nr. Zamora, Río Bombuscaro, [4°6'48"S,78°57'54"W], 1000 m, (Willmott, K. R.), 9 Dec 1996, 1♂, (FLMNH); Río Numbala, (Abbé Gaujon), 1885, 1♂, 1♀, (NHMUK); Río Numbala, 850 m, (Abbé Gaujon), Aug 1885, 1♂ [‘Rivière Numbala’], (USNM); Río Zamora, Zamora, [4°4'6"S,78°57'W], 1200 m, (Baron, O. T.), 6♂, 6♀, (NHMUK); between Zamora and Loja, 1500 m, (Mallet, J.), 21 Nov 1993, 1♀, (MUSM); route de Loja, Río Sabanilla, [3°58'12"S,79°3'42"W], 1200 m, (Boyer, P.), 28 Nov 1998, 1♂, (PIBO); Zamora-Romerillos rd. km 12, 1100-1200 m, (Boyer, P.), 29 Nov 1996, 1♀, (PIBO); Valladolid, [4°31'18"S,79°7'48"W], 1800 m, (Boyer, P.), 4 Dec 2002, 1♀, (PIBO); *Not located*: ‘Ecuador’, 2♂, (NHMUK), (Baron, O. T.), 1♂, (NHMUK).

Other records: Ecuador: *Zamora-Chinchi*: nr. Zamora, Río Bombuscaro, [4°6'48"S,78°57'54"W], 1000 m, (Willmott, K. R.), 12 Nov 2010, (W&H); Río Zamora, Zamora, [4°4'6"S,78°57'W], 950-1265 m [det. by Fox as *H. frater mestra*], (AMNH).

Etymology: The name is derived from the feminine latinized Greek adjective ‘leukos’, meaning white, in reference to the HW color of this subspecies.

Taxonomy and variation: *Hyaliris praxilla leuca* n. ssp. shows little variation, in contrast to the species that it apparently mimics, which are frequently apparently dimorphic with yellow or white HW translucent areas (e.g., *Hyaliris antea amarilla*, *Ithomia adelinda theuda* Hewitson, 1872, *Hypoleria alemana* (Hewitson, [1859])). Given that there are no apparent differences in the genitalia, wing venation, androconia or DNA barcodes between *H. praxilla leuca* and *H. mestra mestra* (Fig. 3F), with the former otherwise most obviously differing from the latter in having a white HW translucent area, one hypothesis is that these two are forms of the same species. We regard the two as distinct species, and treat *H. praxilla leuca* as conspecific with *H. p. praxilla*, for the following reasons. Firstly, *H. praxilla leuca* and *H. m. mestra* occur in sympatry with no known intermediates, as do *H. p. praxilla* and *H. mestra personata* Fox, 1971 in central eastern Ecuador, which show more numerous wing and body color pattern differences than are observed within other ithomiine species. Secondly, both sexes of *H. praxilla leuca* and *H. p. praxilla* share several more subtle characters, including whitish translucence at the base of the FW cell (an area lacking yellowish translucence in *H. m. mestra*), followed by a broad, dark, indistinct shadow or bar in the middle of the FW cell (never observed in *H. m. mestra*), and the HW with a rounded whitish translucent spot whose distal edge is parallel with the black distal margin in the tornus (the yellowish spot in *H. mestra* is more triangular, extending to almost touch the black distal margin in the tornus). Finally, *H. p. praxilla* and *H. praxilla leuca* appear to replace one another geographically. Although DNA barcodes do not distinguish the two species (Fig. 21), *Hyaliris latilimbata* is also placed within the same clade and barely differentiated from either *H. mestra* or *H. praxilla* (which occur in the same region but at higher elevations), and other examples are known within Ithomiini of related species that do not differ in DNA barcodes (Elias *et al.*, 2007). Obviously, it would be desirable to test the current taxonomic hypothesis with molecular data from broader sampling across the genome.

Willmott *et al.* (2020: 7) mistakenly cited the name ‘*Hyaliris praxilla personata*’ instead of *H. mestra personata*

while discussing the identity of Hewitson’s (1872: pl. 9, fig. 202) figure of ‘*Ithomia antea*’. That discussion was also mistaken in stating that Hewitson’s figure ‘clearly’ represented the same species as the lectotype of *Ithomia antea* Hewitson, 1869 designated by Willmott *et al.* (2020). In fact, both Willmott and Lamas forgot the fact that they had examined what appears to be Hewitson’s (1872) figured specimen several decades ago at the NHMUK, and GL’s photograph of the specimen is figured in Warren *et al.* (2021) under *H. mestra personata*, which taxon it does indeed represent. This specimen is now a paralectotype of *Ithomia antea*, and serves to underline the taxonomic difficulties, possibilities for confusion and the opportunities for over-confidence that still prevail with regard to the taxonomy of *Hyaliris*.

Distribution and natural history: This taxon is known only from Zamora-Chinchi province in southeastern Ecuador (Fig. 32C), where it is an uncommon inhabitant of cloud forest from 1000-1700 m. We have observed both sexes flying 3-6 m above the ground inside or at the edge of primary forest, and more rarely at the edge of secondary forest, always near rivers.

Hyaliris praxilla abscondita Lamas, Radford & Willmott,
new subspecies
Figs. 3G,H, 32C

Diagnosis and identification: This subspecies is distinguished from the nominate subspecies (Fig. 3I) by the more extensive reddish orange scaling on the hindwing, which extends from the wing base to the tornus and fills the area posterior of vein Cu₂, rather than just being confined to the wing marginal border.

Description: MALE (Fig. 3G): Forewing length 35 mm (mean 34.3 mm, n=3). *Wings:* as illustrated (Fig. 3G), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head, thorax, abdomen:* same as *Hyaliris praxilla leuca* n. ssp. *Genitalia:* not examined.

FEMALE: (Fig. 3H): Forewing mean length 33.7 mm (n=5). *Wings:* as illustrated (Fig. 3H), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: PERU: *Amazonas:* Cordillera del Cóndor, P[uesto de] V[igilancia] 3 (Alfonso Ugarte), [3°55'S,78°26'W], 1000-1200 m, (Lamas, G.), 20-21 Jul 1994, (MUSM).

PARATYPES (3♂, 6♀): Ecuador: *Morona-Santiago:* Cóndor Mirador, [3°37'42"S,78°23'41"W], 1974 m, (Radford, J.), 24 Aug 2010, 1♀ [CON175], (FLMNH); *Zamora-Chinchi:* Refugio de Vida Silvestre Bosque Protector El Zarza, [3°49'3"S,78°34'10"W], 1450 m, (Radford, J.), 26 Septiembre 2008, 1♂ [JR-08-M153A], (FLMNH). Peru: *Amazonas:* same data as HT, 2♂, 5♀, (MUSM).

Etymology: The name is a feminine Latin adjective meaning hidden or secret.

Taxonomy and variation: This taxon is placed as a subspecies of *H. praxilla* for the same reasons discussed above under *H. praxilla leuca* n. ssp., with DNA barcodes placing it within the clade containing *H. praxilla* and *H. mestra* (Fig. 21). Although only relatively few specimens are known, the wing pattern differences are quite distinct and consistent in all examined specimens, while the nominate subspecies shows little variation throughout its range ((Fig. 32C). Furthermore, this new taxon is apparently isolated from the nominate subspecies by being confined to the Cordillera del Cóndor.

Distribution and natural history: This subspecies is only known from three localities in the Cordillera del Cóndor, on both Ecuadorian and Peruvian slopes, where it has been collected in cloud forest habitats from 1000-2000 m (Fig. 32).

Hyalyris ocna equatoria Willmott & Lamas, new subspecies
Figs. 3J,K, 12E-F, 32D

Ceratinia ocna: Haensch (1903: 172; 1909-1910: 133, pl. 35, fig. c)

Hyalyris ocna n. ssp.: Lamas (2004: 177, no. 82b)

Hyalyris [sic] *oulita ocna*: Piñas (2004: 36, fig. 211)

Hyalyris ocna ssp.: Willmott & Mallet (2004: Appendix A)

Hyalyris ocna ssp. n.: Willmott & Freitas (2006: Figs. 9, 10)

Hyalyris ocna: Chazot et al. (2014b)

Diagnosis and identification: This subspecies is distinguished from the nominate subspecies (Fig. 3L) by the reduced yellow translucent area on the HW, which does not extend into cell M_3-M_2 as it does in the latter subspecies, and by the grayish translucent FW, which lacks the weak yellowish translucence of the nominate subspecies.

Description: MALE (Fig. 3J, 12E-F): Forewing length 31 mm (mean 30.3 mm, n=3). *Wings*: as illustrated (Fig. 3J), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head*: eyes brown, bare, with narrow fringe of white scales at base; antennae entirely yellow except dark brown with dark brown scaling in basal 7-8 antennomeres; labial palpi similar to *H. lactea lactea*; top of head with two white spots behind base of antennae and thin white medial stripe between bases of antennae, frons black with two white spots below bases of antennae. *Thorax*: dorsal surface dark brown with thin yellow medial line, ventral surface mesothorax yellow except for brown where legs fold, metathorax brown except for yellow scaling at dorsal edge near base of wing, forelegs entirely dark brown, mid- and hindlegs dark brown with scattered pale scaling ventrally. *Abdomen*: dorsal surface dark brown, ventral surface yellow. *Genitalia* (Fig. 12E-F): notable features include bent aedeagus in lateral view (Fig. 12E) and single pointed posterior projection of valva in dorsal view (Fig. 12F).

FEMALE: (Fig. 3K): Forewing length 33 mm (n=1). *Wings*: as illustrated (Fig. 3K), lacking DHW costal androconial scales. *Head, thorax, abdomen*: similar to male.

Types: HOLOTYPE ♂: **ECUADOR**: Pastaza: Río Pindo Grande, Shell, [1°29'40"S, 78°3'40"W], 1050 m, (Willmott, K. R., Hall, J. P. W.), 7,8 Feb 1995, [Genitalic dissection HYALYRIS-11], (FLMNH, to be deposited in INABIO).

PARATYPES (31♂, 29♀): **Ecuador**: *Sucumbios*: Baeza-Lago Agrio rd., Lumbaqui, [0°2'44"N, 77°20'12"W], 700 m, Sep, (USNM); Baeza-Lago Agrio rd., Lumbaqui, [0°2'44"N, 77°20'12"W], 850 m, (Velástegui, S.), 24 Sep 1973, 1♀, (MUSM); km 16.5 La Bonita-Rosa Florida rd., Río Palmar, [0°25'6"N, 77°32'12"W], 1200 m, (Willmott, K. R.), 23 Nov 1996, 1♀, (FLMNH), (Hall, J. P. W., Willmott, K. R.), 1♂, (MUSM); km 17 La Bonita-Rosa Florida rd., Río Palmar, trail above S. bank, [0°25'24"N, 77°32'24"W], 1450 m, (Willmott, K. R.), 17 Dec 2001, 1♀ [life history voucher KRW-43], (FLMNH), 18 Dec 2001, 1♂ [life history voucher KRW-58-1], (FLMNH), (Willmott, K. R.), 17 Dec 2001, 1♂ [life history voucher KRW-44], (NHMUK); nr. Rosa Florida, Quebrada El Copal, [0°23'24"N, 77°31'18"W], 1100 m, (Willmott, K. R.), 9 Nov 1997, 1♂, (FLMNH); *Napo*: km 34 Loreto-Tena rd., Río Pingullo, [0°44'20"S, 77°33'11"W], 1000 m, (Warren-Gash, H.), 17 Aug 2010, 2♂, (HAWA); km 34 Loreto-Tena rd., Río Pingullo, [0°44'20"S, 77°33'11"W], 950 m, (Neild, A. F. E.), 17 Aug 2010, 1♂, (INABIO); km 49 Tena-Loreto rd., [0°42'51"S, 77°44'26"W], 1350 m, (Hall, J. P. W., Willmott, K. R.), 7-11 Oct 1996, 1♀ [FLMNH-MGCL-219019], (FLMNH); 'Río Hollín' [=km 49 Tena-Loreto rd.], [0°42'51"S, 77°44'26"W], 1350 m, (Jasinski, A.), 3 May 1997, 1♀, (MZUJ); Río Jatunyacu, Pimpilala, [1°43'1"S, 77°56'13"W], 600-700 m, (Aldaz, E.), Nov 2003, 1♂, 1♀, (PIBO); 'Río Misahuallí, Tena' - (error), May 1989, 1♀, (HAWA); 'Río Napo', 7 Feb 1936, 1♀, (NHMUK); Tena-Loreto rd., Río Chalayacu, [0°43'3"S, 77°40'56"W], 1000 m, (Warren-Gash, H.), 25 Aug 2010, 1♂, 1♀, (HAWA); Tena-Loreto rd., Río Hollín, [0°41'13"S, 77°44"W], (Elias, M., Toporov, S., Santacruz, P.), 2010, 1♀, (INABIO), 12 Feb 2010, 1♀, (FLMNH), 1♀, (MNHN), 14 Mar 2010, 1♂, (FLMNH), 1♀, (MNHN), 22 Mar

2010, 2♂, (MNHN), 27 Feb 2010, 1♀, (MNHN); *Orellana*: Reserva Biológica del Río Bigal, main campsite, [0°31'30"S, 77°25'4"W], 950 m, (Segebarth, C.), 1 Nov 2011, 1♀ [FLMNH-MGCL-153515], (FLMNH), (Standridge, M.), 27 Oct 2011, 1♀ [FLMNH-MGCL-154032], (FLMNH); *Pastaza*: Alpayacu, [1°28'S, 78°7'W], 1098 m, Jul 1910, 1♂ [FLMNH-MGCL-219018], (FLMNH); Alpayacu, [1°28'S, 78°7'W], 1100 m, Jul, 1♂ ['3000 ft'], (FLMNH), (Palmer, M. G.), 5♂ [Genitalic dissection BM-6658], 5♀ [Genitalic dissection BM-6668], (NHMUK); km 25 Puyo-Tena rd., [1°19'42"S, 77°56'W], 900 m, (Covell, C.V.), 12 Nov 1988, 1♂ [FLMNH-MGCL-219017], 1♀ [FLMNH-MGCL-219020], (FLMNH); nr. San José, km 25 Puyo-Tena rd., Río Llandia, [1°19'59"S, 77°55'52"W], 1000 m, (Warren-Gash, H.), 25 Aug 2010, 2♀, (HAWA); Río Pindo Grande, Shell, [1°29'40"S, 78°3'40"W], 1050 m, (Willmott, K. R., Hall, J. P. W.), 7,8 Feb 1995, 1♂, (FLMNH), 2 Oct 1996, 1♀, (MUSM); *Tungurahua*: Topo, [1°25'S, 78°10'W], 1400 m, (Büche, M.), 18 Feb 1993, 1♂, (MUSM); Río Topo, [1°24'36"S, 78°11'30"W], 1250 m, (Neukirchen, W.), 12 Feb 1992, 1♀, (MUSM); *Morona-Santiago*: Parque Nacional Sangay, Sardinayacu, [2°5'55"S, 78°9'21"W], 1450 m, (Boyer, P.), 31 Jul 2010, 1♂, (PIBO).

Other records: **Ecuador**: *Sucumbios*: Baeza-Lago Agrio rd., Cascada de San Rafael, [0°5'48"S, 77°34'54"W], 1200 m, (Willmott, K. R., Hall, J. P. W.), 24 Aug 1999, (W&H); Cerro Lumbaqui Norte, [0°1'42"N, 77°19'W], 800-950 m, (Willmott, K. R., Hall, J. P. W.), 21-23 Aug 1999, (sight record) (W&H); *Napo*: Baeza-Tena rd., Río Jondachi, [0°43'S, 77°48'W], 1000 m, Oct, (USNM); km 49 Tena-Loreto rd., [0°42'51"S, 77°44'26"W], 1300 m, (Willmott, K. R., Hall, J. P. W.), Oct, (W&H); Río Jatunyacu, Pimpilala, [1°43'1"S, 77°56'13"W], 600-650 m, (Willmott, K. R., Hall, J. P. W.), 20 Oct 1996, (W&H); Río Urcusiqui, Baeza-Tena rd., Sarayacu, [0°40'30"S, 77°49'12"W], 1300-1400 m, (Willmott, K. R., Hall, J. P. W.), Mar, (W&H); nr. Cascada de San Rafael, 15 km SW Reventador, [0°5'54"S, 77°35'29"W], (AMNH); San Rafael, [0°6'15"S, 77°35'12"W], 1550 m, (Piñas, F.), 7 Sep 1999, 1 specimen [FDPR-7342], (FRPI); San Rafael, [0°6'15"S, 77°35'12"W], 1550-1150 m, (Piñas, F.), 7 Sep 1999, 1 specimen [FDPR-7343], (FRPI); Tena-Baeza rd., Cotundo, [0°50'42"S, 77°47'44"W], 800 m, Dec, (USNM); Tena-Loreto rd., Río Hollín, [0°41'13"S, 77°44"W], (Elias, M., Toporov, S., Santacruz, P.), 12 Feb 2010, 1♀, (sight record) (Elias, M., unpublished data), 22 Mar 2010, 1♂, 1♀, (sight record) (Elias, M., unpublished data), (Hill, R.), 14 Mar 2010, 1♂ [RH10-141], 1♂ [RH10-142], 1♂ [RH10-144], 1♂ [RH10-145], 1♂ [RH10-146], 1♂ [RH10-152], (RYHI or sight record) (Hill, R., unpublished data); *Pastaza*: Alpayacu, [1°28'S, 78°7'W], 1140 m, 1♂, (collection unknown) (Fox & Real, 1971); ENE of Mera, Río Puyo, [1°25'42"S, 78°2'48"W], 1300 m, (Willmott, K. R., Hall, J. P. W.), 3 Oct 1996, (W&H); Río Pindo Grande, Shell, [1°29'40"S, 78°3'40"W], 1050 m, (Willmott, K. R., Hall, J. P. W.), 12, 19 Apr 1995, (sight record) (W&H), 2 Oct 1996, (sight record) (W&H); San Ramón, 900 m, (Piñas, F.), 30 Nov 2001, 1 specimen [FDPR-7339], (FRPI); Shell, Río Pindo, [1°29'40"S, 78°3'40"W], 1050 m, (Hall, J. P. W., Willmott, K. R.), 8 Feb 1995, 1♀ [INABIO-TABDP-20787], (INABIO); *Tungurahua*: El Topo, [1°24'36"S, 78°11'30"W], 1150 m, (Piñas, F.), 24 Aug 2001, 1 specimen [FDPR-7341], (FRPI); nr. Río Negro, Santa Inéz, [1°24'44"S, 78°13'43"W], 1300 m, Nov, (collection unknown) (Haensch, 1903); Río Huaguayacu, [1°25'S, 78°1'W], 900 m, (AMNH); Río Pastaza, Abitagua, [1°27'S, 78°9'W], 1200 m, Apr, (USNM); Río Pastaza, Abitagua, [1°27'S, 78°9'W], 1250 m, Jun, (AMNH); Río Topo, [1°24'21"S, 78°11'50"W], 1200 m, (Piñas, F.), 11 Oct 2001, 1 specimen [FDPR-7338], (FRPI), 19 Feb 2003, 1 specimen [FDPR-7337], (FRPI); San Francisco, [1°24'20"S, 78°15'20"W], 1200 m, (Piñas, F.), 13 Sep 2005, 1 specimen [FDPR-7336], 1 specimen [FDPR-7340], (FRPI); tributary of Río Pastaza, Río Margarjitas, [1°24'18"S, 78°14'24"W], (AMNH).

Etymology: The name is derived from the feminine Latin adjective 'equatoria', meaning of the equator, in reference to the restricted latitudinal range of this subspecies.

Taxonomy and variation: This subspecies is associated with *H. ocna ocna* because the two taxa share a unique wing pattern within *Hyalyris*, namely orange along the HW anal margin, yellow in the HW discal area, and a colorless or only weakly tinged FW translucent area. Furthermore, at least among north Andean species, they are distinctive in sharing antennae that are mostly yellow, rather than having yellow confined to the distal portion. The two taxa also appear to occur at similar elevations in the eastern Andes. No differences were observed between

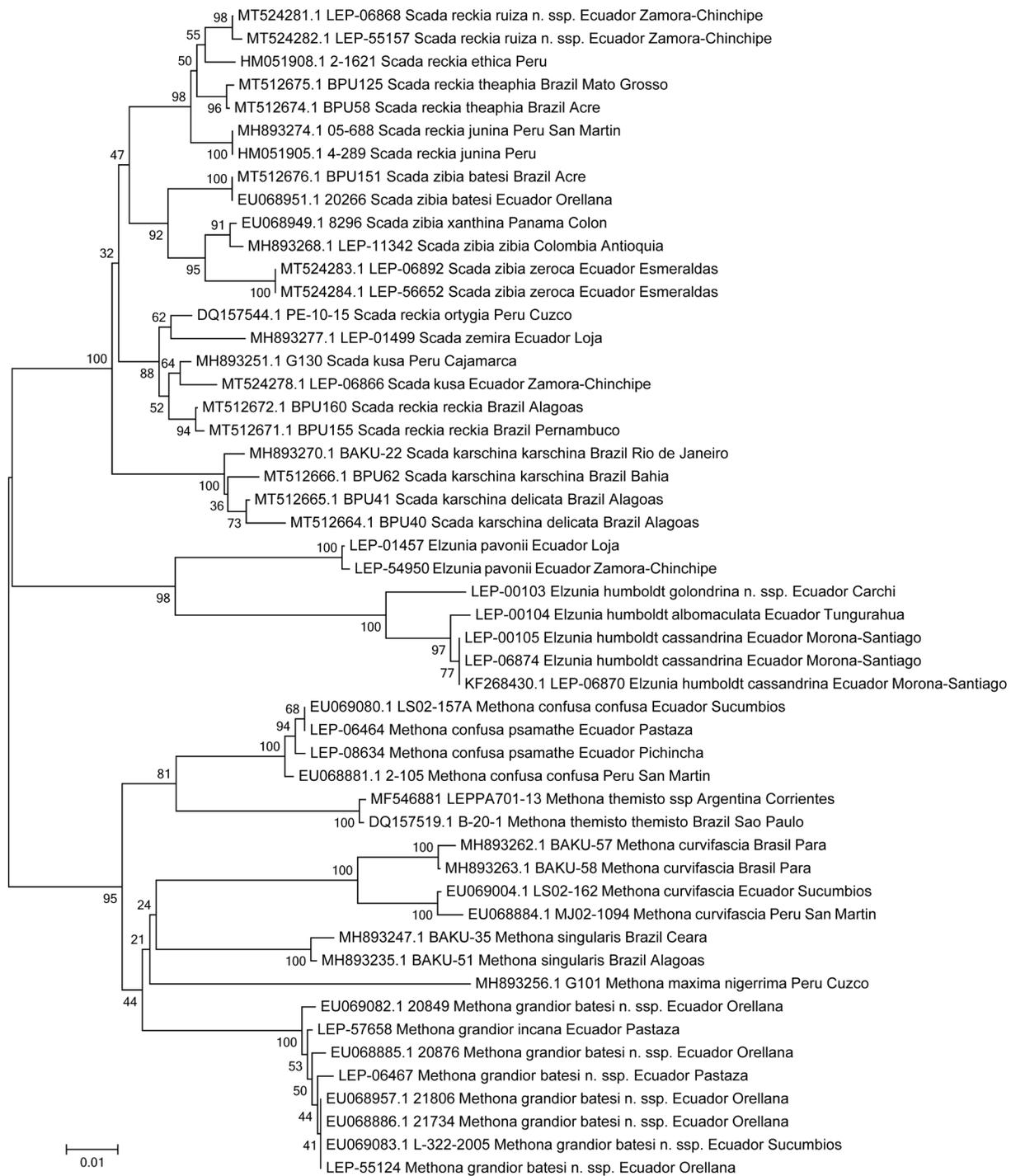


Fig. 19. Neighbor-joining tree (Kimura 2-parameter) for select *Scada*, *Methona* and *Elzunia* based on analysis of 633 bp of COI (barcode region). Bootstrap values (%) are shown by branches.

the two taxa in genitalia, wing venation or androconia. DNA sequence data support a close relationship between *H. oca equatoria* n. ssp. and *H. oca oca* (Fig. 21), as well as with *H. yasunina*. Willmott *et al.* (2020) discussed reasons for treating *H. yasunina* as a distinct species, in particular the fact that it occurs in lowland Amazonian forest rather than the east Andean foothills where both *H. o. equatoria* and *H. o. oca* occur.

No notable variation was observed among the relatively large series of specimens examined of both the new subspecies

and the nominate subspecies, supporting their taxonomic separation despite the relatively few differences in wing pattern.

Distribution and natural history: *Hyalyris oca equatoria* n. ssp. replaces the east Colombian nominate subspecies in eastern Ecuador, where it has been recorded as far south as northern Morona-Santiago (Fig. 32D). It occurs in cloud forest from 600-1450 m, along trails with secondary growth and the edges of forests, both near and away from rivers. In northeastern

Ecuador, solitary eggs were found 1 m above the ground under leaves of *Solanum asperum* Rich. and *Solanum* sp. (section *torvum*) (Solanaceae), on plants growing in an overgrown field near the edge of secondary forest, and in the understorey of primary forest on a steep slope, at the edge of a trail and in a tree-fall light gap.

Hyaliris ocna aurea Lamas & Willmott, **new subspecies**
Figs. 3M,N, 32D

Hyaliris ocna n. ssp.: Lamas (2004: 177, no. 82c)

Diagnosis and identification: This subspecies is distinguished from both other subspecies of *H. ocna* (Fig. 3K,L,M) by the lack of any orange markings on the HW, thus closely resembling *Hyaliris antea amarilla* (Fig. 3O), which lacks a yellow stripe at the base of the VHW costa and has largely or completely brown antennae.

Description: MALE (Fig. 3M): Forewing length 32 mm (n=1). *Wings:* as illustrated (Fig. 3M), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head, thorax, abdomen:* same as *H. ocna equatoria* n. ssp. *Genitalia:* not examined.

FEMALE (Fig. 3N): Forewing length 33 mm (n=1). *Wings:* as illustrated (Fig. 3N), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

HOLOTYPE ♂: **PERU:** Amazonas: P[uesto de] V[igilancia] 3 (Alfonso Ubgarte), Cordillera del Cóndor, [3°55'S,78°26'W], 1000-1200 m, (Lamas, G.), 21 Jul 1994, (MUSM).

PARATYPES (4♂, 4♀): **Ecuador:** Zamora-Chinchipec: nr. Paquisha, Chinapintza, [3°55'18"S,78°36'54"W], 1000 m, (Willmott, K. R.), 29 Sep 1997, 1♀, (FLMNH). **Peru:** same data as HT, 4♂, 1♀, (MUSM), 20 Jul 1994, 1♀ (MUSM). **Country unknown:** *Not located:* no data, 1♀, (NHMUK).

Etymology: The name is a feminine Latin adjective 'aurea', meaning golden, in reference to the distinctive coloration of the HW in this subspecies.

Taxonomy and variation: The taxon is associated with other *H. ocna* subspecies because of the almost entirely yellow antennae and similarity in size, HW venation and the elevation at which it flies. The nine known specimens of this taxon show little variation.

Distribution and natural history: The female Ecuadorian paratype was collected in the understorey of primary forest a few meters in from the edge of the forest at a road, flying 1 m above the ground, near a small, shaded stream gully. All known localities for this taxon are in the Cordillera del Cóndor (Fig. 32D), and it is notable that no *H. ocna* have been recorded to date in a number of well-sampled localities around 1000 m elevation in Ecuador in the adjacent Río Zamora valley.

Hypothyris cantobrica zamorita Willmott, Boyer & Vitale,
new subspecies
Figs. 4A,B, 12G-H, 32E

Rhodussa pamina: Piñas (2004: 33, fig. 178), misidentification.

Diagnosis and identification: This subspecies is most similar to the neighboring *H. cantobrica schunkeae* (Lamas, 1979) (Fig. 4C), which occurs in central Peru (western San Martín south to western Cuzco). It differs in the marginal spots on both wings being smaller (almost obsolete on the DFW), and white

ventrally rather than yellow; in the DFW basal half lacking yellow markings in the discal cell and cell Cu₂-Cu₁; in the DHW lacking a translucent pale yellowish orange discal band, instead being the same shade of orange as the remainder of the wing; and in the orange VFW subapical venal stripes being reduced.

Description: MALE (Fig. 4A, 12G-H): Forewing length 26 mm (mean 26 mm, n=3). *Wings:* as illustrated (Fig. 4A), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes brown, bare, with narrow fringe of yellow scales at base; antennae yellowish brown except basal third dark brown; labial palpi black with yellow scaling along inner ventral edge and along dorsal edge; top of head with thin yellow medial stripe between bases of antennae, two yellow spots behind eyes, frons broadly dark brown in middle with yellow at edges. *Thorax:* dorsal surface dark brown with broad yellow medial stripe, yellow scaling laterally and dorsally in middle and towards posterior edge, tegula orange with yellow spot ventrally, pronotum orange dorsally and yellow laterally, ventral surface yellow except for dark brown where legs fold, forelegs dark brown except ventral femur with dense yellow scales and tarsus white, mid- and hindlegs dark brown with scattered cream scaling ventrally. *Abdomen:* dorsal surface dark brown, ventral surface pale yellow. *Genitalia* (Fig. 12G-H): notable features include very broad curving aedeagus, very narrow vinculum bowed anteriorly, elongate base to valva (Fig. 12G), and lateral 'pockets' in soft tissue between vinculum and valva (Fig. 12H).

FEMALE (Fig. 4B): Forewing mean length 27.3 mm (n=3). *Wings:* as illustrated (Fig. 4B), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **ECUADOR:** Morona-Santiago: [c. 26 km S] Méndez, 'Cunza' [=Río Cumtsa], [2°51'56"S,78°20'38"W], 800-1200 m, (Aldaz, E.), Sep-Oct 2003, [Genitalic dissection KW-21-02], (FLMNH, to be deposited in INABIO).

PARATYPES (2♂, 3♀): **Ecuador:** Morona-Santiago: [c. 26 km S] Méndez, 'Cunza' [=Río Cumtsa], [2°51'56"S,78°20'38"W], 800-1200 m, (Aldaz, E.), Sep-Oct 2003, 1♀, (FLMNH); Zamora-Chinchipec: km 6 Los Encuentros-El Panguí, [3°43'50"S,78°36'32"W], 800-850 m, (Willmott, K. R., J. C. R., J. I. R.), 22 Jun 2013, 1♂ [FLMNH-MGCL-157584], 1♀ [FLMNH-MGCL-157585], (FLMNH); Los Encuentros, 900 m, (Boyer, P.), 2 Dec 1998, 1♂, 1♀, (PIBO).

Etymology: The subspecies name is derived from the Spanish diminutive form of 'Zamora', the name of the river valley which approximately represents the known range of the taxon, and it is treated as a feminine noun in apposition.

Taxonomy and variation: This taxon is treated as a subspecies of *H. cantobrica* (Hewitson, 1876), which it apparently replaces in Ecuador, because it shares with that species highly distinctive male genitalia, which exhibits numerous characters unique within the Ithomiini, in particular the very narrow, elongate vinculum that is bowed anteriorly away from the valva, and the very elongate, narrow basal portion of the valva. The taxa also share similar hindwing venation, androconial scale morphology, and the unusual character of orange venal stripes in the VFW subapical area. Finally, DNA barcodes recovered *H. cantobrica zamorita* n. ssp. and other *H. cantobrica* taxa (including the nominate subspecies), as a single, well-supported clade (Fig. 22), albeit with rather large sequence divergence between *H. cantobrica zamorita* and the remaining taxa, which perhaps merits future investigation. Specimens from Zamora-Chinchipec differ from those from Morona-Santiago in having a slightly narrower yellow DFW postdiscal band and less extensive orange along the DFW anal margin, but more material is needed to better assess the nature of this variation.

Distribution and natural history: This subspecies is known from a restricted area in southeastern Ecuador, from south of the

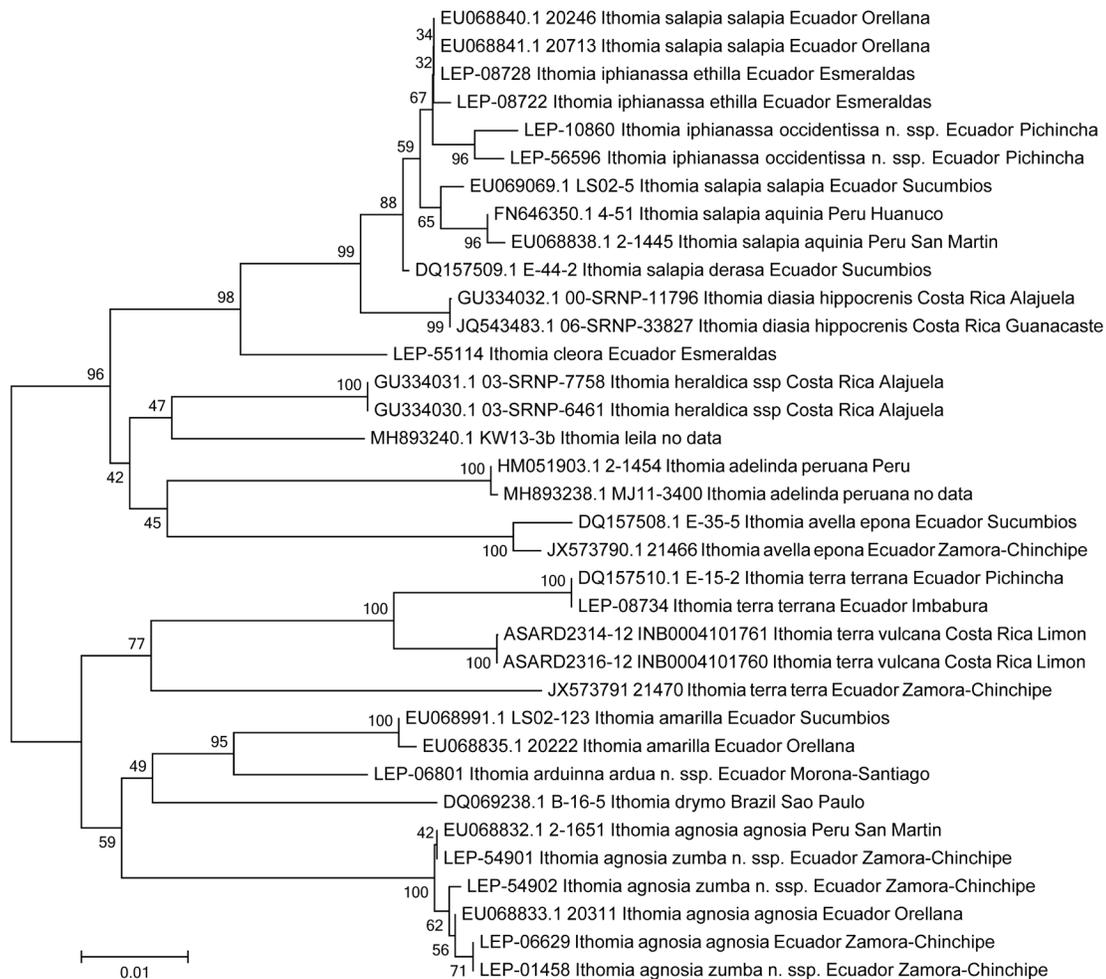


Fig. 20. Neighbor-joining tree (Kimura 2-parameter) for select *Ithomia* based on analysis of 633 bp of COI (barcode region). Bootstrap values (%) are shown by branches.

town of Méndez to near the town of Los Encuentros, along the valley of the Río Zamora and lower Río Upano (Fig. 32E). The distribution seems notably disjunct in comparison with other subspecies, which are not known north of San Martín in Peru, a distance of c. 400 km. Within the isolated Zamora-Upano valley it occurs at elevations from 800-900 m, where it has been recorded within small patches of highly disturbed forest. A female was collected by J. I. Robinson Willmott at 14:55 hrs flying 0.3 m above the ground at the edge of an orchard, and a male nearby at 15:25 hrs flying 1 m above the ground at the edge of secondary forest. The male and female collected by PB were flying in a patch of forest near a pasture, and were the only ithomiines observed there. Given the apparent ability of this taxon to tolerate such disturbed habitats, and the prevalence of such habitats throughout its limited distribution, it is a mystery why this subspecies is so rarely encountered in the field. In flight it is indistinguishable from *Hypothyris euclea pyrippe* (Hopffer, 1874), with which it flies and is presumably involved in mimicry.

Napeogenes glycera mirador Lamas, Willmott & Radford,
new subspecies
 Figs. 4D,E, 32F

Napeogenes glycera n. ssp.: Lamas (2004: 178, no. 92f)

Diagnosis and identification: This new subspecies differs from the most similar related taxon, *N. glycera nausica* Weymer, 1899 (Fig. 4F), in having broader orange in the hindwing tornus, which extends basally to tint the base of cell 2A-Cu₂, which in *N. glycera nausica* has only black scales. On the FW, *N. glycera mirador* n. ssp. has diffuse black scaling extending from the black anal marginal border into the base of cell Cu₂-Cu₁.

Description: MALE (Fig. 4D): Forewing length 32 mm (n=1). *Wings:* as illustrated (Fig. 4D), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes brown, bare, with isolated white scales at base; antennae dark brown becoming slightly paler brown in distal half; labial palpi black with sparse white scaling dorsally; top of head with two white spots behind base of antennae and thin white medial stripe between bases of antennae, frons dark brown with two white spots below bases of antennae. *Thorax:* dorsal surface dark brown, ventral surface dark brown with white spot in middle of mesothorax, forelegs, mid- and hindlegs dark brown. *Abdomen:* dorsal surface dark brown, ventral surface dark brown with sparse white scales laterally on edge of sternites towards posterior half of each sternite. *Genitalia:* not examined.

FEMALE: (Fig. 4E): Forewing length 33 mm (n=1). *Wings*: as illustrated (Fig. 4E), lacking DHW costal androconial scales. *Head, thorax, abdomen*: similar to male.

Types: HOLOTYPE ♂: **PERU**: Amazonas: P[uesto de] V[igilancia] 3 (Alfonso Ugarte), Cordillera del Cóndor, [3°55'S, 78°26'W], 1000-1200 m, (Lamas, G.), 21 Jul 1994, (MUSM).

PARATYPES (1♂, 2♀): **Ecuador**: Morona-Santiago: Cóndor Mirador, [3°37'42"S, 78°23'41"W], 1972 m, (Radford, J.), 27 Aug 2010, 1♀ [CON285], (FLMNH) (CULEPEX Expedition, 2010). **Peru**: Amazonas: same data as HT, 20 Jul 1994, 1♂, 1♀, (MUSM).

Etymology: The subspecies name is derived from the Spanish word 'mirador', meaning a viewpoint, in reference to the distribution of this subspecies in the isolated Cordillera del Cóndor, and part of the name of the only current known locality for the taxon in Ecuador.

Taxonomy and variation: This taxon is associated with *N. glycera* Godman, 1899 based on its similar habitat (cloud forest), size, wing shape (relatively elongate FW), wing pattern (broad black borders and translucent HW cell M₁-Rs), and wing venation (angled FW discocellular veins and gently curving posterior edge to the HW discal cell). We have found the male genitalia to be of little use in diagnosing most *Napeogenes* taxa. *Napeogenes glycera mirador n. ssp.* is sympatric with the only other somewhat similar east Andean *Napeogenes* that occurs at similar elevations, *N. harbona chiguinda* Willmott & Vitale, 2008.

We have only examined four specimens of this new subspecies and two specimens of *N. glycera nausica*. Of the latter taxon, the female is the holotype specimen in the MfN labeled "Ecuador", while the male was collected by PB at km 25 Macas-Nueve de Octubre; the distribution presumably matches that of other co-mimics, such as *Hyalyris praxilla praxilla*, in extending throughout Morona-Santiago province. The differences separating *N. glycera mirador* and *N. glycera nausica* are slight, and variation is difficult to assess with the few specimens available for examination. Nevertheless, given the consistency of the observed differences between the two taxa, and their geographic isolation, we decided to recognize them as distinct subspecies.

Distribution and natural history: *Napeogenes glycera mirador n. ssp.* is known only from the somewhat isolated Cordillera del Cóndor in southeastern Ecuador and northeastern Peru (Fig. 32F), in cloud forest from 1000-1972 m.

Hyposcada illinissa morona Lamas & Willmott, **new subspecies**

Figs. 5A,B, 13A-B, 33A

Hyposcada illinissa n. ssp.: Lamas (2004: 182, no. 160r)

Diagnosis and identification: This new subspecies is distinguished from *H. illinissa margarita* Fox, 1941 (Fig. 5C) from northern Peru (San Martín) by the broader, more intensely white-tinged translucent markings, especially the FW postdiscal spots and the HW discal band. In addition, the white subapical spots in FW cells M₃-M₂ to M₁-R₅ are visible, even if only as a trace in some specimens. *Hyposcada illinissa ida* Haensch, 1903 from further north in eastern Ecuador differs primarily in having the three white FW postdiscal spots at the

costa fused into a single spot, whereas in *H. illinissa morona n. ssp.* they form two more or less separate spots (as in *H. illinissa margarita*). The HW translucent discal band is typically slightly more opaque in *H. illinissa morona* than in *H. illinissa ida*.

Description: MALE (Fig. 5A, 13A-B): Forewing length 24 mm (mean 24 mm, n=4). *Wings*: as illustrated (Fig. 5A), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head*: eyes brown, bare, with narrow fringe of white scales at base; antennae dark brown; labial palpi white except for black laterally; top of head black with white medial stripe between bases of antennae, two white spots behind eyes, frons black with white lateral stripes. *Thorax*: dorsal surface dark brown with broad white medial stripe and scattered white lateral scales, pronotum dark brown dorsally and white laterally, tegula black with scattered white scaling, ventral surface white except for black where the legs fold, with some scattered white lateral scaling, forelegs, mid- and hindlegs black with mixed white scaling. *Abdomen*: dorsal surface dark brown, ventral surface white with scattered white scaling extending laterally. *Genitalia* (Fig. 13A-B): notable features include narrow upper valva projection and short, curved uncus (Fig. 13A).

FEMALE: (Fig. 5B): Forewing mean length 25.2 mm (n=5). *Wings*: as illustrated (Fig. 5B), lacking DHW costal androconial scales. *Head, thorax, abdomen*: similar to male.

Types: HOLOTYPE ♂: **ECUADOR**: Morona-Santiago: km 3 Puerto Morona-San José de Morona, [2°54'44"S, 77°42'25"W], 210 m (J. Hall, K.R., J.C.R., J.I.R. Willmott), 30 July 2016, [FLMNH-MGCL-284025; Genitalic dissection KW-21-03], (FLMNH, to be deposited in INABIO).

PARATYPES (7♂, 12♀): **Ecuador**: Morona-Santiago: 2.5 km N Puerto Morona, [2°54'8"S, 77°44'31"W], 200 m, (Hall, J. P. W., Willmott, K. R., J. C. R., J. I. R.), 5,6 August 2015, 1♂, [FLMNH-MGCL-283631], 1♀ [FLMNH-MGCL-283632], 1♀ [FLMNH-MGCL-283633] (FLMNH), 1♂ (INABIO); forest nr. San José de Morona, [2°53'17"S, 77°41'52"W], 215 m, (Aldaz, R.), 9 Jun 2009, 1♀ [FLMNH-MGCL-153140], (FLMNH), (Gallice, G.), 5 Jun 2009, 1♂ [FLMNH-MGCL-153138], (FLMNH), 6 Jun 2009, 1♂ [FLMNH-MGCL-153139], 1♀ [FLMNH-MGCL-153141], (FLMNH), 7 Jun 2009, 1♀ [FLMNH-MGCL-153142], (FLMNH); km 3 Puerto Morona-San José de Morona, [2°54'44"S, 77°42'25"W], 210 m (Hall, J. P. W., Willmott, K. R., J. C. R., J. I. R.), 30 July 2016, 1♀ [FLMNH-MGCL-284026] (FLMNH), 4 August 2016, 1♀ [FLMNH-MGCL-284027] (FLMNH); Río Santiago, Santiago, [3°2'11"S, 78°2'W], 350 m, (Willmott, K. R.), 28 Sep 1996, 1♂, (FLMNH).

Etymology: The subspecies name is derived from that of Morona, a town in Ecuador and also the name of the river near which the majority of specimens were collected. It is treated as a feminine noun in apposition.

Taxonomy and variation: This taxon is treated as a subspecies of *Hyposcada illinissa* (Hewitson, [1852]) because it shares with that species distinctive characters in the male genitalia (an elongate projection from the upper posterior part of the valva, a short curving uncus, and a short, narrow aedeagus), wing pattern (white ventral marginal spots, absent in the otherwise similar *H. kena* (Hewitson, 1872)), and DNA barcodes (which group it with other taxa currently treated as *H. illinissa* subspecies; Fig. 23). Nevertheless, as noted by De-Silva *et al.* (2010), it is quite likely that the taxonomy of *H. illinissa* will need revision when molecular data are available for more taxa, given the partial sympatry between some very distinctive taxa (e.g., *H. illinissa napoensis* Vitale & Bollino, 2001 and *H. illinissa ida*) and deep divergence in DNA barcodes (Fig. 23).

The clearest character distinguishing this subspecies from neighboring *H. illinissa ida* is the split translucent white postdiscal spots at the DHW costa. Although this might seem a minor character, it is very constant within, and often differs between, other *H. illinissa* subspecies. Furthermore, DNA barcodes suggest *H. illinissa ida* and *H. illinissa morona n.*

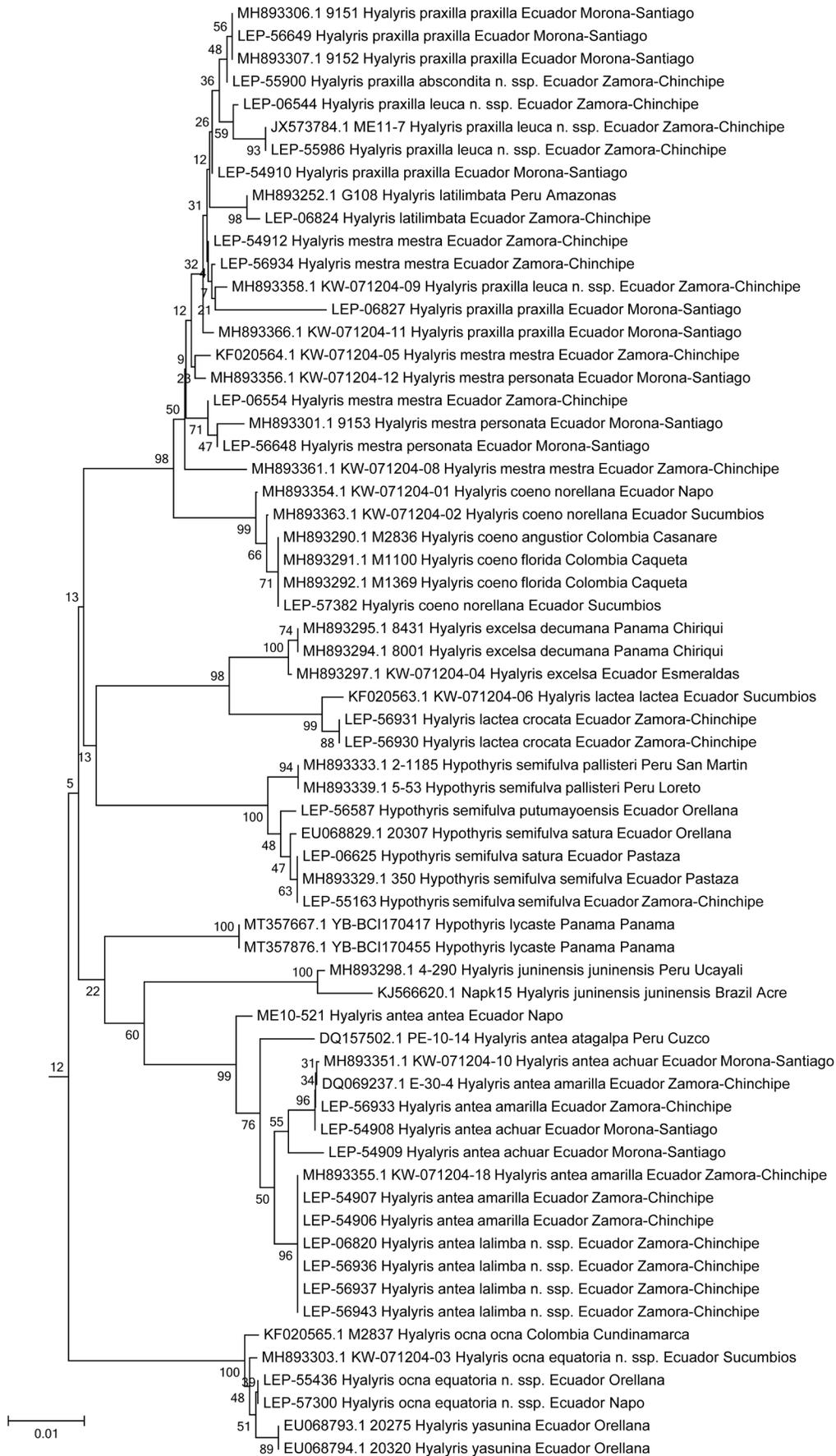


Fig. 21. Neighbor-joining tree (Kimura 2-parameter) for select *Hyalyris* and *Hypothyris* based on analysis of 633 bp of COI (barcode region). Bootstrap values (%) are shown by branches.

ssp. may not be closely related (Fig. 23), since the latter instead grouped with a number of Peruvian taxa, including *H. illinissa margarita*. Slight variation was observed in the width of the translucent white HW postdiscal band in *H. illinissa morona*, but no specimens approached *H. illinissa margarita* in the narrowness of this band.

Distribution and natural history: This subspecies is known to date from southeastern Ecuador in Morona-Santiago, in the vicinity of Río Santiago and Río Morona (Fig. 33A). It is replaced further north in Ecuador, in Pastaza, by *H. illinissa ida*, which also occurs further east, away from the Andes, where the Río Pastaza crosses the Ecuador-Peru border. Both sexes can be found flying in the understorey of relatively undisturbed lowland rain forest, from 200-350 m, being rather local and occurring typically on flat terrain near streams and rivers.

Hyposcada kena unki Lamas, Willmott & Boyer, **new subspecies**
Figs. 5D,E, 13C-D, 33B

Diagnosis and identification: This new subspecies is distinguished from the neighboring and otherwise similar nominate subspecies (Fig. 5F) by the orange subapical markings on the DFW extending broadly into the black space between the translucent white apical spots and postdiscal band, and by the orange marginal band of *H. kena kena* being absent or strongly reduced.

Description: MALE (Fig. 5D, 13C-D): Forewing length 24 mm (mean 23.5 mm, n=2). *Wings:* as illustrated (Fig. 5D), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head, thorax, abdomen:* same as *Hyposcada illinissa morona n. ssp.* *Genitalia* (Fig. 13C-D): notable features include very long and broad aedeagus and uncus distant from valva dorsal edge (Fig. 13C).

FEMALE: Forewing mean length 22 mm (n=1). *Wings:* similar to male, lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **PERU:** Amazonas: Cerro Unki, km 44 Sarameriza-Chiriaco, [4°37'S,77°40'W], 790 m, (Mallet, J, Eeley, H.), 10 Jun 1986, (MUSM).

PARATYPES (6♂, 1♀): **Ecuador:** Morona-Santiago: km 27 Santiago-San José de Morona, Río Kusumi, [2°58'25"S,77°49'23"W], 350 m, (Hall, J. P. W., Willmott, K. R., J. C. R., J. I. R.), 30 July 2016, 1♂ [FLMNH-MGCL-284024; Genitalic dissection KW-21-04], (FLMNH); [Río Shangaimé], km 73 Puyo-Macas rd., [1°57'15"S,77°51'25"W], 750 m, (Boyer, P.), 2 Mar 1998, 1♂, (PIBO). **Peru:** Amazonas: same data as HT, 3♂, (MUSM); Monterrico, km 81 Chiriaco-Sarameriza, [4°54'S,78°02'W], 300 m, (Mallet, J., Eeley, H.), 6 June 1986, 1♀, (MUSM); Loreto: Borja, [4°28'S,77°32'W], 210-250 m, (Lamas, G.), 14 Feb 1978, 1♂, (MUSM).

Etymology: The subspecies name is derived from that of the type locality and it is treated as a masculine noun in apposition.

Taxonomy and variation: This taxon is treated as a subspecies of *Hyposcada kena* because it shares with that species distinctive characters in the male genitalia (in particular a very long, broad aedeagus) and wing pattern (no white ventral marginal spots, present in the otherwise similar *H. illinissa*). Although relatively few specimens of this taxon have been collected, they are similar and consistently differ from many more examined (> 70) of the nominate subspecies throughout its relatively broad range in eastern Ecuador and Peru.

Distribution and natural history: This new subspecies is known from only a few localities in northern Peru and southern Ecuador (Fig. 33B). A male specimen typical of *H. k. kena* was collected in Santiago, west of one of the two Ecuadorian localities, and another female in the OUM was collected by Pearce in 'Gualaquiza', suggesting that the nominate subspecies also occurs widely in the valleys of the Río Upano and Río Zamora, an area of marked endemism for ithomiine subspecies. If so, then *H. kena unki* apparently occupies a very limited distribution in southeastern Ecuador and northeastern Peru, where the final ridges of the eastern Andes meet the adjacent lowlands. One Ecuadorian male was collected in the shady understorey of lowland rainforest flying at 0.5 m above the ground along a streamside trail at midday, while the other was also collected in forest near a stream, flying with a number of other ithomiines.

Hyposcada taliata laetitia Lamas & Willmott, **new subspecies**
Figs. 5G,H, 13E-I, 33C

Hyposcada taliata n. ssp.: Lamas (2004: 182, no. 162b)

Hyposcada taliata ssp. nov.: De-Silva *et al.* (2010: supplementary information)

Hyposcada taliata: Chazot *et al.* (2014b)

Hyposcada taliata ssp. nov.: De-Silva *et al.* (2015: Appendix S1a)

Diagnosis and identification: This new subspecies is distinguished from the nominate (Fig. 5I), which replaces it to the south, by the reduced black in the basal area and discal cell of the HW. It is most easily identified from numerous other similar sympatric ithomiines, mostly in the genus *Oleria*, by the complete series of white DFW marginal spots.

Description: MALE (Fig. 5G, 13E-I): Forewing length 35 mm (mean 34.5 mm, n=2). *Wings:* as illustrated (Fig. 5G), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes brown, bare, with narrow fringe of white scales at base; antennae dark brown; labial palpi white except for medium long black hair-like scales ventrally on middle and terminal segment; top of head black with white medial stripe between bases of antennae, two white spots behind eyes, frons black with white lateral stripes. *Thorax:* dorsal surface dark brown with white medial stripe and scattered white lateral scales, pronotum dark brown dorsally and white laterally, tegula black with scattered white scaling, ventral surface white except for black where the legs fold, with some scattered white lateral scaling, forelegs, mid- and hindlegs black with mixed white scaling. *Abdomen:* dorsal surface dark brown, ventral surface white with scattered white scaling extending laterally and broad dark brown stripe down middle of abdomen. *Genitalia* (Fig. 13E-I): notable features include 'cup-and-flange' tip to valva (Fig. 13E-F).

FEMALE: (Fig. 5H): Forewing mean length 36 mm (n=3). *Wings:* as illustrated (Fig. 5H), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **ECUADOR:** Morona-Santiago: km 14 Limón-Gualaceo rd., [3°0'36"S,78°30'W], 1950 m, (Willmott, K. R., Hall, J. P. W.), 30 Sep 1997, [Genitalic dissection OLERIA-39], (FLMNH, to be deposited in INABIO).

PARATYPES (10♂, 12♀): **Ecuador:** Morona-Santiago: Guarumales/Hidropaute, [2°34'16"S,78°30'56"W], 2100-2200 m, (Boyer, P.), 18-20 Jan 2011, 1♀, (PIBO); km 14 Chigüinda-Gualaquiza rd., [3°15'45"S,78°39'4"W], 1300 m, (Willmott, K. R., J. C. R., J. I. R.), 15 Jun 2013, 1♀ [FLMNH-MGCL-157898], (FLMNH); km 14 Limón-Gualaceo rd., [3°0'36"S,78°30'W], 1950 m, (Willmott, K. R., Hall, J. P. W.), 30 Sep 1997, 1♀, (FLMNH); km 19 Macas-Nueva de Octubre rd., Río Abanico, [2°15'18"S,78°12'W], 1600 m, (Willmott, K. R.), 12,13 Nov 1996, 1♂, 1♀, (FLMNH), (Warren-Gash, H.), 17,18 Sep 2011, 1♀, (HAWA), 28 Aug 2010, 3♂, (HAWA); km. 9.5 Chigüinda-Gualaquiza rd., hillside, [3°14'38"S,78°40'W], 1750 m, (Willmott, K. R.), 12 Oct 2007, 1♀ [FLMNH-MGCL-113454], (FLMNH); Zamora-Chinchipe:

Ollantaya olerioides baeza Willmott & Lamas, **new subspecies**

Figs. 5J,K, 13J-K, 33D

Ollantaya olerioides n. ssp.: Lamas (2004: 184, no. 195b)

Ollantaya olerioides ssp. nov.: De-Silva *et al.* (2010: Fig. 1, supplementary information)

Ollantaya olerioides: Chazot *et al.* (2014b)

Ollantaya olerioides: Brower *et al.* (2014)

Ollantaya olerioides ssp. nov.: De-Silva *et al.* (2015: Appendix S1a)

Diagnosis and identification: This subspecies is distinguished from the nominate subspecies from Bolivia (Fig. 5L) by the more reddish (rather than orange) brown ventral markings, by the straighter basal edge of the dark HW distal marginal border (rather than being more indented in cell Cu_1-M_3), and by the more extensive translucent white scaling on the HW, which extends into the HW discal cell. The taxon is very similar to numerous sympatric ithomiines, mostly *Oleria*, from which it is most easily distinguished by the translucent white marking in cell M_1-Rs on the HW, with this cell being opaque black in other similar species. The subspecies is replaced to the south in Peru by a further undescribed subspecies, which resembles *H. taliata taliata* and can be distinguished in the same way as the latter taxon from *H. taliata laetitiae* n. ssp.

Description: MALE (Fig. 5J, 13J-K): Forewing length 29 mm (mean 31 mm, n=3). *Wings:* as illustrated (Fig. 5J), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes brown, bare, with narrow fringe of white scales at base; antennae dark brown; labial palpi white with broad black on ventral outer edge with black medium length ventral hair-like scales; top of head black with white medial stripe between bases of antennae, two white spots behind eyes, frons black with white lateral stripes. *Thorax:* dorsal surface dark brown with broad white medial stripe and scattered white lateral scales, pronotum dark brown dorsally and white laterally, tegula black with scattered white scaling, ventral surface white except for black where the legs fold, with some scattered white lateral scaling, forelegs, mid- and hindlegs black with mixed white scaling. *Abdomen:* dorsal surface dark brown, ventral surface white with scattered white scaling extending laterally. *Genitalia* (Fig. 13J-K): notable features include slender, elongate uncus and upper valva projections (Fig. 13J-K).

FEMALE: (Fig. 5K): Forewing mean length 29.7 mm (n=3). *Wings:* as illustrated (Fig. 5K), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **ECUADOR:** *Morona-Santiago:* km 19 Macas-Nueve de Octubre rd., Río Abanico, [2°15'18"S, 78°12'W], 1600 m, (Willmott, K. R.), 1 Nov 1996, [Genitalic dissection OLERIA-15], (FLMNH, to be deposited in INABIO).

PARATYPES (30♂, 19♀): **Colombia:** *Antioquia:* Jardín, [5°35'49"N, 75°49'4"W], 1700-1900 m, (Rodríguez, G.), 28 Jul 2002, 1♀, (FAVI); Quebrada Las Ánimas, La Estrella, Medellín, [6°10'N, 75°39'W], 1♀, (ZSBS); *Huila:* San José de Isnos, [1°57'N, 76°13'W], 2050 m, 1♂, (IAVH). **Ecuador:** *Sucumbios:* nr. La Bonita, Río Sucio, [0°28'30"N, 77°33'18"W], 1800 m, (Willmott, K. R.), 12 Dec 2001, 1♀, (FLMNH), 15 Dec 2001, 1♀, (FLMNH), (Boyer, P.), 21 Nov 1999, 1♂, (PIBO); nr. La Bonita, Río Sucio, [0°28'30"N, 77°33'18"W], 1800-2000 m, (Willmott, K. R.), 15 Dec 2001, 1♀, (NHMUK), (Willmott, K. R.), 15 Dec 2001, 1♂, (FLMNH); *Napo:* Baeza, [0°28'S, 77°53'W], 2000 m, (Velástegui, D.), 15 Oct 1979, 2♂, (MUSM); Baeza-Tena rd., Cocodrilo, [0°38'57"S, 77°47'27"W], (Elias, M., Toporov, S., Santacruz, P.), 12 Mar 2010, 2♂, (MNHN), 4 Mar 2010, 1♂, (FLMNH); km 6 Baeza-Tena rd., El Arrayán, [0°28'22"S, 77°52'36"W], 2200 m, (Hall, J. P. W., Willmott, K. R.), 25 Oct 1996, 1♀, (MUSM), (Willmott, K. R.), 25 Oct 1996, 1♀, (FLMNH); nr. Cosanga, Estación Científica Yanayacu, [0°35'24"S, 77°53'W], (Elias, M., Toporov, S., Santacruz, P.), 2010, 1♂, (INABIO), 28 Feb 2010, 1♀, (MNHN); *Tungurahua:* Machay, [1°23'20"S, 78°16'49"W], 1700 m, (Boyer, P.), 18 Nov 1996, 1♂, (PIBO); "environs d'Ambato" - (error), (Blanc, R. P. I.), 1♂, (NHMUK); "Río Topo" - (error), (Palmer, M. G.), 1♂, (NHMUK); *Morona-Santiago:* km 19

Macas-Nueve de Octubre rd., Río Abanico, [2°15'18"S, 78°12'W], 1600 m, (Hall, J. P. W., Willmott, K. R.), 12-13 Nov 1996, 2♂, (MUSM), (Willmott, K. R.), 9 Dec 1996, 2♂, 1♀, (FLMNH); *Zamora-Chinchipec:* km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S, 79°5'42"W], 2000-2100 m, (Willmott, K. R.), 5 Dec 2006, 1♀ [FLMNH-MGCL-112191], (INABIO), (Willmott, K. R., Aldaz, R.), 14 Oct 2006, 1♀ [FLMNH-MGCL-112192], (FLMNH), 23 Oct 2006, 1♀ [FLMNH-MGCL-112193], (FLMNH); *Zamora-Loja* rd., San Francisco, canal subterráneo, [3°58'44"S, 79°5'W], 1900 m, (Willmott, K. R., Aldaz, R.), 20 Oct 2006, 1♂ [FLMNH-MGCL-112194], (FLMNH); *Loja:* Loja, [3°59'23"S, 79°12'17"W], 1♂, (USNM); Santa Bárbara, Aug [18]96, 1♂, (NHMUK); *Not located:* 'Ecuador', 1♂, (SMF). **Peru:** *Amazonas:* Alva, nr. Chachapoyas, [5°56'1"S, 78°0'25"W], (Mittermeier, R. A.), 3 May 1974, 2♀, (MUSM); 'Cedro de Piruro' (= El Cedro), [6°23'S, 77°26'W], 2000 m, (Calderón, B.), Apr 2002, 2♀, (PIBO); *Cajamarca:* 16 km W La Coipa, [5°23'S, 78°58'W], 2050 m, (Lamas, G.), 24 Jun 1995, 1♂, (MUSM); Río Tabaconas, [5°19'S, 79°17'W], 1800 m, (Pratt, A. E. & F.), 1912, 1♀, (NHMUK).

Other records: **Ecuador:** *Napo:* Baeza, [0°28'S, 77°53'W], 2000 m, (Piñas, F.), 20 Dec 2000, 1♂ [FDPR-13950], 1♂ [FDPR-13951], 1♂ [FDPR-13953], 1♂ [FDPR-13955], 1♂ [FDPR-13957], (FRPI), 6 Dec 2002, 1♂ [FDPR-13952], 1♂ [FDPR-13954], (FRPI); Baeza-Tena rd., Cocodrilo, [0°38'57"S, 77°47'27"W], (Elias, M., Toporov, S., Santacruz, P.), 12 Mar 2010, 1♀, (sight record) (Elias, M., unpublished data), (Hill, R.), 12 Mar 2010, 1♀ [RH10-74], (RYHI or sight record) (Hill, R., unpublished data); 'Cimarrones C.', 2100 m, (Oña, P., Lloren, J.), 2 Nov 2000, 1♂ [FDPR-13956], (FRPI); nr. Cosanga, Estación Científica Yanayacu, [0°35'24"S, 77°53'W], (Elias, M., Toporov, S., Santacruz, P.), 15 Mar 2010, 1♂, (sight record) (Elias, M., unpublished data); *Sucumbios:* nr. La Bonita, Quebrada El Garrapatal, [0°29'18"N, 77°33'12"W], 2200 m, (Willmott, K. R.), 21 Dec 2001, (sight record) (W&H).

Etymology: The species name is derived from that of the town of Baeza, a popular collecting locality from the time of the earliest entomologists to visit Ecuador, and in the vicinity of which a number of type specimens were collected.

Taxonomy and variation: Molecular data (De-Silva *et al.*, 2010) and the hindwing venation and characters of the genitalia place this taxon within *Ollantaya* Brown & Freitas, 1994 (Willmott & Freitas, 2006). Aside from wing pattern, there are no significant morphological differences between *O. olerioides baeza* n. ssp. and *O. olerioides olerioides* (d'Almeida, 1952), with the two taxa sharing a relatively short posterior projection from the posterior tip of the valva and short uncus in comparison with congeners. Given the otherwise slight differences in wing pattern, which are similar to those observed in a number of other sympatric co-mimic species, we treat the two taxa as conspecific.

Distribution and natural history: This subspecies ranges from the northern Cordillera Central in Colombia (Antioquia) through eastern Ecuador to extreme northern Peru (Cajamarca and Amazonas) (Fig. 33D). It inhabits relatively undisturbed cloud forest habitats from 1600-2200 m, both along ridge tops and in river valleys. Both sexes are typically encountered flying from 1-4 m above the ground in shady forest understorey throughout the middle of the day, although one female was recorded flying 15 m above the ground in hillside forest at 13:37 hrs on a bright but cloudy day.

Oleria tremona benigna Lamas & Willmott, **new subspecies**
Figs. 6A,B, 13L-M, 33E

Oleria tremona n. ssp.: Lamas (2004: 184, no. 209e)

Oleria tremona ssp. nov.: De-Silva *et al.* (2010: supplementary information)

Oleria tremona: Chazot *et al.* (2014b)

Oleria tremona ssp. nov.: De-Silva *et al.* (2015: Appendix S1a)

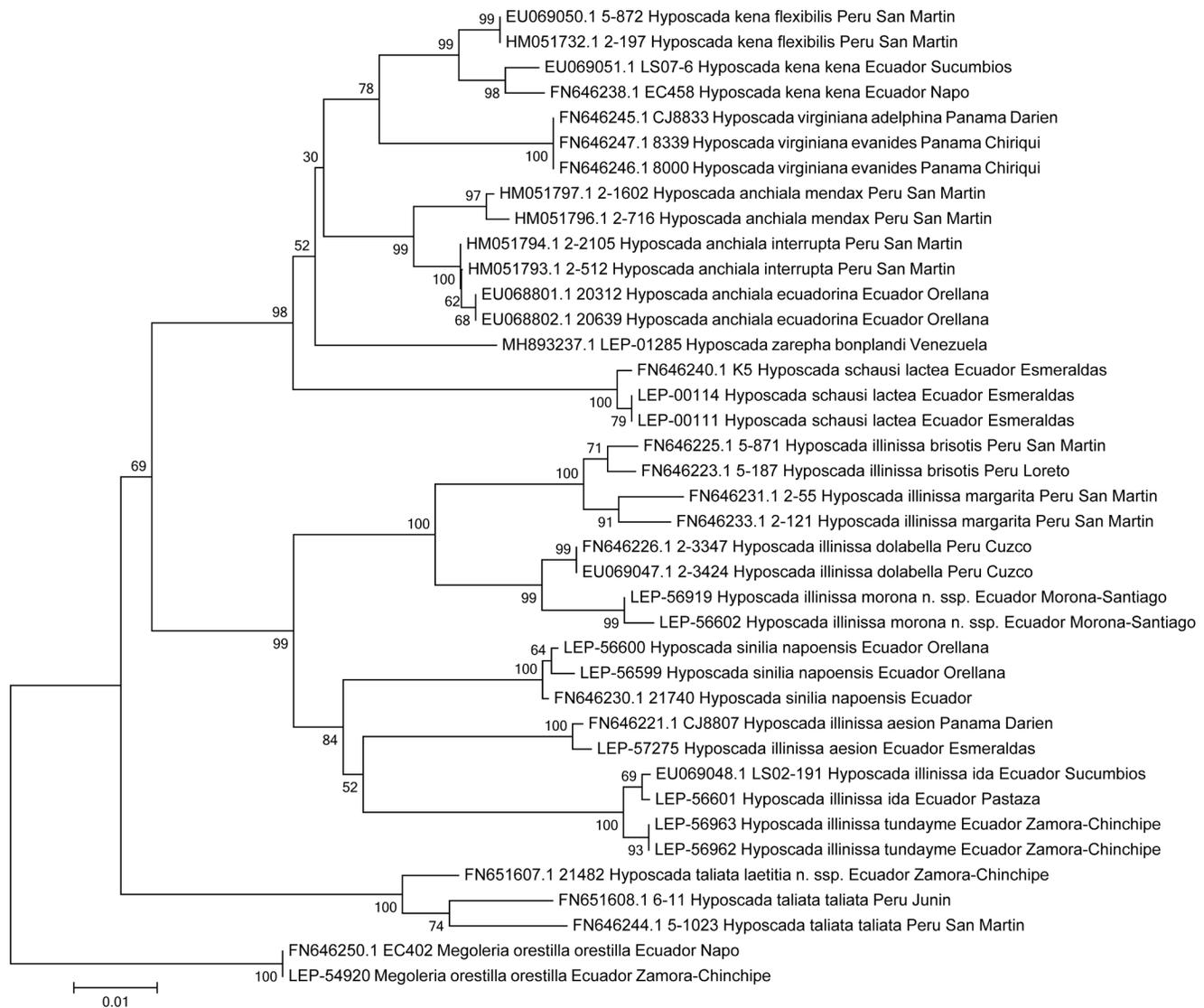


Fig. 23. Neighbor-joining tree (Kimura 2-parameter) for select *Hyposcada* based on analysis of 633 bp of COI (barcode region). Bootstrap values (%) are shown by branches.

Diagnosis and identification: This subspecies is very similar to the nominate subspecies (Fig. 6C), which replaces it to the north, but may be distinguished in the male by the more reddish (rather than orange) ventral brown markings and by the slightly broader white VHW marginal spots. The female has the FW translucent areas ‘cleaner’, lacking scattered black scaling in the middle of the wing, especially in cell Cu_1-M_3 . *Oleria tremona benigna n. ssp.* is otherwise very similar to several sympatric species, especially *Ollantaya olerioides baeza n. ssp.* (see above), *Oleria makrena* (Hewitson, 1854) (which has the inner edge of the dark distal marginal border not basally indented in cell Cu_1-M_3), *Oleria athalina* (Staudinger, [1884]) (which has single, rather than divided, white VHW marginal spots in each cell), and *Oleria santineza* (Haensch, 1903) (which has the anterior half of the HW discal cell much shorter in the male).

Description: MALE (Fig. 6A, 13L-M): Forewing length 29 mm (mean 31 mm, $n=3$). *Wings:* as illustrated (Fig. 6A), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head, thorax, abdomen:* same as in *Ollantaya olerioides baeza n. ssp.* *Genitalia* (Fig. 13L-M): notable features

include almost symmetrical tegumen and uncus in dorsal view with narrow, elongate appendices angulares and double point (inner longer) to valva (Fig. 13M).

FEMALE: (Fig. 6B): Forewing mean length 29.7 mm ($n=3$). *Wings:* as illustrated (Fig. 6B), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **ECUADOR:** *Zamora-Chinchipe:* nr. Romerillos, P. N. Podocarpus, Quebrada Las Dantas, [4°14'26"S, 78°56'W], 1700 m, (Willmott, K. R.), 30 Oct 1997, [Genitalic dissection OLERIA-24], (FLMNH, to be deposited in INABIO).

PARATYPES (76♂, 61♀): **Ecuador:** *Azuay:* ‘nr. Gualaceo’ - (error), 1♂, (FLMNH); Río Paute, 1400 m, Dec, 1♂, (ZSBS); *Zamora-Chinchipe:* above Valladolid, [4°31'18"S, 79°7'48"W], 2000 m, (Hall, J. P. W.), 19 May 1994, 1♂, (FLMNH); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S, 79°5'42"W], 2000 m, (Aldaz, R.), 07 Feb 2002, 3♀, (FLMNH), 13 Jan 2002, 1♂, (FLMNH); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S, 79°5'42"W], 2000-1900 m, (Aldaz, R.), 13 Oct 2006, 1♂ [FLMNH-MGCL-112219], 1♀ [FLMNH-MGCL-112216], (FLMNH); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S, 79°5'42"W], 2000-2100 m, (Willmott, K. R.), 2 Dec 2006, 1♂ [FLMNH-MGCL-112246], 1♀ [FLMNH-MGCL-112249], (FLMNH), 1♀ [FLMNH-MGCL-112244], 1♀ [FLMNH-MGCL-112247], (INABIO), 5 Dec 2006, 1♂ [FLMNH-MGCL-112238], 1♀ [FLMNH-MGCL-112240], 1♀ [FLMNH-MGCL-112242],

1♀ [FLMNH-MGCL-112245], (FLMNH), 1♂ [FLMNH-MGCL-112237], 1♂ [FLMNH-MGCL-112241], 1♀ [FLMNH-MGCL-112239], (INABIO), (Willmott, K. R.), 21 Sep 2007, 1♂ [FLMNH-MGCL-113452], (INABIO), (Willmott, K. R., Aldaz, R.), 10 Oct 2006, 1♀ [FLMNH-MGCL-112220], (FLMNH), 11 Oct 2006, 1♀ [FLMNH-MGCL-112225], (FLMNH), 1♂ [FLMNH-MGCL-112228], 1♂ [FLMNH-MGCL-112232], (INABIO), 6 Nov 2006, 1♀ [FLMNH-MGCL-112218], (FLMNH), 9 Oct 2006, 1♀ [FLMNH-MGCL-112233], (FLMNH), (Elias, M.), 7 -21 Dec 2006, 1♂ [FLMNH-MGCL-112235], 1♀ [FLMNH-MGCL-112243], (FLMNH), 1♂ [FLMNH-MGCL-112236], 1♀ [FLMNH-MGCL-112234], (INABIO), (Aldaz, R.), 30 Oct 2006, 1♂ [FLMNH-MGCL-112248], 1♂ [FLMNH-MGCL-112251], 1♀ [FLMNH-MGCL-112250], 1♀ [FLMNH-MGCL-112252], (FLMNH), 30 Sep 2006, 1♂ [FLMNH-MGCL-112217], (FLMNH), 1♂ [FLMNH-MGCL-112215], (INABIO), 4 Oct 2006, 1♂ [FLMNH-MGCL-112226], 1♂ [FLMNH-MGCL-112230], 1♂ [FLMNH-MGCL-112231], 1♀ [FLMNH-MGCL-112221], 1♀ [FLMNH-MGCL-112229], (FLMNH), 1♂ [FLMNH-MGCL-112224], 1♀ [FLMNH-MGCL-112227], (INABIO); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2000-2150 m, (Aldaz, R.), 07 Feb 2002, 1♂, 2♀, (NHMUK), 07 Feb 2002, 1♀, (FLMNH), 13 Jan 2002, 1♂, (NHMUK); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2050 m, (Radford, J.), 21 Sep 2007 [90], (JARA); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2100 m, (Willmott, K. R., Aldaz, R.), 12 Oct 2006, 1♀ [FLMNH-MGCL-112222], (FLMNH); km 4.3 San Andrés-Jimbura rd., [4°47'59"S,79°18'18"W], 2020 m, (Willmott, K. R.), 13 Oct 2010, 1♀ [FLMNH-MGCL-146789], 1♀ [FLMNH-MGCL-146821], (FLMNH); nr. Romerillos, P. N. Podocarpus, Quebrada Las Dantas, [4°14'26"S,78°56'W], 1700 m, (Willmott, K. R.), 30 Oct 1997, 1♂, (FLMNH); Reserva Tapichalaca, Quebrada Honda trail, [4°28'21"S,79°7'18"W], 1900-2100 m, (Willmott, K. R.), 30 Nov 2005, 1♂ [FLMNH-MGCL-ECD-292], (INABIO); Reserva Tapichalaca, Quebrada Honda trail, [4°28'21"S,79°7'18"W], 2000 m, (Willmott, K. R.), 30 Nov 2005, 1♀ [FLMNH-MGCL-ECD-294], (FLMNH); Reserva Tapichalaca, Quebrada Honda trail, [4°28'21"S,79°7'18"W], 2300 m, (Willmott, K. R.), 30 Nov 2005, 1♂ [FLMNH-MGCL-ECD-377], (FLMNH); ridge to west of Romerillos, [4°13'17"S,78°56'45"W], 1600 m, (Willmott, K. R.), 1 Jul 1997, 1♂, (FLMNH); Río Jamboe, Zamora-Romerillos rd., [4°9'S,78°56'30"W], 1200 m, (Willmott, K. R., Hall, J. P. W.), 25 Jul 1993, 1♂, (FLMNH); Río San Francisco, Estación Científica (EC) San Francisco, [3°58'18"S,79°4'36"W], 1950 m, May, 1♂, (SMNS); 'Río Zamora, Zamora' - (error), 1♀, (NHMUK); Loja: 'environs of Loja' - (error), [18]88, 1♂, (NHMUK), 1889, 1♀, (NHMUK); Quebrada Angashcoala, [4°33'53"S,79°22'10"W], 2600 m, (Willmott, K. R., J. C. R., J. I. R.), 13 Jun 2014, 1♂ [FLMNH-MGCL-280514], 1♂ [FLMNH-MGCL-280515], (FLMNH); *Pastaza*: 'Río Bobonaza, Sarayacu' - (error), (Buckley, C.), 1879, 1♂, (NHMUK). **Peru**: *Amazonas*: Quebrada Chido, [5°50'S,78°0'W], 2300-2500 m, (Grados, J., Calderón, B.), 24 Aug 1998, Aug 2000, 2♀, (MUSM); Choctamal, [6°23'S,77°59'W], 2600-2750 m, (Calderón, B.), 9 Apr 2005, 1♀, (MUSM); *Cajamarca*: Manchara, [5°20'S,79°14'W], 2100 m, Sep, 1♀, (NHMUK); Naranja, [6°16'S,78°51'W], 2300 m, (Lamas, G.), 6 Nov 1998, (MUSM); Río Tabaconas, [5°19'S,79°17'W], 1800 m, 2♂, 2♀, (NHMUK); Río Tabaconas, [5°19'S,79°17'W], 1900 m, (Pratt, A. E. & F.), 1♀, (BMB). **Country unknown**: *Not located*: "Amazon", 1♂, (NHMUK); no data, 2♂, 2♀, (FLMNH).

Other records: **Ecuador:** *Zamora-Chinchi*: km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2000-2100 m, (Willmott, K. R.), 28 Nov 2003, (sight record) (W&H), (Willmott, K. R.), 15 Nov 2006, 1♂, (W&H), 17 Oct 2006, 3♂, 3♀, (W&H), 19 Oct 2006, 1♂, 4♀, (W&H), 2 Nov 2006, 1♂, 1♀, (W&H), (Willmott, K. R., Aldaz, R.), 11 Oct 2006, 4♂, 4♀, (W&H), 14 Oct 2006, 2♀, (W&H), 15 Oct 2006, 1♂, 3♀, (W&H), 22 Oct 2006, 3♂, 1♀, (W&H), 23 Oct 2006, 13♂, (W&H), 27 Oct 2006, 1♂, (W&H), 31 Oct 2006, 5♂, 1♀, (W&H), 6 Nov 2006, 2♂, 1♀, (W&H); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2100 m, (Willmott, K. R.), 24 Nov 2003, (sight record) (W&H), 25 Nov 2003, (sight record) (W&H), (Willmott, K. R.), 26 Oct 2006, 2♂, (W&H).

Etymology: This subspecies name is derived from the feminine Latin adjective 'benigna', meaning mild or kind.

Taxonomy and variation: This taxon shares with *O. tremona tremona* (Fig. 6C; Venezuela to central eastern Ecuador) a short cell M₁-Rs on the HW in the male (longer in *O. santineza*, *O. radina* (Haensch, 1909), and *O. baizana* (Haensch, 1903)),

indented dark distal margin in FW cell M₃-M₂ (not indented in *O. makrena*), and elongate white marginal dashes on the VHW (spots in *O. athalina*), in addition to similarities in the male genitalia (valva with broad posterior point in lateral view ending in longer and shorter inner projections in dorsal view, rather symmetrical tegumen, and long, slender appendices angulares in dorsal view). DNA barcodes also support a close relationship (Fig. 24).

Despite the very slight differences between this subspecies and the nominate subspecies, they were found to be consistent within a large number of examined specimens. In fact, the differences in the white VHW marginal spots between the two taxa are of an extent often seen in other similar species of *Oleria* that are sympatric and co-mimetic, and initially it seemed possible that they might represent distinct species. However, the absence of any significant differences in the male genitalia, and clustering of DNA barcode sequences (Fig. 24), support our decision to treat them as conspecific.

Distribution and natural history: This subspecies replaces the nominate on the east Andean slopes in southern Ecuador, from at least the Río Paute valley southwards, as far as extreme northern Peru (Cajamarca and Amazonas) (Fig. 33E). Surprisingly, we have examined no specimens in collections from Morona-Santiago, which separates this subspecies from the nominate. It occurs in cloud forest from 1200-2750 m, although most records are from 1600-2200 m. We recorded both sexes commonly throughout the day, from 09:45 to 16:30 hrs, flying at heights from 0.2-10 m above the ground, although they are most often observed from 11:00-15:00 hrs within 1-2 m of the ground. Males perched throughout the latter time and height range on tops of leaves in the understorey of tall forest, with the wings held open at approximately 45 degrees in a posture typical of *Oleria*, mostly in leks involving conspecific males as well as those of other ithomiine species. Males were also commonly seen on sunny mornings feeding on white flowers of weedy Asteraceae, as well as on flowering bushes of Asteraceae within the forest. Eggs were laid and caterpillars were found feeding on unidentified species of *Solanum* L. and *Lycianthes* (Dunal) Hassl. (Solanaceae) in the forest understorey at San Francisco (Ecuador, Zamora-Chinchi) (Elias & Willmott, unpublished data).

Oleria radina *bonita* Willmott & Lamas, new subspecies

Figs. 6D,E, 13N-O, 33F

Oleria radina n. ssp.: Lamas (2004: 184, no. 202c)

Oleria solida: Piñas (2004: 31, fig. 155), misidentification

Oleria radina ssp. nov.: De-Silva *et al.* (2010: supplementary information); De-Silva *et al.* (2015: Appendix S1a)

Oleria radina: Chazot *et al.* (2014b)

Diagnosis and identification: Males of this taxon are distinguished from all other described *Oleria* by the combination of an orange-yellow translucent hindwing and a grayish white translucent forewing. In *O. radina radina* the FW is similar, but the HW is transparent with a grayish white translucent postdiscal band (Fig. 6F). The female of *O. radina bonita* n. ssp. is very similar to that of *O. r. radina*, but the few examined specimens of the latter have slightly smaller and more isolated

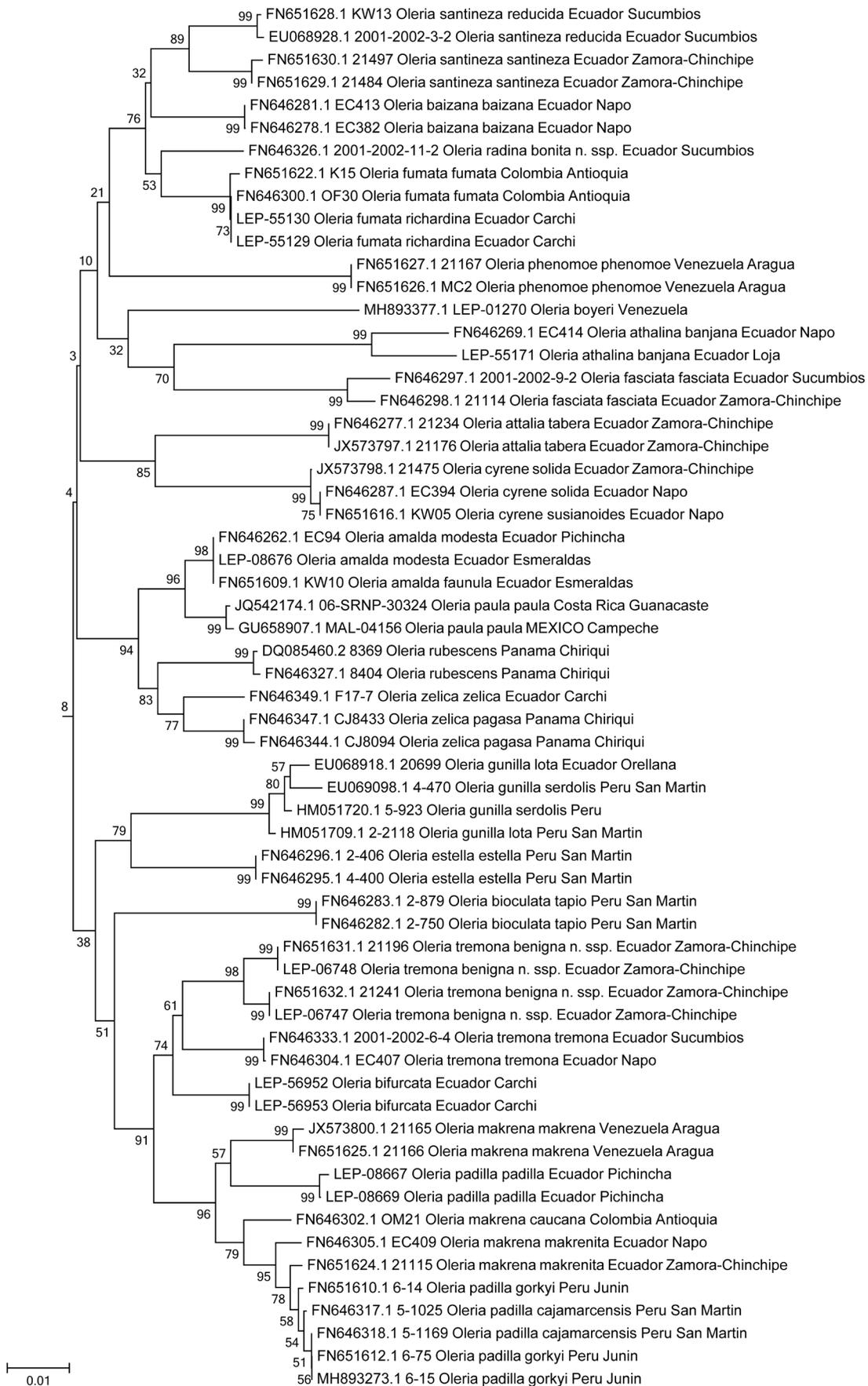


Fig. 24. Neighbor-joining tree (Kimura 2-parameter) for select *Oleria* based on analysis of 633 bp of COI (barcode region). Bootstrap values (%) are shown by branches.

whitish postdiscal spots on the FW. Female *O. radina bonita* is also similar to several sympatric ithomiines, and in particular *O. baizana baizana*; it can be distinguished from that taxon by lacking white DFW apical and DHW marginal spots.

Description: MALE (Fig. 6D, 13N-O): Forewing length 28 mm (mean 28.8 mm, n=6). *Wings:* as illustrated (Fig. 6D), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head, thorax, abdomen:* same as in *Ollantaya olerioides baeza n. ssp.* *Genitalia* (Fig. 13N-O): notable features include strongly asymmetrical tegumen and uncus in dorsal view with reduced/absent appendices angulares (Fig. 13O), elongate posterior projection near middle of valva in lateral view (Fig. 13N).

FEMALE: (Fig. 6E): Forewing mean length 30 mm (n=2). *Wings:* as illustrated (Fig. 6E), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **ECUADOR:** *Sucumbios:* nr. La Bonita, Río Sucio, [0°28'30"N, 77°33'18"W], 2000 m, (Willmott, K. R., Hall, J. P. W.), 11 Nov 1996, [Genitalic dissection KW-21-05], (FLMNH, to be deposited in INABIO).

PARATYPES (20♂, 10♀): **Colombia:** *Nariño:* Monopamba, [0°46'N, 77°7'W], 1700 m, 24 Feb 1986, 1♂, (IAVH). **Ecuador:** *Sucumbios:* km 19 La Bonita-Tulcan rd., old rd. to La Alegría, [0°33'30"N, 77°31'42"W], 2400 m, (Willmott, K. R.), 12 Dec 2001, 2♂, (FLMNH), 13 Dec 2001, 2♂, (FLMNH), 22 Dec 2001, 1♂, (FLMNH), (Willmott, K. R.), 12 Dec 2001, 2♂, (NHMUK); km 2 La Bonita-Tulcán rd., [0°28'48"N, 77°32'24"W], 2000 m, (Willmott, K. R.), 21 Dec 2001, 2♂, (FLMNH); km 6 La Bonita-Rosa Florida rd., [0°27'N, 77°31'45"W], 2000 m, (Boyer, P.), 23 Nov 1999, 1♂, 1♀, (PIBO); nr. La Bonita, Quebrada El Garrapatal, [0°29'18"N, 77°33'12"W], 2100-2200 m, (Willmott, K. R.), 21 Nov 1996, 1♂, (FLMNH), (Willmott, K. R.), 20 Dec 2001, 2♀, (NHMUK); nr. La Bonita, Quebrada El Garrapatal, [0°29'18"N, 77°33'12"W], 2200 m, (Willmott, K. R.), 20 Dec 2001, 3♀, (FLMNH), 21 Dec 2001, 1♀, (FLMNH), 31 Dec 2001, 1♀, (FLMNH); nr. La Bonita, Río Sucio, [0°28'30"N, 77°33'18"W], 1800 m, (Willmott, K. R.), 12 Dec 2001, 1♂, 1♀, (FLMNH); nr. La Bonita, Río Sucio, [0°28'30"N, 77°33'18"W], 2000 m, (Willmott, K. R., Hall, J. P. W.), 11 Nov 1996, 1♂, (FLMNH); Qbda. El Morro, km 9 La Bonita-Tulcán rd., El Higuierón, [0°30'54"N, 77°32'12"W], 2200 m, (Willmott, K. R.), 21 Dec 2001, 3♂, 1♀, (FLMNH); Qbda. El Morro, km 9 La Bonita-Tulcán rd., El Higuierón, [0°30'54"N, 77°32'12"W], 2200-2400 m, (Hall, J. P. W., Willmott, K. R.), 10 Nov 1997, 1♂, (FLMNH), 1♂, (MUSM), (Willmott, K. R.), 22 Nov 1996, 1♂, (FLMNH).

Etymology: The subspecies name is derived from that of the village of La Bonita, in the vicinity of which most of the type specimens were collected.

Taxonomy and variation: This taxon is treated as a subspecies of *O. radina* on the basis of its similar hindwing venation, male genitalia and female wing pattern. The male hindwing discal cell is relatively short, so that the transparent area in cell M_2-M_1 appears as a trapezium, with the transparent area bordering vein M_1 for some distance. In most other similar species (e.g., *O. tremona* (Fig. 6A,C), *O. makrena*, *O. athalina*, and *O. bifurcata* Willmott & Lamas, 2020) this transparent area appears as a triangle, since the discocellular vein 1d is located nearer the apex. *Oleria fumata* (Haensch, 1905), *O. santineza* and *O. baizana* have similar hindwing venation to *O. radina*, and indeed these four species form a clade based on DNA sequence data (Chazot *et al.*, 2019). *Oleria radina* is sympatric with *O. fumata* in western Colombia and with *O. santineza* and *O. baizana* in eastern Colombia and eastern Ecuador. Most subspecies of *Oleria radina* have notably bowed and strongly marked veins Cu_1 , M_3 and M_2 in the FW subapical area (including the nominate subspecies and *O. radina bonita n. ssp.*). In comparison with *O. fumata*, *O. santineza* and *O. baizana*, the male genitalia of *O. radina* (including the nominate subspecies and *O. radina bonita*) are distinctive in

the valva posterior projection being relatively short and broad in lateral view, and straight and broad in dorsal view, the dorsal portion of the right valva being broad and extending dorsally, the tegumen being large and rounded, and the appendices angulares being absent or vestigial. The female of *O. radina bonita* is very similar to that of the nominate subspecies; aside from an overall similar wing pattern, distinctive shared features include the almost fused, rounded double white VHW marginal dots in cells Cu_2-M_3 , black basal two-thirds of FW cell Cu_1-M_3 , and triangular orange VHW submarginal marking over vein M_3 . No notable variation was observed in the examined specimens of this new subspecies.

Haensch (1909-1910: 148) described the nominate subspecies of this species as *Leucothyris cyrene* form *radina* Haensch, 1909, from an unspecified number of specimens from Colombia. The description mentions the HW translucent band slightly broadening at the base, and corresponds to the lectotype, a female, in the MFN, designated by Lamas (1994). We have examined six additional similar female specimens in collections, two of which are labeled “Bogotá”, and one of which is labeled “La Aguadita” (both in Colombia, Cundinamarca). Despite these vague and imprecise localities, they suggest that the nominate subspecies occurs in the Colombian Cordillera Oriental. A single male in the MFN labeled “Bogotá” is assumed to represent *O. radina radina* (Fig. 6F), and it is similar in wing venation and genitalia (Genitalic dissection BERL-10) to *O. radina bonita*, as discussed above. This male differs from males from the Colombian Cordillera Central and Occidental in having the whitish translucent band on the hindwing distal to the discal cell, rather than in the basal half of the wing filling the distal cell, further supporting the inference that it comes from the Cordillera Oriental and represents the nominate subspecies, and is not a mislabeled specimen from elsewhere in Colombia.

Distribution and natural history: This subspecies occurs on the east Andean slopes from extreme southern Colombia (Nariño) to northern Ecuador (Sucumbios) (Fig. 33F). It occurs from 1800-2400 m in relatively undisturbed cloud forest, both along rivers as well as on ridges. The sexual dimorphism in mimicry pattern exhibited by this species is matched within the Ithomiini only by that of its close relative, *O. baizana*, with which it flies. However, although the females of these two species are very similar, and apparently involved in mimicry with one another as well as a number of other oleriines (e.g., *Oleria cyrene* (Latreille, [1809]) and *Megoleria susiana* (C. Felder & R. Felder, 1862)), the males apparently belong to different mimicry rings. *Oleria radina bonita n. ssp.*, with its white translucent FW spots and yellow HW, is a member of a mimicry ring that mainly involves species in the subtribes Godyridina (e.g., *Hypomenitis ortygia ortygia* (Weyer, 1890) and *Hypomenitis enigma pseudortygia* (Neild & Willmott, 2008)) and Dircennina (e.g., *Pteronymia ticida ticida* (Hewitson, 1869) and *Hyalenna sulmona tersa* Willmott & Lamas, 2006)). This divergence in mimicry pattern might be explained by differences in the preferred microhabitats between the sexes, with each microhabitat associated with different mimicry patterns and predator communities (Willmott *et al.*, 2017). We observed males flying from 2-6 m in the understory and perching 6-8 m high on the tops of bushes. Most oleriine

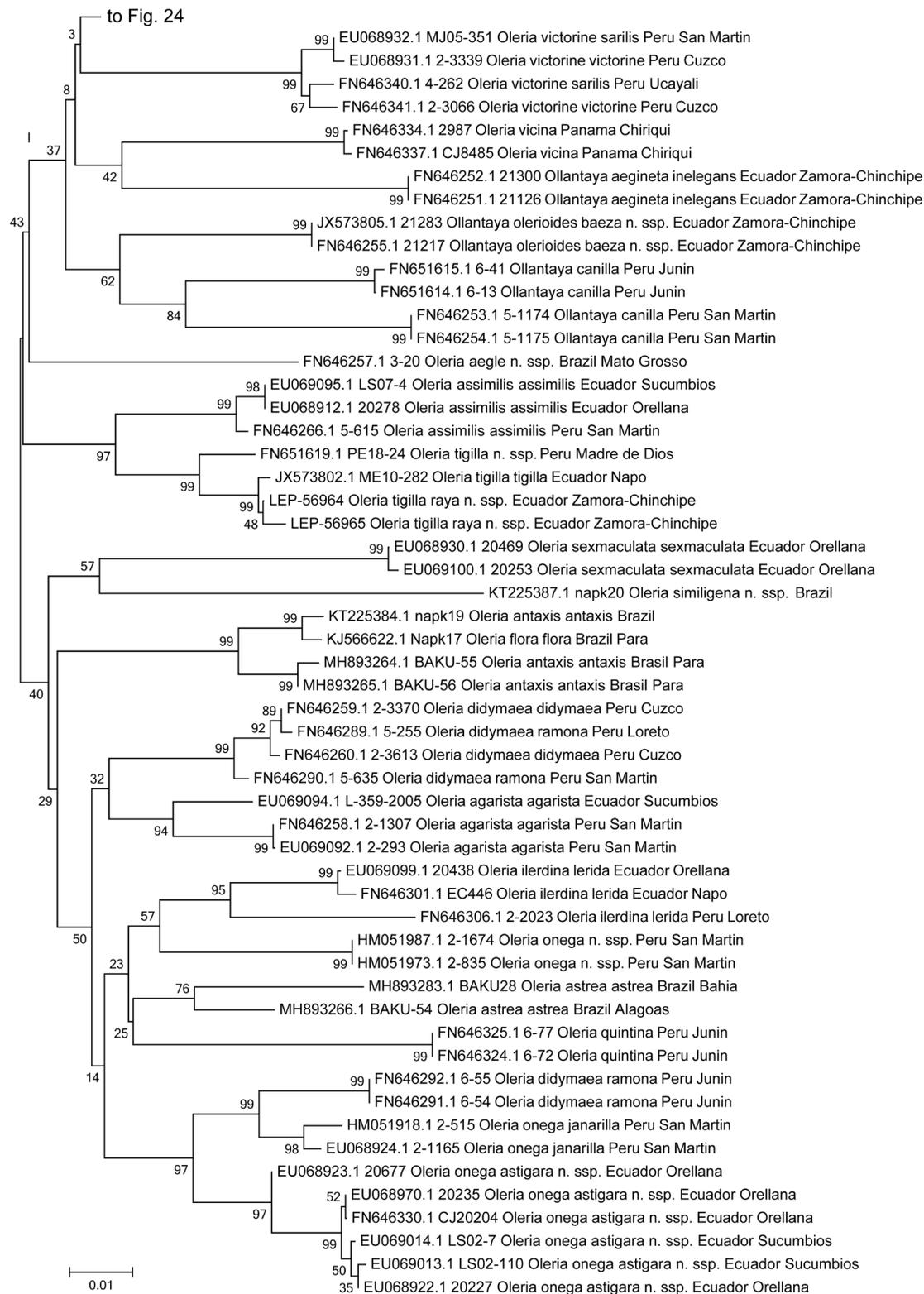


Fig. 25. Neighbor-joining tree (Kimura 2-parameter) for select *Oleria* and *Ollantaya* based on analysis of 633 bp of COI (barcode region). Bootstrap values (%) are shown by branches.

males perch within 2 m of the ground, but many Godyridina and Dircennina perch higher, similar to *O. radina*. Females were typically encountered flying lower in the understory, from 2-4 m, at a height typical of other cloud forest oleriines. A male was found feeding on Asteraceae flowers along a wide trail at 09:00 hrs.

Oleria tigilla raya Lamas & Willmott, **new subspecies**

Figs. 6G,H, 13P-Q, 34A

Oleria tigilla n. ssp.: Lamas (2004: 184, no. 208b)

Diagnosis and identification: This subspecies is distinguished from the nominate subspecies (Fig. 6I) by the entirely black

DFW apex, which lacks an orange subapical band. It is distinguished from other similar *Oleria* by the white translucent FW postdiscal spots occurring in the middle of the cells (in *O. onega* (Hewitson, [1852]) and *O. ilderina* (Hewitson, 1858), vein M_3 cuts through the middle of a spot) and by the short hindwing discal cell.

Description: MALE (Fig. 6G, 13P-Q): Forewing length 27 mm (mean 26.7 mm, n=3). *Wings:* as illustrated (Fig. 6G), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head, thorax, abdomen:* same as in *Ollantaya olerioides baeza n. ssp.* except hair-like scales ventrally on labial palpi shorter. *Genitalia* (Fig. 13P-Q): notable features include strongly asymmetrical tegumen and uncus in dorsal view, with reduced/absent appendices angulares, visible base to gnathos arms (Fig. 13Q), and slightly forked tip to uncus (Fig. 13P).

FEMALE (Fig. 6G): Forewing length 25 mm (n=1). *Wings:* as illustrated (Fig. 6G), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **PERU:** Pasco: Río Raya, km 28 Repartición-Iscozacán, [10°20'S, 75°06'W], 350 m, (Mallet, J.), 22 Aug 1984, (MUSM).

PARATYPES (36♂, 27♀): **Ecuador:** *Morona-Santiago:* nr. Yaupi, Río Wampis, [2°51'16"S, 77°56'48"W], 350-400 m, (Gallice, G.), 2 Jul 2009, 1♂ [FLMNH-MGCL-153551], (FLMNH); Yaupi-Yaapi trail, [2°49'58"S, 77°56'28"W], 320-340 m, (Gallice, G.), 15 Jun 2009, 1♂ [FLMNH-MGCL-153549], 1♂ [FLMNH-MGCL-153550], (FLMNH); *Zamora-Chinchipec:* Río Nangaritzá, 3 km N Las Orquídeas, Reserva Maycú, [4°12'44"S, 78°38'30"W], 850 m, (Willmott, K. R., J. I. R., J. C. R.), 28 Jun 2014, 1♂ [FLMNH-MGCL-280533]; *Genitalic dissection* KW-21-06], (FLMNH); lower Río Numpatakaima, c. 3 km S Shaime, [4°21'S, 78°39'28"W], 900 m, (Willmott, K. R., Hall, J. P. W.), 31 Jul 2009, 1♂ [FLMNH-MGCL-144401], 1♂ [FLMNH-MGCL-144402], 1♂ [FLMNH-MGCL-144403], 1♂ [FLMNH-MGCL-144404], (FLMNH); upper Río Nangaritzá, 3 km N Las Orquídeas, Reserva Maycú, [4°12'44"S, 78°38'30"W], 850 m, (Willmott, K. R., J. I. R., J. C. R.), 28 Jun 2014, 1♂ [FLMNH-MGCL-280532], (FLMNH). **Peru:** *Amazonas:* 15 km E Paraíso, [4°48'S, 78°9'W], 330 m, (Lamas, G., Grados, J., Joron, M., Chang, F.), 14 Nov 1996, 2♂, 6♀, (MUSM); Río Santiago, [4°26'S, 77°38'W], Nov, 4♂, 2♀, (AMNH); upper Río Marañón, Dec, 1♂, 1♀, (AMNH); Wawico, [4°56'S, 78°12'W], 300 m, (Pintado, J.), 2012, 2♂, 3♀, (MUSM); *Huánuco:* Panguana, [9°37'S, 74°56'W], (Koeppke, H.-W.), Jan 1969, 1♂, 3♀, (MUSM); 260 m, (Diller, J.), 6-17 Apr 2003, 1♂, (MUSM); *Loreto:* Cerros de Orellana, 'Lupunay', 120 m, (Hocking, P.), 15 Jul 1988, 1♀, (MUSM); *Pasco:* Chuchurras, [10°9'S, 75°14'W], 1♀, (FLMNH); same data as HT, 1♂, (MUSM); Oxapampa, [10°35'S, 75°24'W], 1945, 1♂, (MUSM); Río Palcazu, Río Chuchurras, [10°7'S, 75°10'W], 320 m, (Hoffmanns, W.), 2♂, (NHMUK); Parque Nacional Yanachaga-Chemillén, Estación Biológica Paujil, [10°19'25"S, 75°15'48.8"W], 375 m, (Grados, J., Carbonell, S., Calderón, C.), 22, 23 May 2008, 6♂, 3♀, (MUSM); Pampa Pescado, [10°2'33.4"S, 75°14'36.4"W], 400-450 m, (Grados, J., Carbonell, S.), 16, 18 Sep 2007, 2♂, (MUSM); *San Martín:* Moyobamba, [6°2'S, 76°58'W], (Mathan, M. de), Sep 1887, 1♂, (NHMUK); Quebrada San Roque, [6°23'S, 76°26'W], 500 m, (Gallusser, S.), 14 Dec 2000, 1♂, 1♀, (MUSM); Tarapoto, [6°29'S, 76°22'W], 430-590 m, (Lamas, G.), 31 Aug 1968, 1♂, 1♀, (MUSM); San Miguel, Río Biabo, [ca. 7°25'S, 76°25'W], 300 m, (Calderón, A.), 11-12 Jan, 8-10 Nov 2007, 5♂, 2♀, (MUSM); Yacusisa, [6°46'S, 76°49'W], (Calderón, A.), 20 Dec 2007, 1♀, (MUSM); Chasuta, [6°34'S, 76°08'W], 150 m, (Tafur, A.), 25 Jan 2011, 1♂, (MUSM); *Ucayali:* nr. Pucallpa, Neshuya, [8°39'S, 74°58'W], 200 m, Aug, 1♂, 1♀, (ZSM); *Not located:* 'Peru', 1♂, (SMNS), (Mathan, M. de), 1♀, (NHMUK).

Etymology: The subspecies name is derived from that of the Río Raya in Pasco, Peru, one of the localities for this subspecies.

Taxonomy and variation: This taxon is treated as a subspecies of *O. tigilla* (Weymer, 1899) because, aside from having the same pattern of white translucent FW subapical spots as the nominate subspecies, it also has the same distinctive male wing venation, with a notably short HW discal cell (1d not shifted apically) and correspondingly long vein M_1 . This character distinguishes it from its sister species *O. assimilis* (Haensch, 1903) (De-Silva et al., 2010; Fig. 25), which is otherwise similar but has

1d placed much nearer the wing apex. These two species also share several genitalic characters that distinguish them from other related lowland *Oleria*, including the more visible base of the gnathos in dorsal view (almost hidden in other species) and typically bifid tip to the uncus (latter apparently present in at least some individuals of *O. assimilis*). Finally, DNA barcodes show a close relationship with the nominate subspecies (Fig. 25).

Although only a single wing pattern character distinguishes this taxon from the nominate subspecies, this character was found to be stable within long series of examined specimens from multiple localities. Furthermore, it coincides with parallel differences between co-mimetic subspecies of other *Oleriina* species, such as *O. onega janarilla* (Hewitson, 1863)/*O. onega astigara n. ssp.*, *O. gunilla lota* (Hewitson, 1872)/*O. gunilla serdolis* (Haensch, 1909), *Hyposcada kena kena*/H. *kena flexibilis* (Haensch, 1909), and others.

Distribution and natural history: This subspecies occurs from southern Ecuador (southeastern Morona-Santiago and Zamora-Chinchipec) to central Peru (Huánuco, Pasco and Ucayali) (Fig. 34A), in lowland forests typically near the base of the eastern Andes, from 120-900 m. Like the nominate subspecies, it is local but not uncommon, in the understorey of disturbed forest near to rivers and streams.

Oleria onega astigara Willmott & Lamas, new subspecies Figs. 6J,K, 13R-S, 34B

Leucothyris agarista: Haensch (1903: 189; 1909-1910: 146)

Oleria agarista: D'Abreu (1984: 238)

Oleria onega n. ssp.: Lamas (2004: 184, no. 196i)

Oleria onega agarista: Piñas (2004: 30, fig. 135); Galluser et al. (2004)

Oleria assimilis: Piñas (2004: 30, fig. 139), misidentification

Oleria janarilla: Piñas (2004: 31, fig. 147), misidentification

Oleria onega ssp.: Willmott & Mallet (2004: Appendix A); Elias et al. (2007: supplementary information)

Oleria onega: Elias et al. (2008: S1); Willmott et al. (2011); Chazot et al. (2014b)

Diagnosis and identification: This subspecies is distinguished from the neighboring and otherwise most similar subspecies, *O. onega janarilla* (Fig. 6L), by the possession of a curving orange subapical band or line on the DFW. The taxon is very similar to the sympatric *O. ilderina lerida* (Kirby, 1878), which may be distinguished by having the orange DFW subapical stripe broader and closely bordering the distal edge of the subapical translucent spot in both cells M_2 - M_1 and M_1 - R_5 ; in *O. onega astigara n. ssp.* the orange marking is closer to the subapical spot in cell M_1 - R_5 than it is in M_2 - M_1 .

Description: MALE (Fig. 6J, 13R-S): Forewing length 23 mm (mean 23.2 mm, n=9). *Wings:* as illustrated (Fig. 6J), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head, thorax, abdomen:* same as in *Oleria tigilla raya n. ssp.* *Genitalia* (Fig. 13R-S): notable features include slightly asymmetrical tegumen and uncus in dorsal view, with short appendices angulares and base to gnathos arms not visible (Fig. 13S).

FEMALE (Fig. 6K): Forewing mean length 24 mm (n=6). *Wings:* as illustrated (Fig. 6K), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **ECUADOR:** Napo: km 14 Tena-Puyo rd., Apuya, [1°6'18"S, 77°46'42"W], 600 m, (Willmott, K. R., Hall, J. P. W.), 3 Dec 1997, [Genitalic dissection OLERIA-33], (FLMNH, to be deposited in INABIO).

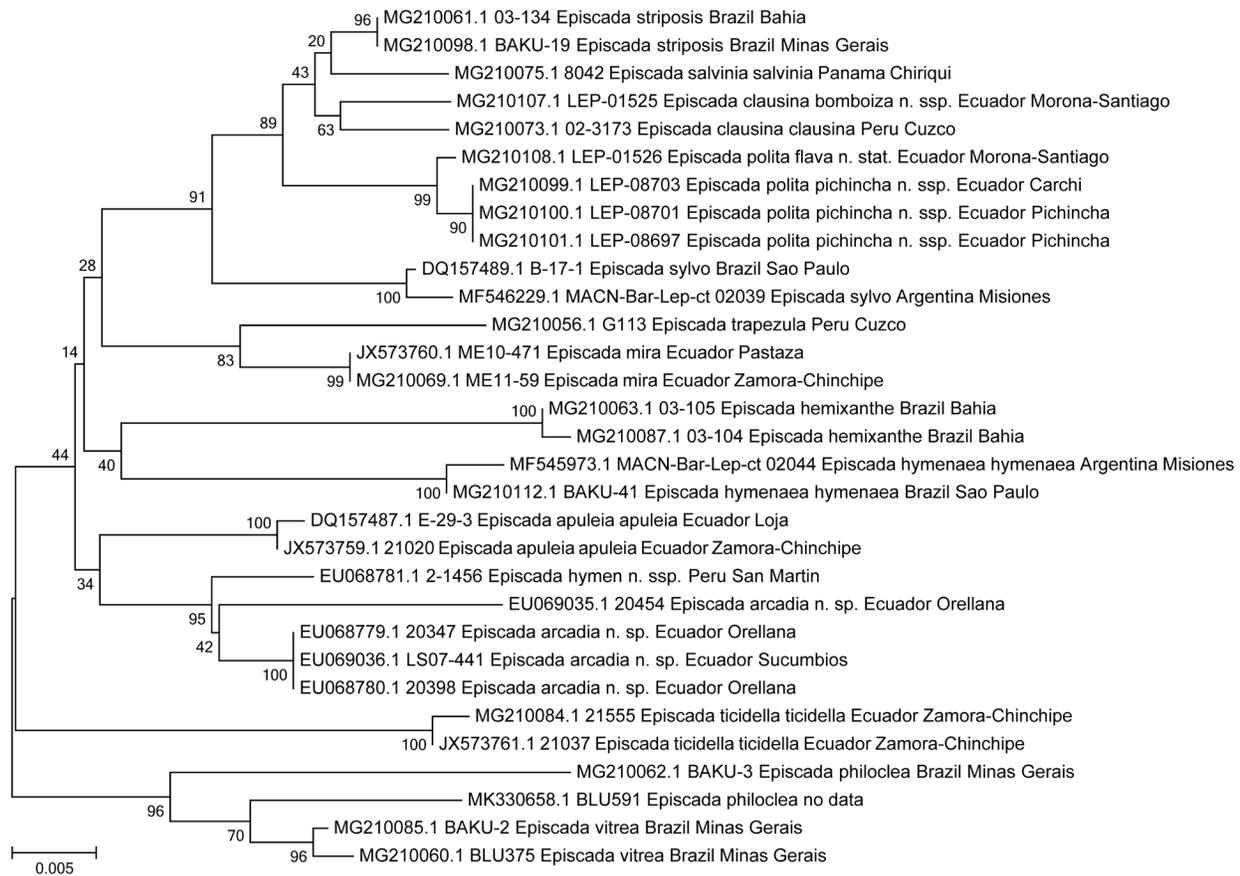


Fig. 26. Neighbor-joining tree (Kimura 2-parameter) for select *Episcada* based on analysis of 633 bp of COI (barcode region). Bootstrap values (%) are shown by branches.

PARATYPES (270♂, 210♀): **Ecuador: Sucumbios:** Añangu, Garzacochoa, [0°1'S,76°11'W], 250 m, (Hesterberg, R.), 16-22 Sep 1994, 1♂ [FLMNH-MGCL-256258], (FLMNH); Garzacochoa, Río Napo, La Selva, [0°29'53"S,76°22'25"W], 250 m, Sep, 1♂, (FLMNH); Lago Agrio, (Villafructe, I. A.), 2,3,4 Apr 1990, 1♂ [FLMNH-MGCL-263646], 1♀ [FLMNH-MGCL-263649], (FLMNH), 22-31 May 1990, 1♂ [FLMNH-MGCL-263671], 1♀ [FLMNH-MGCL-263677], (FLMNH); Lago Agrio, (Mauffray, W.), 8 Jun 1995, 1♀ [FLMNH-MGCL-263678], (FLMNH); Río Napo, Limoncocha, [0°24'S,76°37'W], 240 m, (Covell, C. V.), 24 Jun 1980, 1♂ [FLMNH-MGCL-263659], 1♂ [FLMNH-MGCL-263672], (FLMNH), 24-27 Jun 1980, 1♂ [FLMNH-MGCL-263645], 1♂ [FLMNH-MGCL-263682], 1♀ [FLMNH-MGCL-263680], (FLMNH); Río Napo, Limoncocha, [0°24'S,76°37'W], 300 m, Feb Oct Nov, 15♂, 4♀, (USNM), (Emmel, T. C.), 10 Jul 1973, 1♂ [FLMNH-MGCL-263694], 1♂ [FLMNH-MGCL-263710], 1♂ [FLMNH-MGCL-263711], 1♂ [FLMNH-MGCL-263720], (FLMNH), 10 Sep 1972, 1♂ [FLMNH-MGCL-263733], 1♀ [FLMNH-MGCL-262868], 1♀ [FLMNH-MGCL-263731], (FLMNH), 11 Jul 1973, 1♂ [FLMNH-MGCL-263692], 1♂ [FLMNH-MGCL-263718], 1♂ [FLMNH-MGCL-263719], 1♀ [FLMNH-MGCL-263726], 1♀ [FLMNH-MGCL-263730], (FLMNH), 12 Jul 1973, 1♂ [FLMNH-MGCL-263693], 1♂ [FLMNH-MGCL-263706], 1♂ [FLMNH-MGCL-263707], 1♀ [FLMNH-MGCL-263725], (FLMNH), 12 Sep 1972, 1♂ [FLMNH-MGCL-263734], (FLMNH), 2 Sep 1969, 1♂ [FLMNH-MGCL-263698], (FLMNH), 27 Jun 1980, 1♂ [FLMNH-MGCL-265162], (FLMNH), 28 Jun 1980, 1♂ [FLMNH-MGCL-265160], 1♂ [FLMNH-MGCL-265164], (FLMNH), 29 Jun 1980, 1♂ [FLMNH-MGCL-262804; 'Missed it'], 1♂ [FLMNH-MGCL-262805], 1♂ [FLMNH-MGCL-265156], 1♂ [FLMNH-MGCL-265157], (FLMNH), 29 Sep 1973, 1♂ [FLMNH-MGCL-263712], (FLMNH), 3 Sep 1969, 1♂ [FLMNH-MGCL-265155], 1♂ [FLMNH-MGCL-265163], 1♀ [FLMNH-MGCL-263713], 1♀ [FLMNH-MGCL-263727], 1♀ [FLMNH-MGCL-263728], (FLMNH), 4 Sep 1969, 1♂ [FLMNH-MGCL-263708], 1♂ [FLMNH-MGCL-263714], 1♂ [FLMNH-MGCL-263716], 1♂ [FLMNH-MGCL-263717], (FLMNH), 4 Sep 1972, 1♂ [FLMNH-MGCL-263696], 1♂ [FLMNH-MGCL-263697], 1♂ [FLMNH-MGCL-263715], 1♂ [FLMNH-MGCL-263724], 1♀ [FLMNH-

MGCL-263700], 1♀ [FLMNH-MGCL-263701], 1♀ [FLMNH-MGCL-263704], 1♀ [FLMNH-MGCL-263729], (FLMNH), 5 Sep 1972, 1♂ [FLMNH-MGCL-263695], 1♀ [FLMNH-MGCL-263705], (FLMNH), 7 Sep 1972, 1♂ [FLMNH-MGCL-263709], 1♂ [FLMNH-MGCL-263723], (FLMNH), 9 Sep 1972, 1♂ [FLMNH-MGCL-263721], 1♂ [FLMNH-MGCL-263722], 1♂ [FLMNH-MGCL-263735], 1♀ [FLMNH-MGCL-263699], 1♀ [FLMNH-MGCL-263703], (FLMNH), (Preston, J. & F.), 28 Jun 1980, 1♂ [FLMNH-MGCL-263648], 1♀ [FLMNH-MGCL-263665], (FLMNH), (Vénédictoff, N.), Nov 1972, 1♂ [FLMNH-MGCL-265159], 1♀ [FLMNH-MGCL-265167], (FLMNH), Nov 1972, 1♂ [FLMNH-MGCL-265158], (FLMNH), (Westfall, M.J.), 17 Nov 1980, 1♂ [FLMNH-MGCL-263736], (FLMNH); Río Napo, Pañacochoa, [0°26'11"S,76°4'W], 250 m, (Willmott, K. R., Hall, J. P. W.), 15,16 Oct 1997, 2♂, 1♀, (FLMNH); Río Pañayacu, Laguna de Pañacochoa, [0°23'53"S,76°7'40"W], 250 m, (Hall, J. P. W., Willmott, K. R.), 12-14 Oct 1997, 1♂, (MUSM); *Napo*: 33 km N Tena, 59 km E on Loreto rd., [0°43'54"S,77°30'33"W], 920 m, Nov, 1♀, (AMNH); Aguano, [1°4'S,77°33'W], 1♂, 2♀, (MfN); Baeza-Tena rd., Cocardrilo, [0°38'57"S,77°47'27"W], (Elias, M., Toporov, S., Santacruz, P.), 2010, 1♀, (INABIO); Cordillera Galeras, [0°48'21"S,77°35'14"W], 869 m, (Radford, J.), 11 Aug 2010, 1♀ [GAN34], (FLMNH) (CULEPEX Expedition, 2010); E Archidona, Coral, [0°56'11"S,77°45'31"W], (Elias, M., Toporov, S., Santacruz, P.), 20 Feb 2010, 1♀, (FLMNH), 2♀, (MNHN); E Archidona, Mariposa, [0°54'30"S,77°47'8"W], (Elias, M., Toporov, S., Santacruz, P.), 2010, 1♂, (INABIO), 10 Feb 2010, 1♂, 1♀, (FLMNH), 1♀, (MNHN), 21 Feb 2010, 1♂, (MNHN); Isla Anaconda, [1°3'22"S,77°31'54"W], 350 m, 23 Aug 1976, 1♀ [FLMNH-MGCL-263666], (FLMNH); Jct. of Río Napo and Río Misahuallí, Misahuallí Jungle Lodge, [1°148'S,77°39'30"W], 1700 m, (Emmel, T. C., Schlachta, S. D.), 21 Oct 1998, 1♂ [FLMNH-MGCL-265161], 1♂ [FLMNH-MGCL-265166], (FLMNH); km 34 Loreto-Tena rd., Río Pingullo, [0°44'20"S,77°33'11"W], 950 m, (Neild, A. F. E.), 18 Aug 2010, 1♂, (INABIO); Napo, 1♀, (MfN); nr. Misahuallí, Río Misahuallí, Las Minas, [1°0'30"S,77°40'6"W], 400 m, (Willmott, K. R., Hall, J. P. W.), 17,20,21 Jul 1991, 1♂, (FLMNH); Puerto Misahuallí, [1°1'36"S,77°40'W], Apr Nov, 2♀, (FLMNH), (Jenkins, D. & J.), 6 Nov 1983, 1♀ [FLMNH-MGCL-256262],

- (FLMNH); Puerto Misahuallí, [1°13'36"S,77°40'W], 300 m, (Petit, J.-C.), 20 Nov 2003, 1♂, (JEPE); Puerto Misahuallí, [1°13'36"S,77°40'W], 400 m, (Willmott, K. R., Hall, J. P. W.), 16 Jul 1991, 1♀, (FLMNH); Río Arajuño, Camp Dayuma, [1°53'35"S,77°35'7"W], Apr, 1♂, (USNM); Río Hollín, nr. Archidona, 'Hollín2', [0°55'46"S,77°44'24"W], (Elias, M., Toporov, S., Santacruz, P.), 21 Mar 2010, 1♂, (MNHN); Río Misahuallí 10 min by boat above the junction with Río Napo, [1°02'S,77°40'23"W], 488 m, (Harris, L. N.), 14 Nov 1997, 1♂ [FLMNH-MGCL-263686], 1♀ [FLMNH-MGCL-263667], (FLMNH); Río Misahuallí, Misahuallí, [1°13'36"S,77°40'W], 400 m, (Taylor, T.), 22 May 1971, 1♀ [FLMNH-MGCL-256266], (FLMNH); Río Napo, Misahuallí, [1°13'36"S,77°40'W], 518 m, (Bowe, J. J.), 14 Apr 1999, 1♂ [FLMNH-MGCL-263674], 1♀ [FLMNH-MGCL-263655], 1♀ [FLMNH-MGCL-263679], (FLMNH), 28 Aug 2000, 1♀ [FLMNH-MGCL-263676], (FLMNH), 8 Sep 1998, 1♂ [FLMNH-MGCL-263660], (FLMNH), (Harris, L. N.), 31 Aug 2000, 1♀ [FLMNH-MGCL-263651], (FLMNH); Río Napo, Puerto Napo-Ahuano rd., Jatun Sacha, [1°3'S,77°35'9"W], 400-450 m, (Beccaloni, G. W., Murray, D.), Feb, May, Sep, Oct 1991-1992, 3♂, 4♀, (NHMUK), (Beccaloni, G. W.), Sep 1992, 1♂, 1♀ [I38 ovipositing on aroid leaf overhanging spiny Solanaceae], 4♀ [dissected to obtain ova], (NHMUK), Sep, Oct, 1991, 1992, 3♂ [reared I43a, I45, I46 on plant GB15], 1♀ [reared I39 on plant GB15], (NHMUK); *Orellana*: 48.5 km S Pompeya, Bogi 2 W stream, [0°42'44"S,76°28'29"W], 230 m, (Hall, J. P. W., Willmott, K. R., J. C. R., J. I. R.), 28 Jul 2015, 1♀, (INABIO); Laguna Añangu, Napo Wildlife Center, [0°31'26"S,76°26'26"W], 250 m, (Willmott, K. R.), 12 Oct 2005, 1♂, 1♀, (EUIEB); Laguna Añangu, Napo Wildlife Center, Napo trail, [0°30'35"S,76°26'13"W], 250 m, (Willmott, K. R.), 13 Oct 2005, 1♀, (EUIEB), 16 Oct 2005, 1♂ [FLMNH-MGCL-ECD-305], (FLMNH), 17 Oct 2005, 1♂ [FLMNH-MGCL-ECD-306], 1♂ [FLMNH-MGCL-ECD-308], (FLMNH), 18 Oct 2005, 1♀ [FLMNH-MGCL-ECD-313], (INABIO), 20 Oct 2005, 1♂ [FLMNH-MGCL-ECD-309], (FLMNH), (Elias, M.), 1 Dec 2005, 1♂, 1♀, (EUIEB), 13 Dec 2005, 1♀ [FLMNH-MGCL-ECD-311], (FLMNH); Laguna Añangu, Napo Wildlife Center, Tiputini trail, [0°31'46"S,76°25'11"W], 250 m, (Willmott, K. R.), 11 Oct 2005, 1♀ [FLMNH-MGCL-ECD-310], (FLMNH); lower Río Yasuni, Tambococha, [0°58'42"S,75°25'33"W], 170 m, (Willmott, K. R., J. C. R., J. I. R.), 21 Jul 2015, 1♂, (INABIO); nr. Coca, [0°28'S,76°59'W], 300 m, 1♂, 5♀, (MfN), Feb, 2♀, (USNM); Reserva Biológica del Río Bigal, (FLMNH) (CULEPEX Expedition, 2010); Reserva Biológica del Río Bigal, [0°31'17"S,77°25'10"W], 851 m, (Hartley, E.), 23 Jul 2010, 1♂ [N84], (INABIO) (CULEPEX Expedition, 2010), (Radford, J.), 23 Jul 2010, 1♂ [N92], (FLMNH) (CULEPEX Expedition, 2010); Río Coca, [0°28'S,76°58'W], 300 m, 2♂, 4♀, (FLMNH), (de Lafebre, R.), Jun 1971, 1♂ [FLMNH-MGCL-256260], 1♀ [FLMNH-MGCL-256263], 1♀ [FLMNH-MGCL-256264], 1♀ [FLMNH-MGCL-256265], 1♀ [FLMNH-MGCL-256267], (FLMNH), Jun 1971, 1♂ [FLMNH-MGCL-256259], (FLMNH); Río Cocaya cabañas, [0°55'44"S,75°15'16"W], 180 m, (Willmott, K. R., J. C. R., J. I. R.), 23 Jul 2015, 2♂, 1♀, (INABIO); Río Manduro, Río Napo, Yarina, [0°28'14"S,76°50'W], 300 m, (Gallice, G.), 16 Sep 2010, 1♀ [YL886], (INABIO), 25 Sep 2010, 1♂ [YL1156], (INABIO), 26 Sep 2010, 1♂ [YL1258], (INABIO), 6 Sep 2010, 1♀ [YL546], (INABIO), 8 Sep 2010, 1♂ [YL576], 1♀ [YL577], (INABIO), 9 Sep 2010, 1♂ [YL644], (FLMNH), no data, 1♀ [YL998], (INABIO); Río Napo, Boca del Río Añangu, [0°31'43"S,76°23'41"W], 220-300 m, (Willmott, K. R.), 13 Dec 2005, 1♀ [FLMNH-MGCL-ECD-312], (FLMNH), 22 Nov 2005, 1♂ [FLMNH-MGCL-ECD-307], (FLMNH), 6 Dec 2005, 1♀, (EUIEB), 7 Dec 2005, 1♀, (EUIEB), (Elias, M.), 25 Nov 2005, 1♂, (EUIEB), 28 Nov 2005, 1♂, (EUIEB), 3 Dec 2005, 1♂, (EUIEB); Río Napo, nr. Coca, Laguna Taracoa, 244 m, (Stevens, C.M.), 25 Jun 1980, 1♂ [FLMNH-MGCL-263668], 1♂ [FLMNH-MGCL-263684], 1♂ [FLMNH-MGCL-263732], 1♀ [FLMNH-MGCL-263740], (FLMNH); Taracoa, [0°27'54"S,76°45'50"W], 244 m, (Stevens, C.M.), 25 Jun 1980, 1♂ [FLMNH-MGCL-263661], (FLMNH); Río Napo, Río Yuturi, lodge trail, [0°32'53"S,76°2'W], 250 m, (Willmott, K. R., Hall, J. P. W.), 17-19 Oct 1997, 1♂, (FLMNH); Río Napo, Sacha Lodge, [0°28'14"S,76°27'33"WW], 200 m, (Hall, J. P. W.), 17,18 Feb 2001, 1♂, (FLMNH); Río Napo, Sacha Lodge, [0°28'14"S,76°27'33"WW], 240 m, (Gallice, G.), 16 Oct 2010, 1♀ [SL1636], (FLMNH), 20 Oct 2010, 1♂ [SL1718], (FLMNH), 1♀ [SL1719], 1♀ [SL1748], (INABIO), 22 Oct 2010, 1♀ [SL1872], (INABIO), 26 Oct 2010, 1♀ [SL1978], (INABIO); Río Napo, Tiputini, [0°45'S,75°32'W], 250 m, (Willmott, K. R.), 21 Oct 1997, 1♂, 1♀, (FLMNH); Río Tiputini, Estación Científica Yasuní, camino torre, [0°40'46"S,76°24'W], 260-300 m, (Eliazar, P.J.), 31 Aug 2000, 1♂ [FLMNH-MGCL-265165], (FLMNH); Río Tiputini, Tiputini Biodiversity Station, [0°42'12"S,76°0'30"W], 300 m, (Melo, P.), May-Aug 2002, 2♂, (FLMNH); Estación Científica Yasuní, [0°40'S,76°24'W], 250 m, (Lamas, G.), 25 Nov, 2 Dec 2004 (Lamas, G.), 1♂, 1♀, (MUSM); Río Tiputini, vía Auca, Estación Científica Yasuní, [0°40'27"S,76°23'49"W], 220-250 m, (Gallice, G.), 12 Nov 2010, 1♂ [YN2307], 1♂ [YN2310], (INABIO), 15 Nov 2010, 1♂ [YN2451], (INABIO), 16 Nov 2010, 1♂ [YN2476], 1♀ [YN2475], (INABIO), 19 Nov 2010, 1♂ [YN2573], 1♀ [YN2565], (INABIO), 24 Nov 2010, 1♂ [YN2729], (INABIO), 3 Dec 2010, 1♂ [YN3199], (INABIO), 8 Nov 2010, 1♂ [YN2184], (INABIO), 9 Nov 2010, 1♀ [YN2204], (INABIO), (Harris, L. N.), 4 Oct 1998, 1♂ [FLMNH-MGCL-263644], 1♂ [FLMNH-MGCL-263647], 1♂ [FLMNH-MGCL-263683], 1♂ [FLMNH-MGCL-263689], 1♀ [FLMNH-MGCL-263652], 1♀ [FLMNH-MGCL-263664], 1♀ [FLMNH-MGCL-263688], (FLMNH), 8 Sep 2002, 1♂ [FLMNH-MGCL-263658], 1♂ [FLMNH-MGCL-263673], 1♂ [FLMNH-MGCL-263685], 1♂ [FLMNH-MGCL-263690], 1♀ [FLMNH-MGCL-263650], 1♀ [FLMNH-MGCL-263653], 1♀ [FLMNH-MGCL-263654], 1♀ [FLMNH-MGCL-263675], (FLMNH), (Willmott, J. C. R., J. I. R.), 5 Jul 2014, 1♂, (INABIO); *Pastaza*: km 30 Puyo-Canelos rd., Tinguisa trail, [1°35'54"S,77°47'52"W], 600 m, (Willmott, K. R.), 5 Oct 1996, 1♂, (FLMNH); Mera, nr. trailhead to Río Anzu, [1°25'11"S,78°25'59"W], (Elias, M., Toporov, S., Santacruz, P.), 18 Mar 2010, 1♀, (MNHN); nr. San José, km 25 Puyo-Tena rd., Río Llandia, [1°19'59"S,77°55'52"W], 950 m, (Hall, J. P. W., Willmott, K. R.), 23-26 Aug 1993, 1♀ [FLMNH-MGCL-263702], (FLMNH); Río Bobonaza, Canelos, [1°35'S,77°45'W], 500 m, Dec, 1♀, (AMNH), 1♂, 1♀, (USNM); Río Sarayacu, [1°44'S,77°29'W], 200 m, 1♂, (AMNH), 1♂, 1♀, (USNM); Río Capahuari, Kapawi Lodge, [2°32'30"S,76°51'32"W], 250 m, (Willmott, K. R., Hall, J. P. W.), 21,22,27 Jul 2009, 1♂ [FLMNH-MGCL-144364], 1♂ [FLMNH-MGCL-144366], 1♂ [FLMNH-MGCL-144367], 1♂ [FLMNH-MGCL-144370], 1♀ [FLMNH-MGCL-144344], 1♀ [FLMNH-MGCL-144345], 1♀ [FLMNH-MGCL-144347], 1♀ [FLMNH-MGCL-144351], 1♀ [FLMNH-MGCL-144352], 1♀ [FLMNH-MGCL-144353], 1♀ [FLMNH-MGCL-144354], 1♀ [FLMNH-MGCL-144355], 1♀ [FLMNH-MGCL-144356], (FLMNH); Río Curaray, Curaray, [1°29'S,77°31'W], 250 m, 1♂, 1♀, (NHMUK); *Morona-Santiago*: forest nr. San José de Morona, [2°53'17"S,77°41'52"W], 215 m, (Gallice, G.), 6 Jun 2009, 1♂ [FLMNH-MGCL-153106], 1♀ [FLMNH-MGCL-153111], 1♀ [FLMNH-MGCL-153113], (FLMNH), 7 Jun 2009, 1♂ [FLMNH-MGCL-153104], 1♂ [FLMNH-MGCL-153105], (FLMNH); jct. Río Mayalico-Río Santiago, Isla de las Conchas, [3°21'0"S,77°58'29"W], 250 m, (Hall, J. P. W., Willmott, K. R., J. C. R., J. I. R.), 8,10 Aug 2015, (INABIO); Río Pastaza, playa 2 km W Capitán Chiriboga, [2°33'43"S,76°51'31"W], 250 m, (Willmott, K. R., Hall, J. P. W.), 22,23,25 Jul 2009, 1♂ [FLMNH-MGCL-144361], 1♂ [FLMNH-MGCL-144369], 1♀ [FLMNH-MGCL-144348], 1♀ [FLMNH-MGCL-144349], 1♀ [FLMNH-MGCL-144357], (FLMNH); San José de Morona, [2°52'56"S,77°40'11"W], 210 m, (Gallice, G.), 4 Jun 2009, 1♂ [FLMNH-MGCL-153107], (FLMNH), 9 Jun 2009, 1♀ [FLMNH-MGCL-153109], (FLMNH); Yaupi-Yaupi trail, [2°49'58"S,77°56'28"W], 320-340 m, (Gallice, G.), 15 Jun 2009, 1♀ [FLMNH-MGCL-153108], 1♀ [FLMNH-MGCL-153110], 1♀ [FLMNH-MGCL-153112], (FLMNH); *Not located*: 'Ecuador', 1♂ [PLT *agarista*], 3♂, 1♀, 1♀ [PLT *agarista*], (NHMUK), 1♀ [FLMNH-MGCL-256268], (FLMNH); 'Selva Ecuatoriana, Armitano', 1♂, (ZSBS); *Peru*: *Amazonas*: Río Santiago, [4°26'S,77°38'W], Nov, 1♀, (AMNH); *Loreto*: '20-50 km NE Iquitos' [=55 km NE Iquitos], Explorama Lodge, [3°27'S,72°51'W], 120 m, (Harris, L. & C.), 22-28 Oct 1989, 1♂ [FLMNH-MGCL-263286], 1♀ [FLMNH-MGCL-263277], 1♀ [FLMNH-MGCL-263278], 1♀ [FLMNH-MGCL-263281], (FLMNH); '50 mi. E Iquitos [= Yanamono]' - (error), (Jenkins, D. & J.), 6 Aug 1980, 1♀ [FLMNH-MGCL-263914], (FLMNH); '65 mi E Iquitos' [=34 mi NE Iquitos], Explorama Lodge, [3°27'S,72°51'W], 120 m, (Dow, L.C.), 6 Mar 1984, 1♂ [FLMNH-MGCL-262867; Genitalic dissection DPITH-8], (FLMNH); Arcadia, [0°59'22"S,75°18'33"W], 150 m, (Lamas, G., Robbins, R. K.), 31 Oct-5 Nov 1993, 10♂, 7♀, (MUSM); Castaña, [0°48'13"S,75°14'24"W], 150 m, (Lamas, G., Robbins, R. K.), 18-26 Oct 1993, 7♂, 3♀, (MUSM); Iquitos, [3°45'S,73°15'W], 1♂, (SMTD); lower Río Napo, 1♂, 2♀, (NHMUK); Río Cachiayacu, [5°50'S,76°33'W], 1♀, (NHMUK); Río Tigre, San Jacinto, [2°19'S,75°52'W], (Rich, P.), 18 Apr 1993, 1♂, (MUSM); Río Pucacuro, Coconilla, [2°42'S,75°06'W], 160 m, (Ramírez, J. J.), 24 Jul 2003, 1♂, (MUSM). **Country unknown**: *Not located*: no data, 2♂, (NHMUK), 1♀, (FLMNH), 2♀ [km. 15], (USNM), 1♀, (MfN).

Other examined specimens (not paratypes, see discussion below):
Brazil: *Acre*: Alto Jurua, (May, E.), 1♂, (MNRJ); *Amazonas*: Alto Rio Itacoai, [5°0'S,70°9'W], Jun 1948, 3♂, 1♀, (DZUP); Benjamin Constant, [4°23'S,70°2'W], (Parko), 1♂, (DZUP); nr. Benjamin Constant, Rio Itacoai,

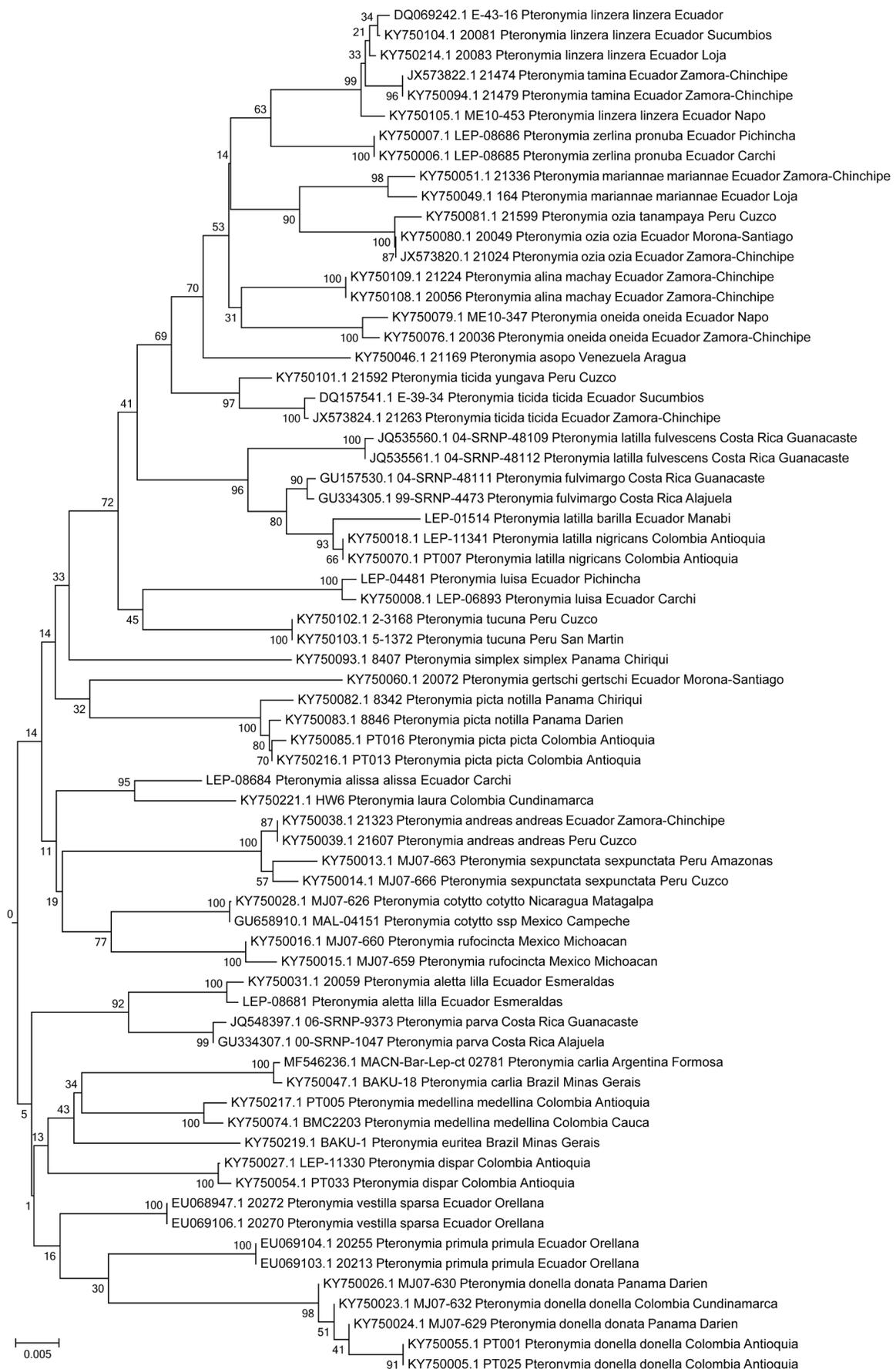


Fig. 27. Neighbor-joining tree (Kimura 2-parameter) for select *Pteronymia* based on analysis of 633 bp of COI (barcode region). Bootstrap values (%) are shown by branches.

[4°20'9"S,70°12'10"W], (Parko), 1♂ [No. 1/699], 1♀ [No. 1/699], (MNRJ); nr. Benjamin Constant, Río Javari, [4°23'S,70°2'W], (Pohl, B.), Aug, Sep 1942, 1♂, 2♀, (MZSP), (Dirings), Feb 1960, 1♂, (MZSP); Río Itacoaí, Campoamor, (Carvalho, J. C., Viegas), 30 May 1930, 1♂, (MNRJ). **Colombia:** *Putumayo:* Puerto Leguizamo, Caucayá, [0°9'S,74°49'W], Sep, Nov, Dec, 10♂, 14♀, (AMNH). **Ecuador:** *El Oro:* 'Bellavista' - (error), 1♀, (FLMNH); *Pichincha:* '12 km E Santo Domingo de los Colorados, [Hotel] Tinalandia' - (error), (Preston, J. & F.), 26 Jun 1980, 1♂ [FLMNH-MGCL-263657], 1♂ [FLMNH-MGCL-263662], 1♂ [FLMNH-MGCL-263663], (FLMNH); *Tungurahua:* 'Bellavista' - (error), (de Lafebre, R.), Apr 1971, 1♀ [FLMNH-MGCL-256261], (FLMNH).

Other records: **Ecuador:** *Sucumbios:* Río Pañayacu, Laguna de Pañacochoa, [0°23'53"S,76°7'40"W], 250 m. (Willmott, K. R., Hall, J. P. W.), 12-14 Oct 1997, (W&H); *Napo:* Aguano, [1°4'S,77°33'W], 350 m. (Galarza, M.), 1 May 1988, 1♂ [FDPR-13383], (FRPI); Aguano, [1°4'S,77°33'W], 400 m. (collection unknown) (Haensch, 1903); 'Coca Iamoe', 350 m. (Salazar, F.), 15 Nov 2000, 1♀ [FDPR-13415], (FRPI); E Archidona, Coral, [0°56'11"S,77°45'31"W], (Elias, M., Toporov, S., Santacruz, P.), 20 Feb 2010, 3♂, 10♀, (sight record) (Elias, M., unpublished data); E Archidona, Mariposa, [0°54'30"S,77°47'8"W], (Elias, M., Toporov, S., Santacruz, P.), 10 Feb 2010, 2♂, (sight record) (Elias, M., unpublished data), 20 Mar 2010, 5♂, 1♀, (sight record) (Elias, M., unpublished data), 21 Feb 2010, 10♂, 6♀, (sight record) (Elias, M., unpublished data); km 14 Tena-Puyo rd., Apuya, [1°6'18"S,77°46'42"W], 600 m. (Willmott, K. R., Hall, J. P. W.), 10 Sep 1996, (W&H), 12-14,24 Feb 1995, (W&H), 16 Apr 1995, (W&H), 28 Aug 1997, (W&H), 6,10,13,19,21,28 Oct 1996, (W&H); km 30 Tena-Puyo rd., Satzayacu, [1°12'35"S,77°51'38"W], 700 m. (Willmott, K. R., Hall, J. P. W.), 13 Sep 1996, (W&H); La Floresta, (Zak, V.), 19 May 1984, 1♂ [FDPR-13392], (FRPI); nr. Misahuallí, Pununo, [1°1'18"S,77°40'12"W], 500 m. (Piñas, F.), 3 Feb 2002, 1♀ [FDPR-13422], (FRPI); nr. Misahuallí, Río Misahuallí, Las Minas, [1°0'30"S,77°40'6"W], 400 m. (Willmott, K. R., Hall, J. P. W.), May, (W&H); Puerto Misahuallí, [1°1'36"S,77°40'W], 500 m. (Piñas, F.), 22 Dec 2001, 1♂ [FDPR-13374], 1♂ [FDPR-13382], 1♂ [FDPR-13404], 1♀ [FDPR-13411], 1♀ [FDPR-13414], (FRPI); Río Hollín, nr. Archidona, 'Hollín2', [0°55'46"S,77°44'24"W], (Elias, M., Toporov, S., Santacruz, P.), 21 Mar 2010, 1♀, (sight record) (Elias, M., unpublished data); Río Jatunyacu, Pimpilala, [1°4'31"S,77°56'13"W], 600-650 m. (Willmott, K. R., Hall, J. P. W.), Sep, (W&H); Río Misahuallí, Misahuallí, [1°1'36"S,77°40'W], 500 m. (Piñas, F.), 12 Jan 2002, 1♂ [FDPR-13387], 1♂ [FDPR-13395], 1♂ [FDPR-13402], 1♂ [FDPR-13403], (FRPI), 2 Feb 2002, 1♂ [FDPR-13376], 1♂ [FDPR-13393], 1♂ [FDPR-13394], 1♂ [FDPR-13397], 1♀ [FDPR-13418], (FRPI), 26 Jan 2002, 1♂ [FDPR-13389], 1♂ [FDPR-13400], (FRPI); Río Napo, Puerto Napo-Ahuano rd., Chichicorrumi, [1°4'11"S,77°37'45"W], 450 m. (Willmott, K. R., Hall, J. P. W.), Sep, (W&H); Río Napo, Puerto Napo-Ahuano rd., Jatun Sacha, [1°3'S,77°35'59"W], 400-450 m. (Beccaloni, G. W.), (collection unknown) (Beccaloni, 1996); Río Sinde, km 12 Tena-Puyo rd., Finca San Carlo, [1°5'18"S,77°47'24"W], 600 m. (Willmott, K. R., Hall, J. P. W.), Feb, Sep, (W&H); Serena, [1°5'25"S,77°55'33"W], 600 m. (Piñas, F.), 11 Oct 2006, 1♂ [FDPR-13401], 1♀ [FDPR-13409], (FRPI); Taracoa, [0°27'54"S,76°45'50"W], 250 m. (Chieruzzi, M.), 21 Dec 1982, 1♂ [FDPR-13386], (FRPI); Tena-Puyo rd., El Capricho, [1°11'14"S,77°49'53"W], 800 m. (Willmott, K. R.), 26 Oct 1996, (W&H); *Orellana:* Coca-Tiguino rd., Río Tiputini, [0°44'3"S,76°53'31"W], 300 m. (Willmott, K. R., Hall, J. P. W.), 1 Jul 1994, (W&H); Laguna Añangu, Napo Wildlife Center, Napo trail, [0°30'35"S,76°26'13"W], 250 m. (Jiggins, C., Sánchez, C.), 15 Dec 2005, 1♂, 1♀, (W&H), (Willmott, K. R.), 24 Oct 2005, 1♀, (W&H), (Elias, M.), 21 Oct 2005, 1♀, (W&H), 22 Oct 2005, 1♂, (W&H); nr. Coca, [0°28'S,76°59'W], 300 m. Mar, (collection unknown) (Haensch, 1903), (Willmott, K. R., Hall, J. P. W.), 11 Aug 1999, (W&H), (Willmott, K. R.), 22 Oct 2005, (W&H); Nueva Providencia, [0°29'37"S,76°28'27"W], 350 m. (Salazar, F.), 25 Oct 2000, 1♀ [FDPR-13416], (FRPI); Pichira, [0°23'2"S,76°36'14"W], (Sandoval, S.), 6 Mar 1990, 1♂ [FDPR-13390], (FRPI); Río Manduro, Río Napo, Yarina, [0°28'14"S,76°50'W], 300 m. (Willmott, K. R.), 23-24 Jul 1998, (W&H); Río Napo, Añangu community, [0°29'37"S,76°25'11"W], 230 m. (Elias, M.), 10 Dec 2005, 1♂, 1♀, (W&H), 8 Dec 2005, 2♀, (W&H), 9 Dec 2005, 2♂, 2♀, (W&H); Río Napo, Boca del Río Añangu, [0°31'43"S,76°23'41"W], 220-300 m. (Willmott, K. R.), 10 Dec 2005, 1♂, 1♀, (W&H), 11 Dec 2005, 1♂, (W&H), 13 Dec 2005, 4♂, 3♀, (W&H), 26 Oct 2005, 1♂, (W&H), 29 Oct 2005, 3♂, 1♀, (W&H), 30 Oct 2005, 1♂, (W&H), 4 Nov 2005, 2♂, (W&H), 6 Dec 2005, 1♂, (W&H), 6 Nov 2005, 1♂, (W&H), 7 Dec 2005, 4♂, 1♀, (W&H), 9 Dec 2005, 1♂, (W&H), 9 Nov 2005, 2♂, (W&H), (Elias, M.), 1 Nov 2005, 1♂, (W&H), 28 Nov 2005, (W&H), 29 Nov 2005, 1♂, (W&H); Río Napo, Río Yuturi, lodge trail, [0°32'53"S,76°2'W], 250 m. (Willmott,

K. R., Hall, J. P. W.), 21-22 Jul 1998, (W&H); Río Napo, Sacha Lodge, [0°28'14"S,76°27'33"W], 240 m. (Gallice, G.), 26 Oct 2010, 1 specimen, (sight record) (Gallice, G., unpublished data), 27 Oct 2010, 1 specimen, (sight record) (Gallice, G., unpublished data); Río Tiputini, Tiputini Biodiversity Station, [0°42'12"S,76°0'30"W], 300 m. (Willmott, K. R.), 10 Feb 2002, (W&H); Río Tiputini, vía Auca, Estación Científica Yasuní, [0°40'27"S,76°23'49"W], 220-250 m. (Gallice, G.), 29 Nov 2010, 1 specimen, (sight record) (Gallice, G., unpublished data); Yasuní, Estación Científica, [0°40'17"S,77°24'2"W], 250 m. (Guevara, D.), 15 Feb 1998, 1♀ [FDPR-13405], (FRPI), (Onore, G.), 6 Mar 1998, 1♀ [FDPR-13420], (FRPI), (Piñas, F.), 18 Feb 1996, 1♂ [FDPR-13399], (FRPI); Yasuní, Estación Científica, [0°40'17"S,77°24'2"W], 300 m. (López, L.), 15 Sep 1995, 1♂ [FDPR-13385], (FRPI), (Onore, G.), 15 Nov 1996, 1♀ [FDPR-13406], (FRPI), (Piñas, F.), 18 Feb 1996, 1♂ [FDPR-13384], (FRPI), 20 Sep 1996, 1♂ [FDPR-13380], (FRPI), 29 Sep 1995, 1♀ [FDPR-13408], 1♀ [FDPR-13417], (FRPI); Yasuní, Estación Científica, [0°40'17"S,77°24'2"W], 300-250 m. (Onore, G.), 31 Mar 1997, 1♀ [FDPR-13421], (FRPI); Yasuní, Estación Científica, [0°40'17"S,77°24'2"W], 350 m. (Guevara, D.), 15 Feb 1998, 1♀ [FDPR-13407], 1♀ [FDPR-13419], (FRPI); *Pastaza:* Mera, nr. trailhead to Río Anzu, [1°25'11"S,78°2'59"W], (Hill, R.), 21 Mar 2010, 1♂ [RH10-292], 1♀, 1♀ [RH10-293], (RYHI or sight record) (Hill, R., unpublished data); Moretocochoa, [1°36'16"S,77°21'12"W], 400 m. (Naranjo, J.), 3 Jul 1996, 1♀ [FDPR-13413], (FRPI); Río Curaray, Lorocachi, [1°37'15"S,75°59'30"W], 210 m. (Carpio, C.), 20 Feb 1996, 1♂ [FDPR-13396], (FRPI); Río Curaray, Lorocachi, [1°37'15"S,75°59'30"W], 250 m. (Willmott, K. R.), 28 Jul 1998, (W&H); Río Matabuno, 350 m. (Manzano, I.), 5 Apr 2000, 1♂ [FDPR-13388], 1♀ [FDPR-13410], 1♀ [FDPR-13412], (FRPI); Río Pastaza, Kapawi village, [2°32'16"S,76°50'10"W], (Willmott, K. R., Hall, J. P. W.), 23 Jul 2009, (W&H); Río Pindo Grande, Shell, [1°29'40"S,78°3'40"W], (Hill, R.), 19 Mar 2010, 1♂ [RH10-266], (RYHI or sight record) (Hill, R., unpublished data); Villano, [1°30'S,77°29'W], (Naranjo, J.), 10 Jul 1996, 1♂ [FDPR-13375], 1♂ [FDPR-13377], 1♂ [FDPR-13378], 1♂ [FDPR-13379], 1♂ [FDPR-13381], 1♂ [FDPR-13398], (FRPI).

Etymology: The name is an anagram of 'agarista', a name which has often been applied to this taxon. It is treated as a feminine noun in apposition.

Taxonomy and variation: This taxon is treated as a subspecies of *O. onega* largely because of its similarity to *O. onegajananilla*, which it appears to replace in the east Ecuadorian lowlands, and with which it clusters based on DNA barcodes (Fig. 25). Nevertheless, the classification of *O. onega* and the closely related species *O. ilderina*, *O. didymaea* (Hewitson, 1876) and *O. alexina* (Hewitson, [1859]) is provisional and needs revision. These species show no morphological differences except in wing pattern, and allopatric taxa are grouped into species on the basis of geographic distributions and occasionally wing pattern characters. DNA sequence data also failed to recover all species as monophyletic (De-Silva *et al.*, 2010; Fig. 25), while a number of key taxa, such as *O. onega onega*, currently lack sequence data. Furthermore, some phenotypically similar and closely allopatric taxa seem to be rather divergent in other respects (e.g., Galluser *et al.*, 2004), and a comprehensive study with molecular, and, if possible, ecological data is needed to clarify the taxonomy.

This taxon is, like *O. tigilla raya* n. ssp., only distinguished from the phenotypically closest subspecies by a single wing pattern character. However, like *O. tigilla raya*, that character is present in long series of individuals from multiple localities, and coincides with similar variation in subspecies of other commimetic ithomiines (see under *O. tigilla raya*). There is some slight variation in the width and extent of the orange subapical band, and a thin orange submarginal line may or may not be present on the DHW.

This taxon was formerly erroneously treated under the name *O. agarista* (e.g., Haensch, 1903, 1909-1910) or *O. onega*

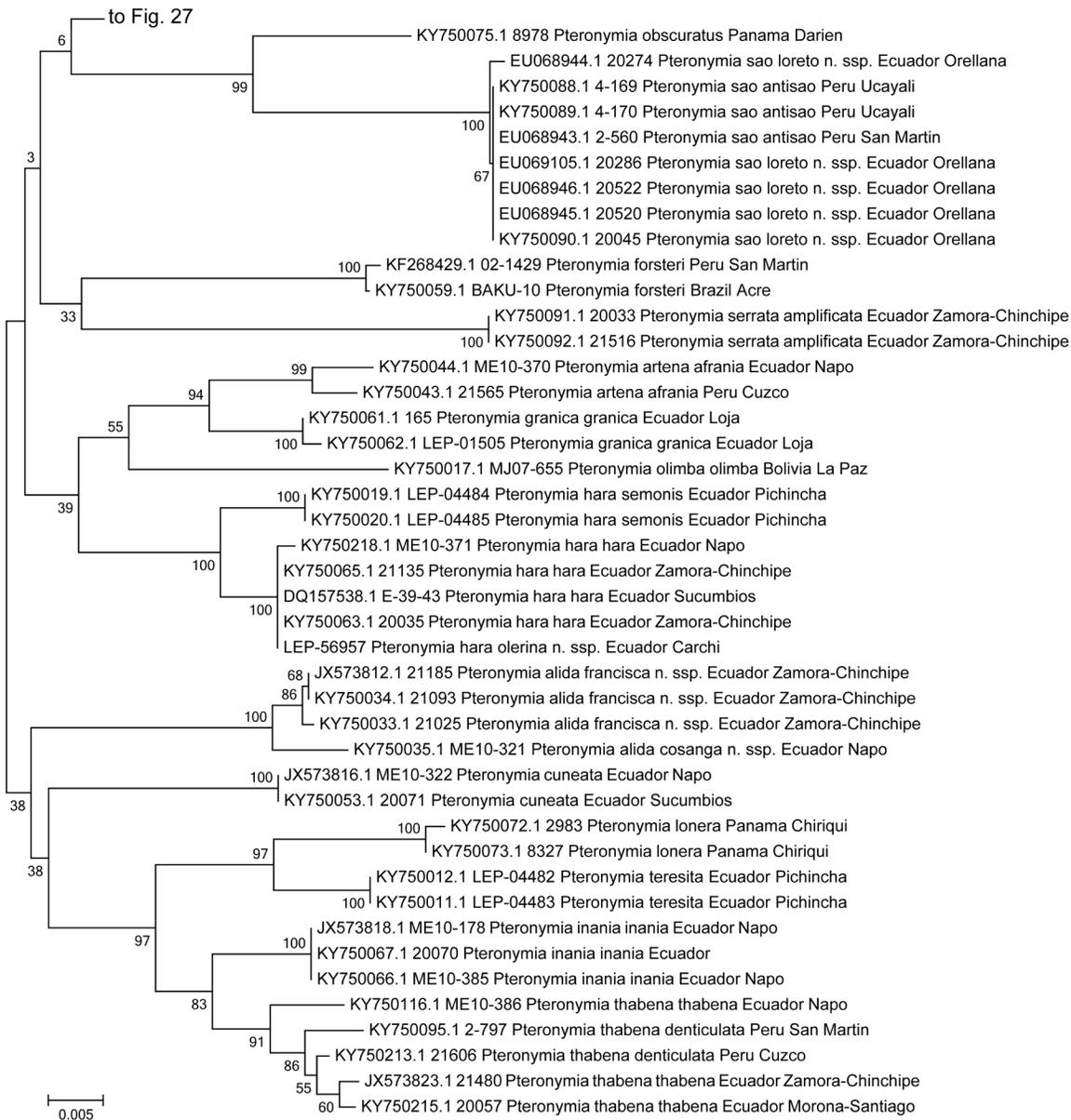


Fig. 28. Neighbor-joining tree (Kimura 2-parameter) for select *Pteronymia* based on analysis of 633 bp of COI (barcode region). Bootstrap values (%) are shown by branches.

agarista (e.g., Galluser *et al.*, 2004; Piñas, 2004), and for this reason has remained without a name despite the numerous specimens in collections. The original description (C. Felder & R. Felder, 1862: 77) of *Ithomia agarista* appeared in a paper on Lepidoptera supposedly from the upper Río Negro in northern Brazil, but which actually appear to have been collected in the Río Huallaga valley above Yurimaguas, in Peru (Lamas, 1976). The description reads: “59. *Ithomia agarista* Nob[is]. Alis supra nigro-fuscis, anticis macula trigona basali, altera obliqua quadrata cellularibus tribusque exterioribus hyalino-albis, utrinque striga externa fulva, posticis fascia lata discali hyalino-alba, litura discocellulari nigra, subtus costa strigaque externa fulvis. ♂ *I. Astreae* Cram. (*Florae* Hew.) valde affinis est, sed maculis alarum anticarum semper distinctae separatis recedit. In republica Ecuador quoque volat, sed specimen nigrinum differt ab his statura minore margineque nigro alarum posticarum multo latiore.” This description corresponds to a

syntype in the NHMUK with three distinct spots outside the discal cell (“cellularibus tribusque exterioribus”), which has the translucent distal half of the FW discal cell extending into the base of cell Cu_2-Cu_1 , a unique character for a rare taxon that is not conspecific with *O. onega*, differing from it in genitalia, wing venation, DNA sequences, and wing pattern. Lamas (2004) thus treated *O. agarista* as a distinct species, and this usage of the name has been followed subsequently (Elias *et al.*, 2007, 2008; De-Silva *et al.*, 2010, 2015; Chazot *et al.*, 2014b, 2016b, 2017; Willmott *et al.*, 2017). The second part of the description differentiated the described specimen from ‘Río Negro’ from Ecuadorian specimens by its broader black HW margin; the four Ecuadorian syntypes in the NHMUK do indeed differ in this manner and actually represent two other species, *O. assimilis assimilis* (one specimen), *O. onega astigara* n. ssp. (two specimens) and *O. onega janarilla* (one specimen). To clarify the identity of *Ithomia agarista* we therefore designate

the female syntype in the NHMUK that corresponds to the first specimen described in the original description and to recent usage as the **lectotype**, with the following label data: “Rio Negro//SYN-TYPE//FELDER COLLN.//ST ♂ *Ithomia agarista* Felder & Felder, 1862 The specimen described first. Det. K. R. Willmott 8/01//It’s a female syntype! LAMAS, G. det. 2002” (Fig. 6M).

Distribution and natural history: This subspecies occurs from extreme southern Colombia, throughout eastern Ecuador and into northern Peru (Fig. 34B), in lowland rainforest below 950 m. Some phenotypically similar specimens from western Brazil (listed above) may also represent the same taxon but are not designated as paratypes given the confusing taxonomy of this and related species. Both sexes are very common in the understorey of disturbed to primary rainforest, where they fly throughout the day, from 08:00 to 16:30 hrs, usually less than 1 m above the ground.

Episcada clausina bomboiza Willmott & Lamas, **new subspecies**
Figs. 7A,B, 14A-B, 34C

Episcada clausina n. ssp.: Lamas (2004: 186, no. 236c)

Episcada clausina ssp. nov.: Chazot *et al.* (2016a: S1)

Diagnosis and identification: This subspecies is distinguished from the nominate (Fig. 7C) by the broader (*c.* twice as broad) yellow DFW postdiscal band. In addition, this band is also more intensely yellow; in the nominate subspecies the veins are clearly differentiated from the adjacent wing cell areas by having denser yellow scaling, whereas in *E. clausina bomboiza* **n. ssp.** the veins are less clearly distinct. The new subspecies also has traces of translucent yellow scaling in the FW submarginal translucent areas in cells Cu_1-M_3 , M_3-M_2 and M_2-M_1 that are absent in the nominate subspecies, and the dark HW marginal border is slightly narrower. The female of *E. clausina bomboiza* is further distinguished from the nominate subspecies by having reduced orange along the DFW anal margin, with the cubital vein bordered posteriorly by a clean black band that is covered in scattered orange scales in the nominate subspecies.

Description: MALE (Fig. 7A,B, 14A-B): Forewing length 23 mm ($n=1$). *Wings:* as illustrated (Fig. 7A), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes brown, bare, with fringe of white scales at base; antennae dark brown; labial palpi white except for black terminal segment; top of head with white medial stripe between bases of antennae, two white spots behind eyes, frons broadly dark brown in middle with white at edges. *Thorax:* dorsal surface dark brown with yellow medial stripe, sparse yellow scaling laterally, tegula yellow with sparse black scaling, pronotum dark brown dorsally and yellow laterally, ventral surface between legs white then yellow laterally except for dark brown where legs fold, legs dark brown with scattered white scaling. *Abdomen:* dorsal surface dark brown, ventral surface pale yellow. *Genitalia* (Fig. 14A-B): notable features include strongly bent aedeagus in lateral view (Fig. 14A).

FEMALE: (Fig. 7B): Forewing mean length 23.3 mm ($n=3$). *Wings:* as illustrated (Fig. 7B), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **ECUADOR:** *Morona-Santiago:* nr. Gualaquiza, Bomboiza, [3°25'36"S, 78°31'W], 850 m, (Hall, J. P. W., Willmott, K. R.), 26-29 Jul 1993, [Genitalic dissection EPISCD-1], (FLMNH, to be deposited in INABIO).

PARATYPES (7♂, 10♀): **Ecuador:** *Morona-Santiago:* 13 km NNW Macas, San Isidro, [2°12'1"S, 78°9'30"W], 1200 m, (Boyer, P.), 1 Aug 2011, 1♀, (PIBO), (Petit, J.-C.), 9 Jan 2012, 1♀, (JEPE); Gualaquiza, [3°25'S, 78°36'W], 800 m, 1♂, 1♀, (NHMUK), (Pearce), 1♂, (NHMUK); km 33 Macas-Puyo rd., [2°3'36"S, 77°58'10"W], 1050 m, (Warren-Gash, H.), 5 Jul 2012, 1♂, 1♀, (HAWA); nr. Gualaquiza, Bomboiza, [3°25'36"S, 78°31'W], 850 m, (Hall, J. P. W., Willmott, K. R.), 26-29 May 1994, 1♀, (FLMNH), 5-6 Nov 1996, 2♀, (FLMNH); Yakunk-Cutucú trail, lower ridge, [2°45'40"S, 78°9'40"W], 1340 m, (Willmott, K. R.), 3 Dec 2003, 1♀ [FLMNH-MGCL-143961], (FLMNH); *Zamora-Chinchipe:* km 12 Zamora-Gualaquiza rd., Hostería El Arenal, [3°59'30"S, 78°52'25"W], 1100 m, (Petit, J.-C.), 9 Dec 2002, 1♀, (JEPE); *Not located:* ‘Ecuador’, 1♂, (NHMUK), 1♂, (MfN), (Higgins), 1870, 1♂, 1♀, (OUM). **Country unknown:** *Not located:* no data, 1♂, (NHMUK).

Etymology: The subspecies name is derived from that of the village of Bomboiza, in the vicinity of which the holotype and several paratypes were collected.

Taxonomy and variation: This taxon is very similar in wing pattern to four other yellow-banded *Episcada* occurring in eastern Ecuador, namely *E. hymenaea mirifica* **n. ssp.** (Fig. 7D,E), *E. pichita* Lamas & Willmott, 2020 (Fig. 7G), *E. mira* (Hewitson, 1877) (Fig. 7H), and *E. polita flava* Winhard, 2021 **n. stat.** (Fig. 7I; see below under *E. p. pichincha* **n. ssp.**). *Episcada trapezula* Brabant & Bischler, 2003 might also occur in eastern Ecuador, based on two specimens labeled ‘Ecuador’ and ‘E Ecuador’ in the MZUJ and SMTD respectively, although no Ecuadorian specimens with reliable, recent data are known. These six species may be most easily distinguished as follows. *Episcada hymenaea* (Prittwitz, 1865) has the male HW androconial hair-like scales divided into two patches, instead of a single patch, a unique character among these species. *Episcada pichita* has a broad yellow FW postdiscal band that is weakly marked, with the veins clearly highlighted with much more intense yellow than the adjacent cell areas. *Episcada mira* and *E. trapezula* have the yellow on the HW costal margin extending right to the wing base, basal of the humeral vein, whereas in the other four species the latter area is orange. *Episcada polita flava* is perhaps the most similar, in the male, but in that taxon the yellow FW postdiscal band extends less far across the wing, and there are no translucent yellow FW submarginal markings. The female of *E. clausina bomboiza* **n. ssp.** is easily distinguished from all of these species by having a broad orange stripe along the DFW anal margin, which it shares with *E. clausina clausina* (Hewitson, 1876). A phylogenetic analysis based on DNA sequence data showed that a single Ecuadorian individual of *E. clausina bomboiza* clustered with a single individual of *E. c. clausina* from southern Peru (Chazot *et al.*, 2017, Fig. 26), and that this sister taxon pair was sister to *Episcada striposis* Haensch, 1909 from southeastern Brazil (Chazot *et al.*, 2017). Male genitalia are relatively uninformative in most *Episcada*, but the more sharply downturned aedeagus in both *E. clausina bomboiza* and *E. c. clausina* may be distinct from that in *E. pichita*, *E. trapezula* and *E. mira*, at least.

Distribution and natural history: This subspecies is known only from the valleys of the Río Zamora and Río Upano in southeastern Ecuador (Fig. 34C), where it occurs very locally from 800-1340 m in remnant patches of disturbed rainforest and lower montane forest. Males were observed in the morning feeding on flowers of a weedy Asteraceae along the edge of a track through a field *c.* 50 m from selectively logged forest at the type locality.

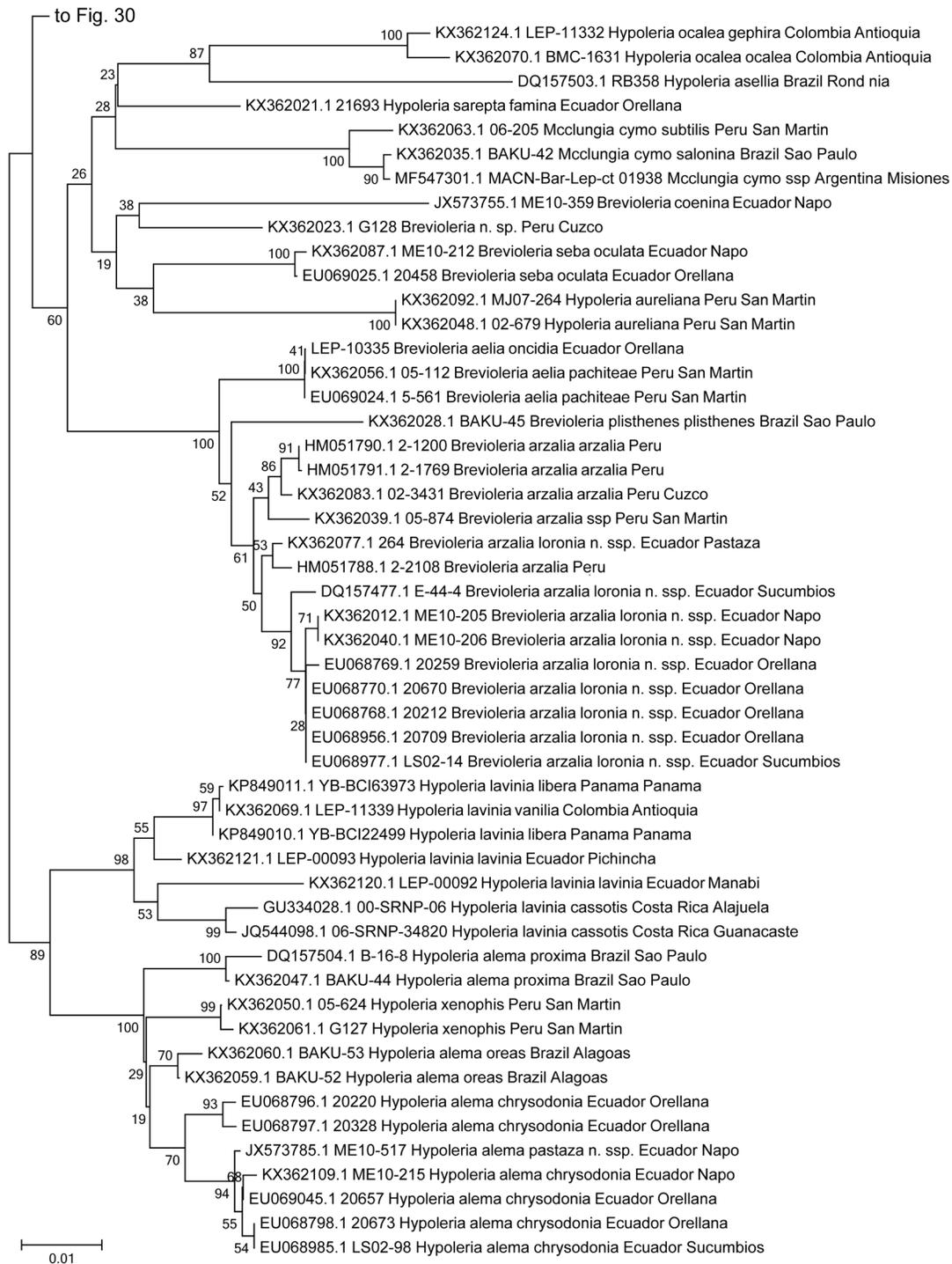


Fig. 29. Neighbor-joining tree (Kimura 2-parameter) for select Godyridina based on analysis of 633 bp of COI (barcode region). Bootstrap values (%) are shown by branches.

Episcada hymenaea mirifica Lamas & Willmott, **new subspecies**

Figs. 7D,E, 14C-D, 34D

Episcada hymenaea n. ssp.: Lamas (2004: 187, no. 240e,f)

Diagnosis and identification: This subspecies is most similar to *E. hymenaea centralis* (Brown & Mielke, 1970) (Fig. 7F), from southwestern Brazil (Goiás, Mato Grosso), but differs from that taxon in lacking any orange scaling on the DFV

costa. Other subspecies of *E. hymenaea* show additional wing pattern differences, and all have the FW yellow band much less intensely marked than in this new subspecies or *E. hymenaea centralis*. *Episcada hymenaea mirifica* n. ssp. (Fig. 7D,E) is also very similar in wing pattern to a number of other sympatric *Episcada* in the eastern Andes. Males are readily distinguished by the additional distal hair pencil on the DHW, which extends well beyond the discocellulars, and by having the space posterior of vein Sc+R₁ on the VHW restricted in the middle,

rather than even throughout, both of which are characteristic of *E. hymenaea* taxa (other similar *Episcada* have a single, unbroken hair pencil patch on the DHW and corresponding even space posterior of vein Sc+R₁ on the VHW). Males of *E. hymenaea*, including *E. hymenaea mirifica*, also often have VHW veins R and Rs lined with yellow, distinct from similar species. The female is perhaps most similar to that of *E. polita flava* n. stat. (Fig. 7I), but may be distinguished by the less elongate FW and narrower dark distal margins on both wings. Putative females of *E. trapezula* are also very similar but lack conspicuous yellow scaling along the posterior edge of the dark costal margin on the HW in cell M₂-M₁.

Description: MALE (Fig. 7D, 14C-D): Forewing length 23 mm (n=1). *Wings:* as illustrated (Fig. 7D), band of androconial hair-like scales in anterior edge of DHW discal cell split into two distinct patches, a paler buff basal patch and a darker gray distal patch, with associated modified wing scales in DHW costal region, as in nominate subspecies. *Head, thorax, abdomen:* same as in *Episcada clausina bomboiza* n. ssp. *Genitalia* (Fig. 14C-D): notable features include lightly bent aedeagus in lateral view (Fig. 14C).

FEMALE: (Fig. 7E): Forewing mean length 22.5 mm (n=2). *Wings:* as illustrated (Fig. 7E), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: PERU: Cuzco: Quebrada Quitacalzón, [13°01'S, 71°30'W], 1100 m, (Lamas, G.), 20 Oct 2005, (MUSM).

PARATYPES (37♂, 15♀): Ecuador: Tungurahua: Río Blanco, [1°22'59"S, 78°21'W], 1900 m, (Lafebre, R. de), Nov 1968, 1♀ [FLMNH-MGCL-282736; Genitalic dissection KW-21-20], (FLMNH), (Lafebre, R. de), Topo, [1°24'36"S, 78°11'30"W], 1200 m, (Velástegui, S. E.), 20 Sep 1972, 1♀, (MUSM); *Not located:* 'Ecuador', 1♀ [ex coll Jasinski], (MZUJ), 1♂, (SMTD). Peru: Amazonas: 9 km SE Omia, Río Gebil, [6°31'S, 77°23'W], 1320 m, (Mallet, J.), 28 Oct 1987, 2♂, (MUSM); 'Rodríguez de Mendoza, San Martín' [= Mendoza], [6°24'S, 77°29'W], 8 Jul 1998, 1♂ [ex coll. G. Ten Broek], (PIBO); Apurímac: Environs Abancay, 1800-2000 m, (Boettger, J.), Apr 2004, 2♀, (PIBO); Cuzco: same data as HT, 1050-1100 m, (Lamas, G., Grados, J., Mielke, O.), 12 May 1984, 23-26 Sep 2004, 20-25 Oct 2005, 12 Nov 2008, 31 Jan, 5 Feb, 23 Oct 2010, 27 Oct 2018, 19♂, (MUSM); San Pedro, [13°03'S, 71°33'W], 1400 m, (Lamas, G.), 6 Nov 2001, 1♂, (MUSM); (West, F. & A.), 4-8 Nov 2007, 1♂, (MUSM); 35 km W Pilcopata, 1190 m, (Heppner, J. B.), 7 Dec 1979, 1♂ [FLMNH-MGCL-282734; Genitalic dissection KW-21-18], (FLMNH). Huánuco: Tingo María, [9°18'S, 76°0'W], 670 m, (Büche, M.), Aug 1990, 1♂, (MUSM); Tingo María, [9°18'S, 76°0'W], 800 m, (Jenkins, D. W. & J.), Jul 1980, 1♀ [FLMNH-MGCL-282735], (FLMNH); Junin: Chanchamayo, Río Utcumayo, Pampa Hermosa, [11°25'S, 74°46'W], 1100-1300 m, (Boyer, P.), 9-12 Jul 2003, 1♀ ['Río Utcumayo, San Ramon'], (PIBO); Chanchamayo, Río Utcumayo, Pampa Hermosa, [11°25'S, 74°46'W], 1200-1400 m, (Boyer, P.), 28 Jan 2003, 1♀ ['24 km N San Ramón'], (PIBO); Mina Pichita, [11°5'S, 75°25'W], 1900-2000 m, (Boyer, P.), 6 Feb 2003, 1♀, (PIBO); *Not located:* 'Peru', 1♂, (SMF), 1♂, (MUSM). Bolivia: Santa Cruz: [nr. Santa Cruz de la Sierra], Bueyes, [17°47'S, 63°10'W], (Garlepp), 1♂, 3♀, (NHMUK); Provincia del Sara, [16°50'S, 63°55'W], Apr-May, 3♂, (NHMUK); *Not located:* 'Bolivia', 2♂, (NHMUK), 1♂, (SMF), 1♂, (SMTD). Country unknown: *Not located:* no data, 1♀, (OUM), 10 Mar 1826, 1♀, (OUM), 20 Mar 1826, 1♀, (OUM).

Etymology: This taxon is named from the Latin feminine adjective 'mirifica', meaning marvelous or wonderful, in allusion to the remarkable similarity of this rare taxon to other east Andean *Episcada* and in particular to the similarly sounding *Episcada mira*.

Taxonomy and variation: This taxon is associated with *Episcada hymenaea* on the basis of the divided DHW androconial hair-like scales, which form a paler basal patch and a darker distal patch. This character is unique within *Episcada* and was the basis for the description of the monotypic genus *Prittwitzia* Brown & Ebert (Brown *et al.*, 1970), but that name

was considered a subjective synonym of *Episcada* by Lamas (2004), a decision supported by phylogenetic analysis of DNA sequence data (Chazot *et al.*, 2017). The nominate subspecies is widespread and abundant, whereas the other four subspecies are uncommon to rare and have isolated distributions, and DNA sequence data would be valuable to examine whether these taxa really do constitute just a single species. In particular, *E. hymenaea mirifica* seems to occur in close proximity, if not sympatry, with *E. h. hymenaea* in Bolivia (Fig. 34D), but locality data are not sufficiently precise or reliable to make any firm conclusions.

There is a reasonable amount of variation among the small number of specimens examined in the width and intensity of the FW yellow band. Unfortunately, the limited series of this taxon in collections and often poor locality data hinder any assessment of the taxonomic significance of this variation. In the northern part of the range, Ecuadorian females vary somewhat in the width of the FW yellow band, but broader-banded specimens are similar to those from Cuzco in southern Peru. A single male from northern Peru ('Rodríguez de Mendoza') in the PIBO has a rather translucent yellow band, very similar to *Episcada pichita*, but no females are known from that area. A male and female pair from Bolivia (Bueyes) in the NHMUK have the narrowest yellow FW bands, about two thirds the width of the band in southern Peruvian specimens. Clearly more material of both sexes is needed from throughout the distribution to examine this variation more closely.

Distribution and natural history: This taxon is known from central Ecuador (Pastaza valley) to Bolivia (Santa Cruz) (Fig. 34D). All known Ecuadorian specimens are from commercial collectors or bear vague data, and the definitive presence of the species in that country requires confirmation. It is evidently a rare taxon which presumably flies with similar congeners and co-mimics between 1000-2000 m in east Andean cloud forest.

Episcada polita pichincha Willmott & Lamas, new subspecies
Figs. 7J,K, 14E-F, 34E

Episcada polita n. ssp.: Lamas (2004: 187, no. 245f)

Diagnosis and identification: This subspecies is distinguished from *E. polita raymondi* Neild, 2008 (Fig. 7L), from the Venezuelan Sierra de Mérida and Cordillera de la Costa (Fig. 34E), by the broader white FW postdiscal band, which is also adjacent to the dark postdiscal bar rather than displaced distally from it in cell M₃-M₂. The white FW postdiscal band distinguishes it from all other *Episcada polita* Weymer, 1899 taxa, in which the band is yellow. The taxon is very similar to *Episcada salvinia apia* (C. Felder & R. Felder, 1865), from Colombia, which differs in having narrower dark apical and distal margins on both wings, a narrower and more translucent white FW postdiscal band, and less prominent pale apical spots on the VFW. The female of the east Andean species *Episcada mira* is also very similar, but has yellow continuing right to the base of the VHW costa, covering the humeral vein. Perhaps the most similar taxon with which this subspecies is sympatric is *Pteronymia alissa* (Hewitson, 1869), which can be readily identified in males by the fusion of HW veins M₁ and Rs, and

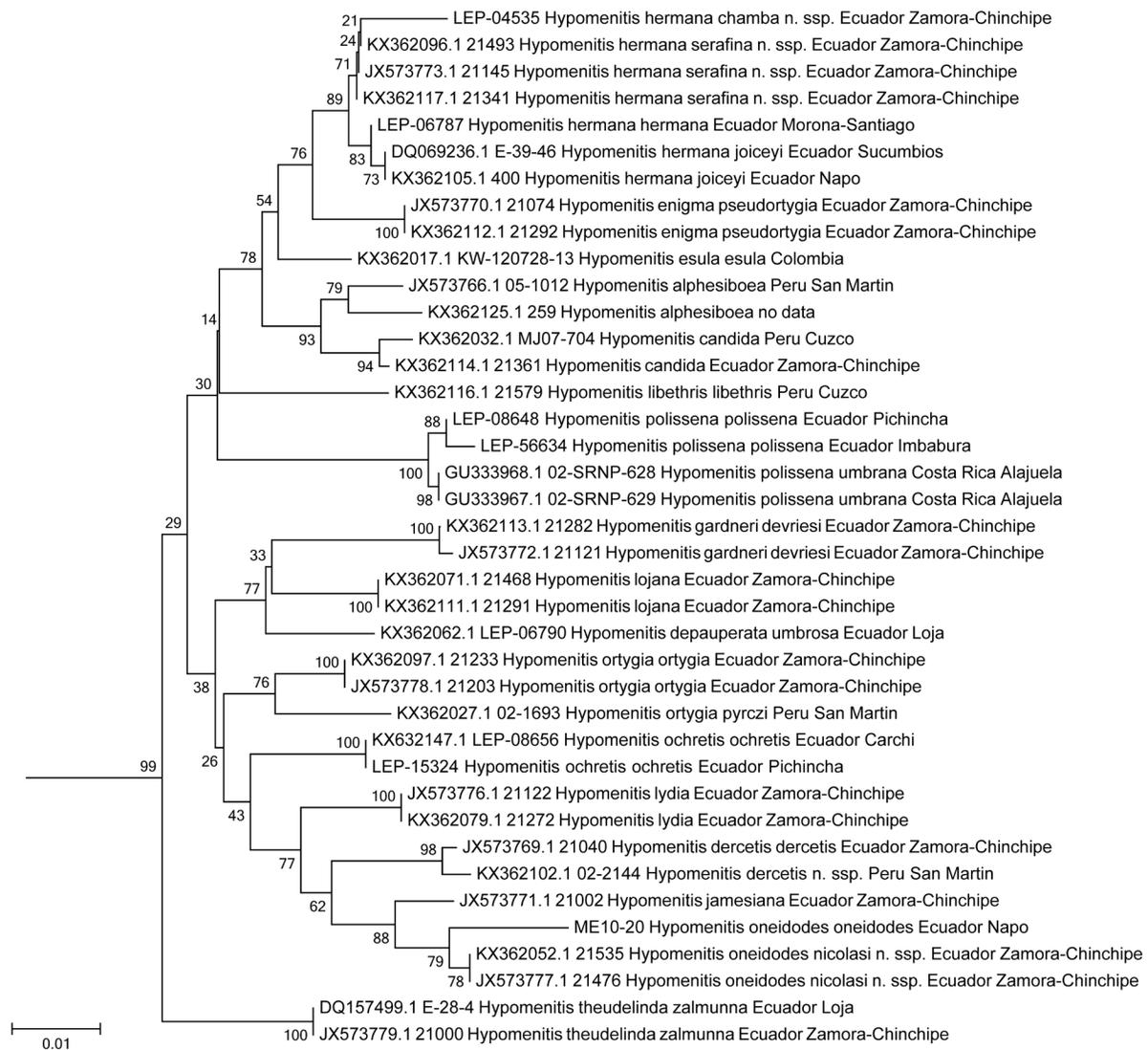


Fig. 30. Neighbor-joining tree (Kimura 2-parameter) for select *Hypomenitis* based on analysis of 633 bp of COI (barcode region). Bootstrap values (%) are shown by branches.

in both sexes by the less elongate HW shape and pure white (rather than yellow or yellowish) ventral abdomen.

Description: MALE (Fig. 7J, 14E-F): Forewing length 23 mm (mean 22.3 mm, n=3). *Wings:* as illustrated (Fig. 7J), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes brown, bare, with fringe of white scales at base; antennae dark brown; labial palpi white except for black terminal segment; top of head with white medial stripe between bases of antennae, two white spots behind eyes, frons broadly dark brown in middle with white at edges. *Thorax:* dorsal surface dark brown with white medial stripe, sparse white scaling laterally, tegula white with sparse black scaling especially in antero-dorsal portion, pronotum dark brown dorsally and white laterally, ventral surface white except for dark brown where legs fold, legs dark brown with scattered white scaling. *Abdomen:* dorsal surface dark brown, ventral surface pale yellow. *Genitalia* (Fig. 14E-F): notable features include strongly bent aedeagus in lateral view (Fig. 14E).

FEMALE: (Fig. 7K): Forewing mean length 22.5 mm (n=4). *Wings:* as illustrated (Fig. 7K), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **ECUADOR:** *Carchi:* Reserva Las Golondrinas, N of La Carolina, Santa Rosa, [0°49'38"N,78°7'42"W], 1700 m, (Hall, J. P. W., Willmott, K. R.), 5 Sep 1996, [Genitalic dissection KW-21-07], (FLMNH, to be deposited in INABIO).

PARATYPES (67♂, 40♀): **Colombia:** *Nariño:* Ricaurte, [1°13'N,77°59'W], 1100 m, Jun 1946, 1♀, (AMNH); Ricaurte, [1°13'N,77°59'W], 1600 m, 1♀, (IAVH). **Ecuador:** *Carchi:* same collection data as HT, 1♂, (MUSM); E Las Juntas, Río Chorro Blanco, [0°48'17"N,78°8'43"W], 1450-1600 m, (Willmott, K. R., Hall, J. P. W.), 16 Jul 2011, 1♂ [FLMNH-MGCL-150841], 1♂ [FLMNH-MGCL-150842], (FLMNH), 1♂ [FLMNH-MGCL-150843], 1♂ [FLMNH-MGCL-150844], 6♂, 2♀, (INABIO); km 16 La Carolina-Las Juntas rd., Finca San Francisco, [0°48'12"N,78°10'15"W], 1300 m, (Willmott, K. R., Hall, J. P. W.), 13,16 Jul 2011, 1♂ [FLMNH-MGCL-150840], (FLMNH); Reserva Las Golondrinas, N of La Carolina, Santa Rosa, [0°49'38"N,78°7'42"W], 1700 m, (Hall, J. P. W., Willmott, K. R.), 5 Sep 1996, 1♂, (FLMNH), (Willmott, K. R.), 5 Sep 1996, 3♀, (FLMNH); *Cotopaxi:* [San Francisco de] Las Pampas, [0°26'S,78°58'W], 1500 m, (Onore, G.), May 1985, 1♀, (DZUP); *Imbabura:* Río Mira, Paramba, [0°49'N,78°21'W], 1050 m, dry season, 12♂, 2♀, (NHMUK); Río Mira, Paramba, [0°49'N,78°21'W], 1200 m, (Rosenberg, W. F. H.), Feb 1897, 2♂, (MNHN); *Pichincha:* 12 km SW Las Tolas, [0°3'3"N,78°50'18"W], 1200 m, (Willmott, K. R., Hall, J. P. W.), 1,3 Aug 2011, 1♂ [FLMNH-MGCL-150845], 1♀ [FLMNH-MGCL-150846], (FLMNH), 4♂, 1♀ [FLMNH-MGCL-150847], 4♀, (INABIO); 16 km E Santo Domingo, [0°19'S,79°0'W], 650 m, 1♂, (ZSBS); km 5 Nanegal-García Moreno rd., Palmito Pamba, [0°9'11"N,78°39'27"W], 1500 m, (Aldaz, R.), 7 Jun 2011, 2♂, (INABIO); km 5 Nanegal-García Moreno rd., Palmito Pamba, [0°9'11"N,78°39'27"W], 1700 m, (Aldaz, R.), 8 Jun 2011, 1♀, (INABIO); km 9 Pacto-Guayabillas rd., [0°9'18"N,78°49'14"W], 1630 m, (Willmott, K.

R., Hall, J. P. W.), 5,6 Aug 2011, 1♀, (INABIO); Nanegal, [0°07'S,78°46'W], 1400 m, (Velástegui, S. E.), 12 Aug 1970, 1♂, (MUSM); 'Quito' - (error), 1♂, (NHMUK); Reserva Las Galarías, [0°039'S,78°43'50"W], 2050 m, (Kell, T.), 31 Jul 2012, 1♀ [FLMNH-MGCL-169423; Nunbird Ridge], (FLMNH); Río Mindo, Mindo, [0°42'0"S,78°45'W], 1300 m, (Willmott, K. R., Hall, J. P. W.), 10 Jul 1998, 1♀, (FLMNH); Río Pilatón, (Lafebre, R. de), 5♂, 2♀, (FLMNH), Nov 1970, 1♂, 2♀, (MUSM); Río Pilatón, Tandapi, [0°27'S,78°46'W], 1500 m, Dec, 2♂, (ZSBS), (Velástegui, D.), 12 Jul 1969, 1♂, 1♀, (MUSM); Río Pilatón, Tandapi, [0°27'S,78°46'W], 1550 m, (Mielke, O.), 22,23 Jun 1987, 7♂, 1♀, (OLMI), (Nicolay, S. S.), 17 Sep 1975, 1♂, 2♀, (USNM); Río Pilatón, Tandapi, [0°27'S,78°46'W], 1550-1700 m, (Willmott, K. R., Hall, J. P. W.), 15 Jul 1994, 1♂, (FLMNH); Río Tandapi, [0°27'S,78°46'W], (Lafebre, R. de), 1♂, (FLMNH); Tandayapa Bird Lodge, [0°07'N,78°40'41"W], 1700 m, (Willmott, K. R., Hall, J. P. W.), 2-5 Aug 2011, 1♀ [FLMNH-MGCL-150848], (FLMNH), 3♀, (INABIO); *Azuay*: 'Sigsig' - (error), (Lafebre, R. de), 1♂, (FLMNH); *Loja*: 'San Pedro de Vilcabamba, Río Uchima' - (error), (Lafebre, R. de), 5♂, 8♀, (FLMNH), 1500 m, Jul 1970, 1♂, (MUSM); *Not located*: 'Ecuador', 1♂, (FLMNH). **Country unknown**: *Not located*: no data, 1♂, (SMNS), 1♂, (USNM).

Other records: **Ecuador:** *Carchi*: Reserva Las Golondrinas, N of La Carolina, Santa Rosa, [0°49'38"N,78°7'42"W], 1600-1700 m, (Hall, J. P. W., Willmott, K. R.), 29 Nov 1996, 1 specimen [INABIO-TABDP-18541], (INABIO); *Pichincha*: km 5 Nanegal-García Moreno rd., Palmito Pamba, [0°9'11"N,78°39'27"W], 1450-1700 m, (Willmott, K. R., Hall, J. P. W.), 11 Jul 1998, (W&H); Tandayapa Bird Lodge, [0°07'N,78°40'41"W], 1700 m, (Willmott, K. R., Hall, J. P. W.), 2-5 Aug 2011, (W&H).

Etymology: This subspecies is named for the province of Pichincha, in which it is particularly common and widespread. The name is treated as a feminine noun in apposition.

Taxonomy and variation: This taxon is allopatric with respect to other *E. polita* taxa (Fig. 34E), shows no morphological differences from them aside from wing pattern, and occurs at similar elevations, in mountain foothills. In comparison with other similar species, *E. polita* taxa have rather rounded forewings and relatively smaller hindwings, with scalloped inner edges to the dark HW marginal border, but these differences are subtle and rather variable, and genitalic characters are typically uninformative within the genus. Unfortunately, DNA barcodes are also not available for any relevant Colombian and Venezuelan *Episcada* taxa, including *E. p. polita*, and the taxonomy is therefore provisional.

The only other taxon that we regard as a subspecies of *E. polita* for which DNA barcodes are available was recently described by Winhard (2021) as "*Episcada clausina flava* spec. [sic] nov." on page 133, and in the legend for figures 6 and 7 as "*Episcada flava* spec. nov.". The figured holotype corresponds to an east Ecuadorian taxon whose DNA barcodes cluster with *E. polita pichincha* n. ssp. (Fig. 26). As discussed above under *E. hymenaea mirifica* n. ssp., this yellow-banded east Ecuadorian taxon differs from *E. mira* in not having solid yellow to the base of the VHW costa, from *E. pichita* in having a solid yellow FW postdiscal band, and from *E. hymenaea mirifica* in not having VHW veins R and Rs lined with yellow almost to the distal edge of cell M₂-M₁, and in having separate white dots in the VFW apex rather than a pale yellowish edge. Winhard (2021) provided no reason for associating *flava* with *Episcada clausina*, and given that *flava* is sympatric with *E. clausina bomboiza* n. ssp., and that the latter taxon grouped with *E. c. clausina* based on DNA barcodes, current evidence suggests that *flava* is not conspecific with *E. clausina*. As *flava* shares similar wing pattern characters with *E. polita pichincha* and *E. p. polita*, and clusters at least with the former based on

DNA barcodes, we treat it as *Episcada polita flava* n. stat.

Episcada polita pichincha is a common taxon in the field and in collections, and the fact that it has no name is presumably a result of its strong similarity to *E. salvinia apia* and other sympatric co-mimics, such as *Pteronymia alissa*. Despite the similarity to *E. polita raymondi*, these two taxa are not neighboring subspecies, being separated geographically in central Colombia by the rather different *E. p. polita* (Fig. 34E).

Distribution and natural history: This subspecies is known only from the west Andean slopes from extreme southern Colombia (Nariño) to northern Ecuador (Cotopaxi) (Fig. 34E). It occurs from 1200-2050 m in cloud forest habitats, typically along the edges of roads and wide trails through primary forest. Males were commonly observed feeding at white Asteraceae flowers in the mid-morning, in overgrown fields near the forest edge. At Tandayapa Bird Lodge in Ecuador, a female was observed inspecting a plant similar to *Solanum aphyodendron* S. Knapp (Solanaceae), where solitary eggs were found under leaves 1 m above the ground. The taxon is sympatric with a number of similar ithomiines with which it is presumably involved in mimicry, especially *Greta andromica andromica* (Hewitson, [1855]), *Hypomenitis polissena polissena* (Hewitson, 1863), and a number of species of *Pteronymia* and *Oleria*.

Episcada arcadia Lamas & Willmott, new species

Figs. 7M,N, 14I-M,R,S,T, 15A-F, 34F

Episcada sulphurea n. ssp.: Lamas (2004: 187, no. 249b)

Episcada sulphurea ssp1: Elias et al. (2007: supplementary information)

Episcada sulphurea: Elias et al. (2008: S1); Chazot et al. (2014b); Willmott et al. (2017)

Diagnosis and identification: This species is distinguished from its likely sister species *Episcada sulphurea* Haensch, 1905 (Fig. 7O) by the following genitalic characters (state in *E. sulphurea* in parentheses): 1. The gnathos is split into two posterior projections (Fig. 14J,O; a single projection in *E. sulphurea* (Fig. 14H) and all other *Episcada*); 2. The valva in lateral view is less elongate and more rounded ventrally (Fig. 14I,N; a parallelogram (Fig. 14G)); 3. The posterior tip of the female abdomen is markedly asymmetrical, twisted to the left (Fig. 15A,G; only slightly asymmetrical (Fig. 16A)); 4. The seventh sternite of the female abdomen is expanded dorso-posteriorly to overlap the ventral edge of the seventh tergite (Fig. 15A,G; not expanded or overlapping (Fig. 16A)); 5. The seventh sternite of the female abdomen is shorter in ventral view and forms a distinct bulge just anterior of the ostium bursae (Fig. 15D,I; not shortened, lacking a bulge (Fig. 16C)); 6. The eighth tergite of the female abdomen is reduced in width and almost or completely fused with the lamella postvaginalis (Fig. 15A,G; less reduced, not fused with lamella postvaginalis (Fig. 16A)). Wing pattern differences are more subtle, but *E. arcadia* n. sp. has a less intense yellow FW translucent postdiscal band, especially near the costa, which is thus similar in color to the remaining yellow areas of the wing, and on the ventral surface the opaque marginal borders and FW discocellular bar are more blackish rather than yellow-brown. Genitalic characters 1 and 4 described above also distinguish this species from all

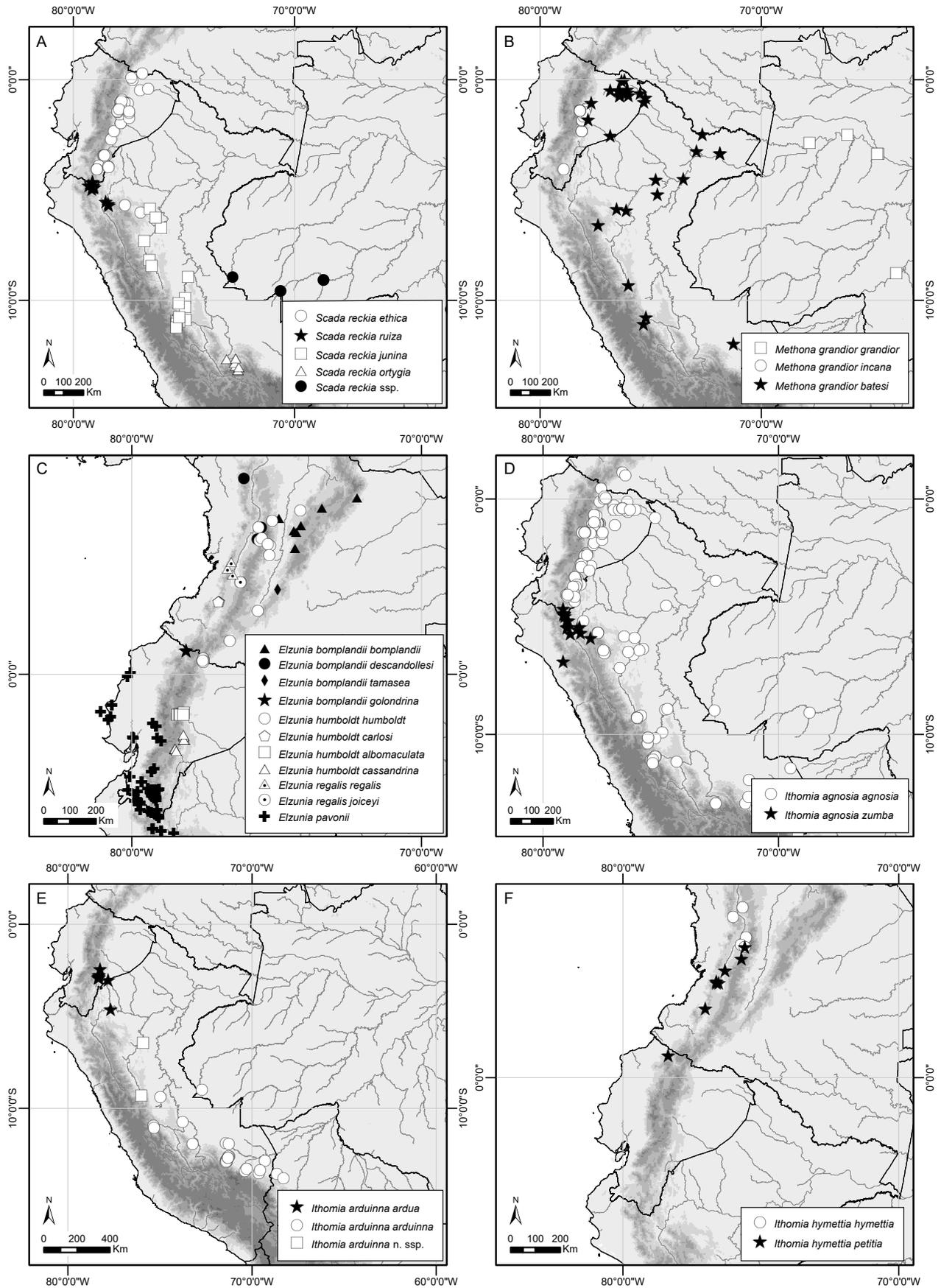


Fig. 31. Distributions of new and related *Scada*, *Methona*, *Elzunia* and *Ithomia* taxa: **A**, *Scada reckia ruiza* n. ssp.; **B**, *Methona grandior batesi* n. ssp.; **C**, *Elzunia bomplandii golondrina* n. ssp.; **D**, *Ithomia agnosia zumba* n. ssp.; **E**, *Ithomia arduinna ardua* n. ssp.; **F**, *Ithomia hymettia petitia* n. ssp.

other *Episcada*, and 1 is unique within the Ithomiini, with only *Pteronymia hara* (Hewitson, 1877) having two projections and these being small bumps rather than long points (Fig. 17L).

This species is also very similar to several sympatric ithomiines, including *Pteronymia vestilla sparsa* Haensch, 1903 and *Pteronymia primula primula* (Bates, 1862). In *E. arcadia*, FW cell Cu_1 - M_3 lacks any yellow color (FW yellow postdiscal band extends into this cell in *P. vestilla sparsa*), vein Cu between the bases of veins Cu_2 and Cu_1 is black (yellow in *P. primula*), and HW vein M_2 meets the discocellulars immediately opposite Mr, rather than anteriorly of Mr. Aside from *E. sulphurea*, discussed above, this last character distinguishes *E. arcadia* from most similar species elsewhere in the Neotropics, except *Episcada hymen* Haensch, 1905 (Fig. 7R) (Peru to Bolivia) and *Episcada doto* (Hübner, [1806]) (Peru, Venezuela). Both of those species have the HW translucent yellow more strongly confined to the anterior part of the wing and yellow scaling along the basal part of the VHW costa; *E. doto* is also larger, has a more rounded HW and has the yellow FW translucent postdiscal band broader, extending anteriorly to fill cell M_2 - M_1 at the distal margin.

Description: MALE (Fig. 7M, 14I-M,R,T): Forewing length 20 mm (mean 20.8 mm, n=4). *Wings:* as illustrated (Fig. 7M, 14R,T), VHW costa entirely orange without trace of yellow scales; venation typical of genus (Willmott & Freitas, 2006), with distinct medial recurrent vein intruding into FW discal cell, and more distinctive placement of HW medial recurrent vein immediately opposite base of vein M_2 (Fig. 14R); continuous band of pale buff, androconial hair-like scales in anterior edge of DHW discal cell, narrowing slightly in middle, covering associated modified wing scales in DHW Rs-Sc+ R_1 that are pale buff, sparse and blade-like in shape (Fig. 14T). *Head, thorax, abdomen:* same as *Episcada clausina bomboiza* n. ssp. *Genitalia* (Fig. 14I-M): notable features include rounded ventral edge to valva and deep gnathos in lateral view (Fig. 14I), gnathos split into two posterior projections (Fig. 14J), aedeagus gently bent near tip (Fig. 14L).

FEMALE: (Fig. 7N, 14S, 15A-F): Forewing mean length 20.6 mm (n=5). *Wings:* as illustrated (Fig. 7N), lacking DHW costal androconial scales, with strong FW medial recurrent vein as in male, and HW veins M_1 -Rs junction distal of discal cell end (Fig. 14S). *Head, thorax, abdomen:* similar to male. *Genitalia* (Fig. 15A-F): notable features include asymmetric tip to abdomen (Fig. 15A,G), seventh sternite expanded dorso-posteriorly to overlap ventral edge of seventh tergite (Fig. 15A,G), seventh sternite shorter in ventral view and forming a distinct bulge just anterior of ostium bursae (Fig. 15D,I), eighth tergite reduced in width and almost or completely fused with lamella postvaginalis (Fig. 15A,G).

Types: HOLOTYPE ♂: **ECUADOR:** *Orellana:* Río Napo, Boca del Río Añangu, [0°31'43"S,76°23'41"W], 220-300 m, (Willmott, K. R.), 17 Nov 2005, [FLMNH-MGCL-ECD-78; Genitalic dissection KW-21-25], (FLMNH, to be deposited in INABIO).

PARATYPES (9♂, 29♀): **Ecuador:** *Napo:* 4 km W Misahuallí, [1°2'18"S,77°41'42"W], 400 m, (Busby, G. W.), 12 Oct 1992, 1♂ [Genitalic dissection KW-21-08], (FLMNH); *E Archidona, Mariposa,* [0°54'30"S,77°47'8"W], (Elias, M., Toporov, S., Santacruz, P.), 22 Feb 2010, 1♀, (FLMNH); *Río Hollín, nr. Archidona, 'Hollín2',* [0°55'46"S,77°44'24"W], (Elias, M., Toporov, S., Santacruz, P.), 21 Mar 2010, 1♀, (MNH); *Río Misahuallí, Misahuallí,* [1°1'36"S,77°40'W], 450 m, (Boyer, P.), Jun 1997, 1♀, (PIBO); *Río Napo, Puerto Napo-Ahuano rd., Jatun Sacha,* [1°3'S,77°35'9"W], 400-450 m, (Beccaloni, G. W.), 16 Sep 1992, 1♀, 1♀ ['feeding on flowers of PA 2'], (NHMUK); *Orellana:* 28 km SE Coca, track NNE of Pindo 13 oil well, [0°39'40"S,76°49'W], 260 m, (Warren-Gash, H.), 19 Aug 2010, 1♂, (HAWA); *nr. Coca,* [0°28'S,76°59'W], 300 m, (Willmott, K. R.), 22 Oct 2005, 1♀ [FLMNH-MGCL-ECD-81], (FLMNH); *Río Manduro, Río Napo, Yarina,* [0°28'14"S,76°50'W], 300 m, (Gallice, G.), 16 Sep 2010, 1♀ [YL869], (FLMNH), 26 Sep 2010, 1♀ [YL1292], (INABIO); *Río Napo, Boca del Río Añangu,* [0°31'43"S,76°23'41"W], 220-300 m, (Willmott, K. R.), 16 Nov 2005, 1♀ [FLMNH-MGCL-ECD-82], (FLMNH), 1♀ [FLMNH-MGCL-ECD-80], (FLMNH), 20 Nov 2005, 1♀, (EUIEB), 27 Oct 2005, 1♂ [FLMNH-

MGCL-ECD-76], (FLMNH), 28 Oct 2005, 1♀ [FLMNH-MGCL-ECD-75; Genitalic dissection KW-21-29], (FLMNH), 6 Nov 2005, 1♀, (EUIEB), 8 Dec 2005, 1♂, (EUIEB), 8 Nov 2005, 1♀, (EUIEB), 9 Nov 2005, 1♀ [FLMNH-MGCL-ECD-83], (FLMNH), (Elias, M.), 1 Nov 2005, 1♂ [FLMNH-MGCL-ECD-77], 1♀ [FLMNH-MGCL-ECD-79], 1♀ [FLMNH-MGCL-ECD-84], (FLMNH), 23 Nov 2005, 1♀, (EUIEB), 24 Nov 2005, 1♀, (EUIEB); *Río Napo, Sacha Lodge,* [0°28'14"S,76°27'33"W], 240 m, (Gallice, G.), 11 Oct 2010, 1♀ [SL1464], (FLMNH); *Morona-Santiago:* km 35 Puyo-Macas rd., [1°41'20"S,77°48'19"W], 650 m, (Boyer, P.), 19 Nov 1998, 1♂, (PIBO); *nr. Yaupi, Río Wampis,* [2°51'16"S,77°56'48"W], 350-400 m, (Gallice, G.), 21 Jun 2009, 1♂ [FLMNH-MGCL-153578; Genitalic dissection KW-21-28], (FLMNH); *Río Santiago, Santiago,* [3°2'11"S,78°2'W], 350 m, (Gallice, G.), 1 Jun 2009, 1♀ [FLMNH-MGCL-153577], (FLMNH); *Pastaza: "Sarayaco" (= Sarayacu),* [1°44'S,77°29'W], 1♀, (MUSM); *Zamora-Chinchipec: Río Zamora, Zamora,* [4°4'6"S,78°57'W], 950-1265 m, (Baron, O. T.), 1♂, (MUSM). **Peru:** *Loreto:* *Arcadia,* [0°59'22"S,75°18'33"W], 150 m, (Lamas, G.), 31 Oct 1993, 1♀, (MUSM).

Other records: **Ecuador:** *Napo:* *E Archidona, Mariposa,* [0°54'30"S,77°47'8"W], (Elias, M., Toporov, S., Santacruz, P.), 23 Feb 2010, 1♀, (sight record) (Elias, M., unpublished data); *Río Napo, Añangu community,* [0°29'37"S,76°25'11"W], 230 m, (Elias, M.), 10 Dec 2005, 1♀, (W&H); *Río Napo, Boca del Río Añangu,* [0°31'43"S,76°23'41"W], 220-300 m, (Willmott, K. R.), 11 Dec 2005, 1♀, 6 Dec 2005, 1♀, 7 Dec 2005, 1♂, 8 Dec 2005, 1♀, (W&H).

Etymology: This subspecies is named for the community of Arcadia, one of the earliest localities where this taxon was collected. The name is treated as a feminine noun in apposition.

Taxonomy and variation: The female genitalia has the inner walls of the antrum covered with minute studs (a synapomorphy for *Episcada*+*Ceratinia* Hübner, 1816) (Fig. 15C; Willmott & Freitas, 2006, character 340:1). The male genitalia has a broadening tip to the aedeagus (Fig. 14M) and large gap between the anterior edge of the valva and the vinculum (Fig. 14I), both also derived characters typical of this clade (Willmott & Freitas, 2006, characters 226:1 and 270:2). *Episcada arcadia* n. sp. possesses a strong additional FW medial recurrent vein anterior of Mr (Fig. 14R,S) (Willmott & Freitas, 2006: char. 112:1) that is typical (but not universal) in *Episcada*. Finally, DNA sequence data support the placement of this species within *Episcada* (Chazot *et al.*, 2017, as '*Episcada sulphurea*'), and as a close relative of *Episcada hymen*, with which this species also shares the medial recurrent vein in the HW discal cell being immediately opposite vein M_2 (Fig. 14R-T).

In fact, the most likely sister species of *E. arcadia* is true *E. sulphurea* (central Peru (Ucayali) to Bolivia (La Paz)), which was not represented in Chazot *et al.* (2017). *Episcada sulphurea* has similar HW venation to *E. arcadia* and *E. hymen*, but the first two species are further distinguished by having somewhat asymmetric female genitalia (although this is more marked in *E. arcadia*), and are otherwise very similar in wing pattern. In fact, given their allopatry, until recently we considered *E. arcadia* to be a subspecies of *E. sulphurea* (Lamas, 2004; Elias *et al.*, 2007, 2008; Chazot *et al.*, 2014b; Willmott *et al.*, 2017). However, while dissecting specimens for this study, we were surprised to find that both the male and female genitalia of *E. arcadia* were remarkably distinct from all other *Episcada*, including *E. sulphurea*, with differences much greater than seen among any other congeners. We regard these differences as sufficient to recognize *E. arcadia* as a distinct species, despite lack of evidence for sympatry with *E. sulphurea*.

Haensch (1905: 171) described *Episcada sulphurea* from a single male from Yungas, Bolivia, collected by Garlepp. In

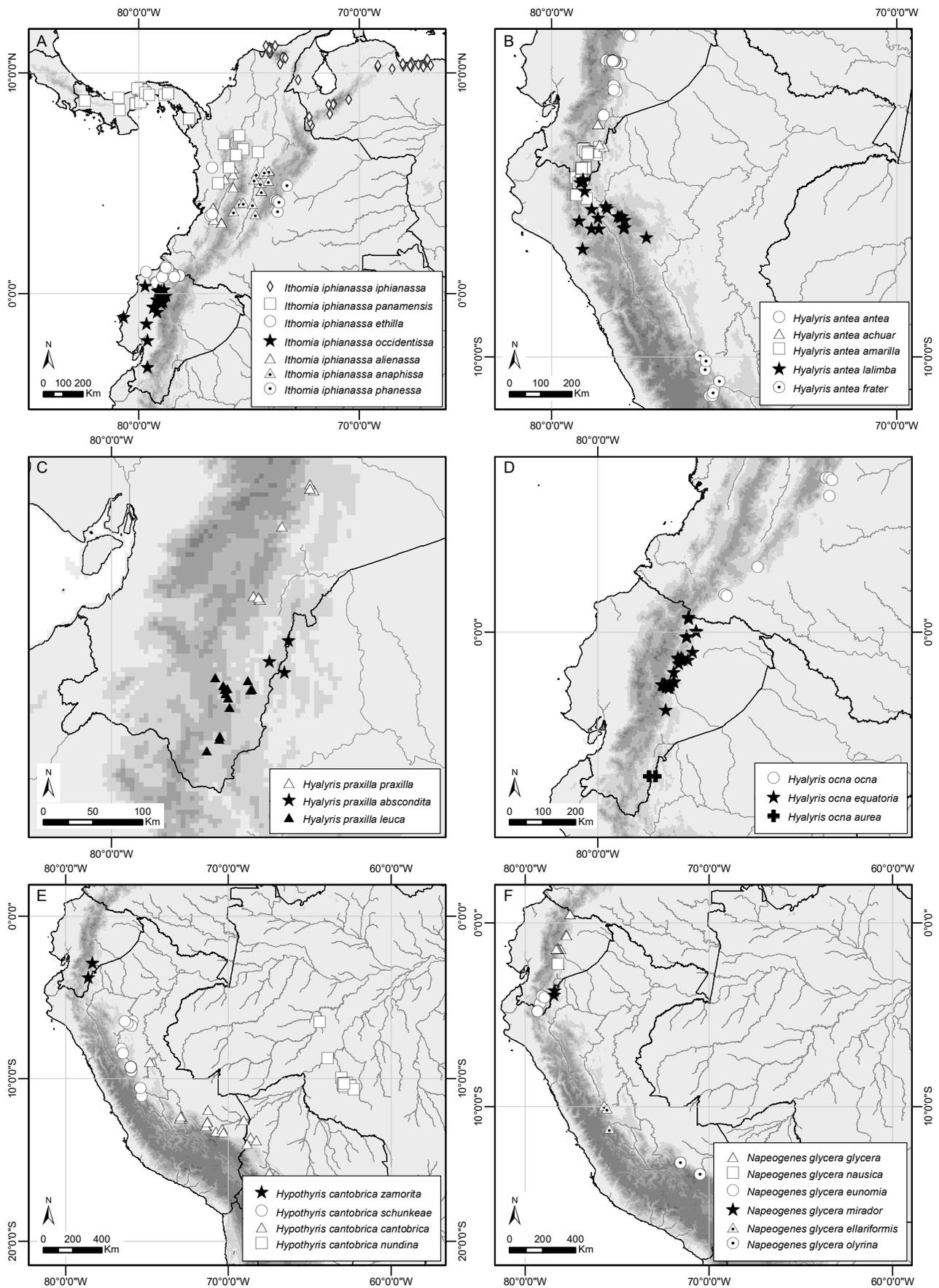


Fig. 32. Distributions of new and related *Ithomia*, *Hyaliris*, *Hypothyris* and *Napeogenes* taxa: **A**, *Ithomia iphianassa occidentissa* n. ssp.; **B**, *Hyaliris antea lalimba* n. ssp.; **C**, *Hyaliris praxilla leuca* n. ssp.; **D**, *Hyaliris ocna equatoria* n. ssp.; *Hyaliris ocna aurea* n. ssp.; **E**, *Hypothyris cantobrica zamorita* n. ssp.; **F**, *Napeogenes glycera mirador* n. ssp.

comparison with his immediately preceding description of *Episcada hymen* (Haensch, 1905: 170), also based on a single male from Bolivia (from San Mateo), he stated that *E. sulphurea* differed by being slightly larger, the wings more elongate, the yellow FW postdiscal band being wider and the yellow overall more extensive, in particular covering the veins, the base of the forewings lacking reddish-brown scaling, and the VHW costa lacking yellow scaling. These descriptions closely correspond to the holotypes in the MfN figured by Warren *et al.* (2021) and to specimens of both species dissected for comparison with *E. arcadia*.

Distribution and natural history: This taxon is known only from eastern Ecuador to northeastern Peru (Loreto) (Fig. 34F). It occurs in lowland forest up to 650 m, but it is most often encountered away from the Andes, below 350 m. The taxon appears to be very local, absent from many sites, and when encountered occurs as solitary individuals in primary forest understorey. In Ecuador, both sexes, but more often females, were found flying from 10:45-16:05 hrs, from 0.7-1.6 m above the ground, frequently near the edges of light gaps or streams. The taxon is involved in mimicry with a number of ithomiines and other butterflies (see Beccaloni, 1997), which together comprise one of the most abundant butterfly mimicry complexes in eastern Ecuador and northeastern Peru. In the vicinity of Laguna Añangu, Ecuador, Elias and Willmott found 12 solitary eggs, 2 first instars, 1 second instar and 1 fifth instar of *E. arcadia n. sp.* under leaves of *Solanum sessile* Ruiz & Pav. (Solanaceae) (determined by S. Knapp), ranging from 1.2-5 m above the ground. The host plants were growing in old secondary growth areas along the Río Napo and in adjacent gardens, and also hosted immatures of the co-mimic *Pteronymia sao* (Hübner, [1813]) (Willmott & Elias, unpublished data).

Episcada arcadia navarro Lamas & Willmott, **new subspecies**
Figs. 7P,Q, 14N-O, 15G-J, 34F

Diagnosis and identification: This subspecies is distinguished from the nominate subspecies by the darker ('smokier') overall appearance of the wings, its yellow areas contrasting sharply with the ground color. In addition, there are slight differences apparent in both male and female genitalia, as detailed in the description below.

Description: MALE (Fig. 7P, 14N-Q): Forewing length 19 mm (mean 20 mm, n=2). *Wings:* as illustrated (Fig. 7P), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head, thorax, abdomen:* same as in nominate subspecies. *Genitalia* (Fig. 14N-Q): similar to nominate subspecies except indentation between posteriorly pointing projections from gnathos slightly less deep (Fig. 14N-Q).

FEMALE: (Fig. 7Q, 15G-J): Forewing length 22 mm (n=1). *Wings:* as illustrated (Fig. 7Q), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male. *Genitalia* (Fig. 15G-J): similar to nominate subspecies except tip of abdomen slightly less asymmetrical, seventh sternite slightly less reduced in width and eighth tergite not so reduced in width and touching or incompletely fused with lamella postvaginalis (Fig. 15G-J).

Types: HOLOTYPE ♂: PERU: *San Martín:* Navarro, [6°21'S, 75°45'W], 400 m, (Lamas, G.), 14-18 Aug 1974, [dissected by KRW], (MUSM).

PARATYPES (1♂, 1♀): Peru: *Loreto:* San Salvador, 5 km NNW Contamana, [7°19'S, 75°01'W], 180 m, (Lamas, G.), 26 Nov 2002, 1♂, (MUSM); *San Martín:* same data as HT, [dissected by KRW], 1♀, (MUSM).

Etymology: The name is derived from that of the type locality and is treated as a masculine noun in apposition.

Taxonomy and variation: *Episcada arcadia navarro n. sp.* shares with *Episcada arcadia n. sp.* all of the diagnostic male and female genitalic traits described under the latter taxon. With no evidence of sympatry or substantial molecular divergence (no DNA sequences are yet available for *E. arcadia navarro*), we treat the two taxa as conspecific.

Distribution and natural history: This taxon is known from only two sites (San Martín and Loreto) in northern Peru (Fig. 34F).

Pteronymia alida luctuosa Willmott & Lamas, **new subspecies**

Figs. 8A,B, 17A-D, 35A

Pteronymia alida n. ssp.: Lamas (2004: 187, no. 261e)

Diagnosis and identification: This subspecies is distinguished from *P. alida zabina* (Hewitson, [1857]) (Fig. 8C), from Colombia, by the more pronounced white postdiscal mark at the FW costa and by the thicker black scaling around the FW discocellulars. The male of *P. a. luctuosa n. ssp.* has a white semi-opaque FW costal bar and translucent white postdiscal scaling in FW cells M₂-R₅, in comparison with a pale yellowish brown translucent FW postdiscal spot at the costa and barely any colored postdiscal scaling in *P. alida zabina*. The marginal translucent colored spots in *P. alida luctuosa* are pale grayish white, compared to pale yellowish brown in *P. alida zabina*. The female of *P. alida luctuosa* differs from *P. alida zabina* in having much broader black marginal and FW discal markings, a more dentate basal edge to the dark HW margin, and heavier white translucent coloring throughout the wings. The taxon is otherwise distinguished from other *P. alida* (Hewitson, 1855) taxa by the FW translucent markings being whitish rather than yellowish. It is also very similar to the co-occurring taxon *P. hara olerina n. ssp.* (Fig. 8N), but may be distinguished by the less well-defined white translucent FW postdiscal band in the male, by the more dentate basal edge to the dark HW margin in the female, and in both sexes by the longer vein Mr intruding into the HW discal cell.

Description: MALE (Fig. 8A, 17A-D): Forewing length 30 mm (n=1). *Wings:* as illustrated (Fig. 8A), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes brown, bare, with narrow fringe of white scales at base; antennae dark brown; labial palpi black with broad white on inner ventral edge, broad white dorsally extending laterally, terminal segment black, long black hair-like scales ventrally; top of head black with white medial stripe between bases of antennae, two white spots behind eyes, frons black with white lateral stripes. *Thorax:* dorsal surface brown with white medial stripe and scattered white lateral scales and long brown hair-like scales, pronotum clothed with very long brown hair-like scales with some lateral white long hair-like scales, tegula clothed with very long brown hair-like scales becoming white in a band in middle, ventral surface white except for black where the legs fold, forelegs dark brown with scattered white scales, mid- and hindlegs dark brown with scattered white scales ventrally on femur and dorsally on tibia and tarsus. *Abdomen:* dorsal surface dark brown, ventral surface white. *Genitalia* (Fig. 17A-D): broad valvae with symmetrical inner dorsal projections (Fig. 17A,B), aedeagus strongly curving upwards except bent downwards at posterior tip and with flared anterior tip (Fig. 17C,D).

FEMALE: (Fig. 8B): Forewing mean length 29.5 mm (n=2). *Wings:* as illustrated (Fig. 8B), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

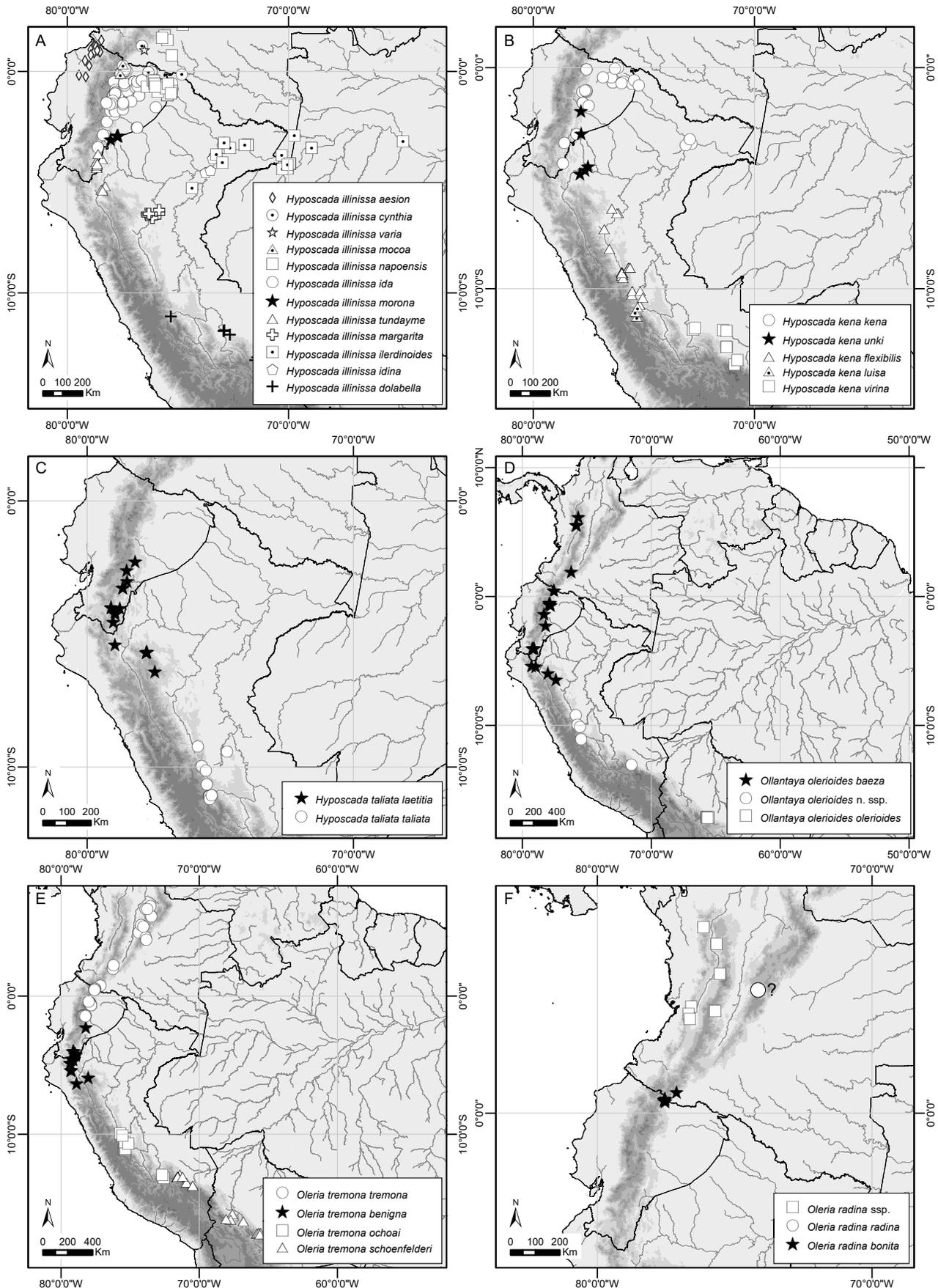


Fig. 33. Distributions of new and related *Hyposcada*, *Ollantaya* and *Oleria* taxa; a dot with ? indicates the likely general region where *O. radina radina* occurs based on vague label data: **A**, *Hyposcada illinissa morona* n. ssp.; **B**, *Hyposcada kena unki* n. ssp.; **C**, *Hyposcada taliata laetitia* n. ssp.; **D**, *Ollantaya olerioides baeza* n. ssp.; **E**, *Oleria tremona benigna* n. ssp.; **F**, *Oleria radina bonita* n. ssp.

Types: HOLOTYPE ♂: **ECUADOR:** *Carchi:* Reserva Las Golondrinas, N of La Carolina, Santa Rosa, [0°49'38"N,78°7'42"W], 1700 m, (Willmott, K. R.), 29 Nov 1996, [Genitalic dissection PTERON-8], (FLMNH, to be deposited in INABIO).

PARATYPES (1♂, 5♀): **Colombia:** *Cauca:* Coconuco, 2200 m, (Warren-Gash, H.), 1 Jun 2007, 1♀, (HAWA); *Valle del Cauca:* Carretera al Mar, La Providencia, [3°42'46"N,76°45'34"W], 1300 m, Sep 1945, 1♀, (AMNH); Tatabro, (Salazar, J.), Jan 1992, 1♀ [‘200 m’], (JELE). **Ecuador:** *Carchi:* Reserva Forestal Golondrinas, [0°49'29"N,78°7'48"W], 1600-1700 m, (Wojtusiak, J., Pyrcz, T.), 26 Jun 1999, 1♂, (MZUJ); Reserva Las Golondrinas, N of La Carolina, Las Juntas, [0°48'48"N,78°9'W], (Boyer, P.), 30 Nov 1996, 1♀, (PIBO); Reserva Las Golondrinas, N of La Carolina, Santa Rosa, [0°49'38"N,78°7'42"W], 1700 m, (Willmott, K. R.), 29 Nov 1996, 2♀, (FLMNH).

Etymology: The name is derived from the feminine Latin adjective ‘luctuosa’, meaning mournful or dark, in reference to the expanded dark wing coloration that is distinctive of this subspecies.

Taxonomy and variation: Morphological characters, in particular the broad, anteriorly extended gnathos and symmetrical dorsal inner projections of the valvae in the male genitalia, show this taxon to belong to a compact group containing seven species of *Pteronymia*, the *P. alida* clade, containing *P. alida*, *P. serrata* Haensch, 1903, *P. cuneata* Willmott, Lamas & Hall, 2020, *P. inania* Haensch, 1903, *P. teresita* (Hewitson, 1863), *P. thabena* (Hewitson, 1869) and *P. lonera* (Butler & Druce, 1872) (De-Silva *et al.*, 2017). All of these species are fairly uniform in terms of wing shape, venation, male androconial hair pencils and genitalia, and with no DNA sequences yet available for either *P. alida luctuosa* or the Venezuelan *P. alida alida* (Cordillera de la Costa and Sierra de Mérida), the taxonomy proposed here is tentative. This taxon is treated as a subspecies of *P. alida* because both taxa have relatively narrow dark HW margins and narrow, straight white VHW marginal dashes, and otherwise appear to occur in similar cloud forest habitats. *Pteronymia alida luctuosa* is not known to be sympatric with any other members of the *P. alida* species group, although *P. teresita* is also present in northwestern Ecuador, at lower elevations.

Distribution and natural history: This taxon is known from the western Andes of Colombia (Cauca and Valle de Cauca) to northern Ecuador (Carchi) (Fig. 35A). It occurs in primary cloud forest habitats from 1300-2200 m. In Ecuador, the holotype male and two paratype females were collected in the afternoon in a subcanopy trap baited with rotting fish, c. 10 m high, at the edge of a wide trail through forest near the Río Santa Rosa. This is highly unusual behavior for an ithomiine (except for the genera *Tithorea* Doubleday, 1847 and *Elzunia*), but the observation suggests that this taxon typically flies high in the subcanopy and canopy, like east Andean *P. alida* (see below), helping to explain its rarity in collections. The female wing pattern is similar to that of several sympatric *Oleria* (e.g., *O. fumata richardina* Lamas, 1994, and *O. bifurcata*), with which the taxon is presumably involved in mimicry.

Pteronymia alida cosanga Willmott & Lamas, new subspecies
Figs. 8D,E, 17E-F, 35A

Pteronymia alida n. ssp.: Lamas (2004: 187, no. 261f)

Episcada apuleia: Piñas (2004: 49, fig. 363), misidentification

Pteronymia alida ssp: Willmott & Mallet (2004: Appendix A)
Pteronymia alida ssp. n.: Willmott & Freitas (2006: Figs. 9, 10)
Pteronymia alida: Chazot *et al.* (2014b)

Diagnosis and identification: This taxon is distinguished from the nominate subspecies from Venezuela (Fig. 8F) by the shorter, narrower, more translucent yellow FW postdiscal band, and from that taxon and *P. alida georgei* Neild, 2008 (also Venezuela) by having a row of prominent translucent yellow HW submarginal spots, and by the remaining transparent area of both wings being suffused with yellow-orange, instead of being largely colorless. The translucent yellow FW postdiscal band and submarginal spots, and HW submarginal spots, in addition to the strong overall yellow-orange translucence, distinguish the taxon from *P. alida infuscans* (Brabant, 2004) (Fig. 8I) (Peru, Huánuco to Junín), which has only a faint yellowish tinge to the wings and almost no translucent colored postdiscal or submarginal spots. The taxon differs from *P. alida francisca* n. ssp. as described under that taxon. *Pteronymia alida cosanga* n. ssp. is most easily distinguished from other similar sympatric congeners by the very narrow, paired white VHW marginal dashes in each cell.

Description: MALE (Fig. 8D, 17E-F): Forewing length 30 mm (mean 29.6 mm, n=5). *Wings:* as illustrated (Fig. 8D), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head, thorax, abdomen:* as in *Pteronymia alida luctuosa* n. ssp. *Genitalia* (Fig. 17E-F): as illustrated, similar notable features to *P. alida luctuosa* n. ssp.

FEMALE: (Fig. 8E): Forewing mean length 30 mm (n=3). *Wings:* as illustrated (Fig. 8E), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **ECUADOR:** *Sucumbios:* nr. La Bonita, Quebrada El Garrapatal, [0°29'18"N,77°33'12"W], 2200 m, (Willmott, K. R.), 21 Dec 2001, [Immature stage voucher KRW-81-1; Genitalic dissection KW-21-09], (FLMNH, to be deposited in INABIO).

PARATYPES (14♂, 6♀): **Ecuador:** *Sucumbios:* nr. La Bonita, Quebrada El Garrapatal, [0°29'18"N,77°33'12"W], 2200 m, (Willmott, K. R.), 21 Dec 2001, 1♀, (FLMNH); *Napo:* Baeza-Tena rd., Cocodrilo, [0°38'57"S,77°47'27"W], (Elias, M., Toporov, S., Santacruz, P.), 12 Mar 2010, 1♂, (MNHN); Hacienda San Isidro (cerca de Cosanga), [0°36'16"S,77°53'2"W], 2000 m, (Boyer, P.), 9 Dec 1996, 1♀, (PIBO); km 6 Baeza-Tena rd., El Arrayán, [0°28'22"S,77°52'36"W], 2200 m, (Willmott, K. R.), 25 Oct 1996, 1♂, 2♀, (FLMNH); nr. Cosanga, Estación Científica Yanayacu, [0°35'24"S,77°53'W], (Elias, M., Toporov, S., Santacruz, P.), 2010, 1♂, (INABIO), 15 Mar 2010, 2♂, (MNHN), 24 Feb 2010, 2♂, (FLMNH), 1♂, 1♀, (MNHN), 28 Feb 2010, 1♂, (FLMNH), 28 Jan 2010, 1♂, (FLMNH); nr. Cosanga, Yanayacu, [0°34'12"S,77°52'12"W], 2000 m, (Greeney, H.), Feb 2005, 1♀ [reared ‘1849’], (FLMNH), Jan 2005, 1♂ [reared C-1025], (FLMNH); Baeza, [0°28'S,77°53'W], 2000 m, 1♂, (MUSM); Estación Biológica Yanayacu, [0°36'S,77°53'W], 2000 m, (Lamas, G.), 24 Nov 2006, 1♂, (MUSM); *Bolívar:* ‘Balzapamba’ - (error), (Haensch), 1♂, (MfN).

Other records: **Ecuador:** *Sucumbios:* Qbda. El Morro, km 9 La Bonita-Tulcán rd., El Higuerón, [0°30'54"N,77°32'12"W], 2200 m, (Willmott, K. R., Hall, J. P. W.), 10 Nov 1997, (sight record) (W&H); *Napo:* Baeza-Tena rd., Cocodrilo, [0°38'57"S,77°47'27"W], (Elias, M., Toporov, S., Santacruz, P.), 12 Mar 2010, 1♂, (sight record) (Elias, M., unpublished data), (Hill, R.), 12 Mar 2010, 1♂ [RH10-65], (Hill, R., unpublished data); nr. Cosanga, Estación Científica Yanayacu, [0°35'24"S,77°53'W], (Elias, M., Toporov, S., Santacruz, P.), 15 Mar 2010, 3♂, (sight record) (Elias, M., unpublished data), 25 Feb 2010, 2♂, (sight record) (Elias, M., unpublished data).

Etymology: The name is derived from that of the town of Cosanga, near which many of the specimens of the type series were collected. It is treated as a feminine noun in apposition.

Taxonomy and variation: As discussed above under *P. alida luctuosa* n. ssp., this taxon is a member of a compact clade

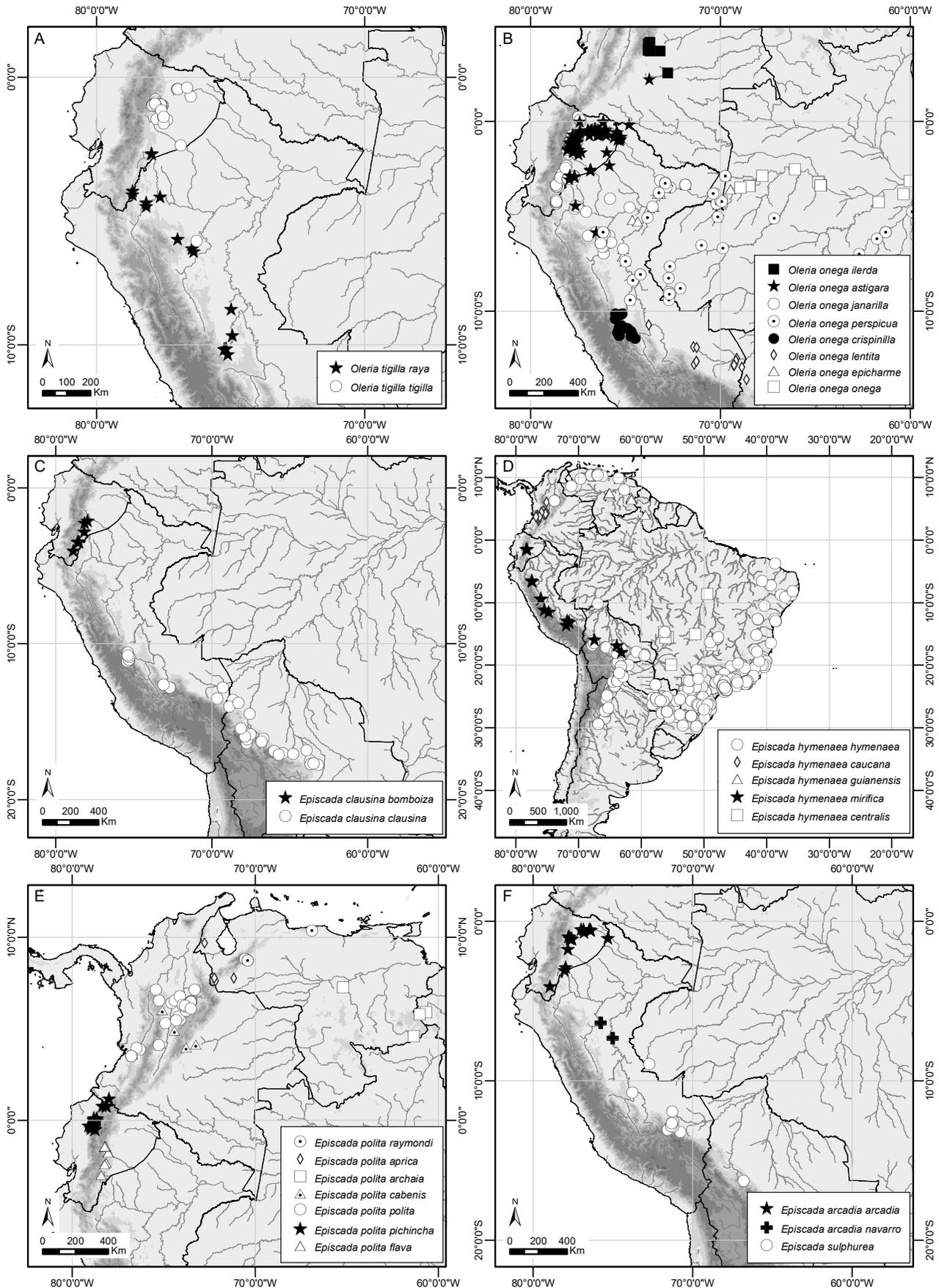


Fig. 34. Distributions of new and related *Oleria* and *Episcada* taxa: **A**, *Oleria tigilla raya* n. ssp.; **B**, *Oleria onega astigara* n. ssp.; **C**, *Episcada clausina bomboiza* n. ssp.; **D**, *Episcada hymenaea mirifica* n. ssp.; **E**, *Episcada polita pichincha* n. ssp.; **F**, *Episcada arcadia* n. sp., *Episcada arcadia navarro* n. ssp.

of seven *Pteronymia* species, the *P. alida* clade (De-Silva *et al.*, 2017). Similarly, it is tentatively associated with nominate *P. alida* for the same reasons as *P. alida luctuosa*, namely the narrow white VHW marginal dashes and similar cloud forest habitat. Unlike *P. alida luctuosa*, however, *P. alida cosanga n. ssp.* is sympatric with a number of other members of the *P. alida* clade, including *P. serrata*, *P. cuneata*, *P. inania*, and *P. thabena* (De-Silva *et al.*, 2017), with *P. teresita* occurring at lower elevations in the western Andes and *P. lonera* endemic to Costa Rica and Panama.

Distribution and natural history: This taxon is known only from northeastern Ecuador, in the provinces of Sucumbíos and Napo (Fig. 35A), where it occurs in primary cloud forest from 1725-2200 m. In Ecuador, both sexes were found flying 2-3 m above the ground across the top of a ridge in a cleared area surrounded by primary forest, as well as in primary forest understorey, often on ridgetops. Males were also found feeding on flowers of weedy Asteraceae along wide trails near forest. At the type locality, two eggs and a first instar were found under leaves of *Solanum nutans* Ruiz & Pav. (Solanaceae) (determined by S. Knapp) in a small, overgrown field, c. 10 m from the forest edge on a steep ridge side, from which one male (the holotype) and one female (paratype) were reared to adults. The taxon is involved in mimicry with numerous sympatric ithomiines, of which the most notable are perhaps *Pteronymia inania inania*, *P. oneida oneida* (Hewitson, 1855), *P. veia linzera* (Herrich-Schäffer, 1865), *Godyris hewitsoni hewitsoni* (Haensch, 1903), *Hypomenitis lydia* (Weyermer, 1899), and males of *Oleria baizana baizana*.

Pteronymia alida francisca Willmott & Lamas, new
subspecies

Figs. 8G,H, 17G-H, 35A

Pteronymia alida n. ssp.: Lamas (2004: 187, no. 261g)

Pteronymia alida ssp.: Willmott & Mallet (2004: Appendix A)

Pteronymia alida: Chazot *et al.* (2014b); Chazot *et al.* (2016a: S1)

Diagnosis and identification: This taxon differs from *P. alida cosanga n. ssp.* (Fig. 8D,E) (northeastern Ecuador) by the reduced translucent yellow FW postdiscal band and by the lack of a strong yellow-orange suffusion throughout the wings, in this respect more closely resembling *P. alida infuscans* from Peru (Fig. 8I) (Huánuco to Junín). It may be distinguished from the latter taxon by the row of translucent yellow submarginal spots on both wings, paler ventral margins, larger white VHW marginal dashes (barely or not visible in *P. alida infuscans*), and less well-defined yellow triangle at the base of the VHW costa. *Pteronymia alida francisca n. ssp.* is also similar to a number of other sympatric congeners but may be distinguished in the same way as *P. alida cosanga* (see under that taxon).

Description: MALE (Fig. 8G, 17G-H): Forewing length 30 mm (mean 30.2 mm, n=6). *Wings:* as illustrated (Fig. 8G), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head, thorax, abdomen:* as in *Pteronymia alida luctuosa n. ssp.* *Genitalia* (Fig. 17G-H): as illustrated, similar notable features to *P. alida luctuosa n. ssp.*

FEMALE: (Fig. 8H): Forewing mean length 29.7 mm (n=7). *Wings:* as illustrated (Fig. 8H), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **ECUADOR:** *Zamora-Chinchi*: km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2000-2100 m, (Willmott, K. R.), 28 Nov 2003, [Genitalic dissection KW-21-10], (FLMNH, to be deposited in INABIO).

PARATYPES (16♂, 15♀): **Ecuador:** *Morona-Santiago:* Guarumales/Hidropaute, [2°34'16"S,78°30'56"W], 2030 m, (Willmott, K. R.), 7 Nov 2010, 1♀ [FLMNH-MGCL-146793], (FLMNH); Guarumales/Hidropaute, [2°34'9"S,78°30'49"W], 1700 m, (Boyer, P.), 10 Aug 2010, 1♀, 2100-2200 m, (Boyer, P.), 18-20 Jan 2011, 1♀, (PIBO); km 25 Macas-Nueve de Octubre rd., [2°15'42"S,78°12'54"W], 1600-2100 m, (Boyer, P.), 6 Dec 1998, 1♀, (PIBO); *Zamora-Chinchi*: km 18 Yacuambi-Saraguro rd., Cascada Hampik Yaku, [3°33'56"S,78°58'6"W], 2000 m, (Willmott, K. R., J. C. R., J. I. R.), 21 Jun 2013, 1♀ [FLMNH-MGCL-157936], (FLMNH); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2000-2100 m, (Willmott, K. R.), 28 Nov 2003, 1♀, (FLMNH), (Willmott, K. R.), 17 Oct 2006, 1♂ [FLMNH-MGCL-112393], 1♂ [FLMNH-MGCL-112405], 1♀ [FLMNH-MGCL-112396], (FLMNH), 2 Nov 2006, 1♂ [FLMNH-MGCL-112403], (FLMNH), (Willmott, K. R., Aldaz, R.), 11 Oct 2006, 1♀ [FLMNH-MGCL-112404], (FLMNH), 12 Nov 2006, 1♂ [FLMNH-MGCL-112395], 1♂ [FLMNH-MGCL-112406], (FLMNH), 14 Nov 2006, 1♂ [FLMNH-MGCL-112409], (FLMNH), 15 Oct 2006, 1♂ [FLMNH-MGCL-112399], 1♂ [FLMNH-MGCL-112402], 1♀ [FLMNH-MGCL-112401], (FLMNH), 22 Oct 2006, 1♂ [FLMNH-MGCL-112397], 1♀ [FLMNH-MGCL-112408], (FLMNH), 1♂ [FLMNH-MGCL-112400], 1♂ [FLMNH-MGCL-112407], 1♀ [FLMNH-MGCL-112394], (INABIO), 27 Oct 2006, 1♂ [FLMNH-MGCL-112392], (FLMNH), 6 Nov 2006, 1♂ [FLMNH-MGCL-112398], (INABIO); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2100 m, (Willmott, K. R.), 25 Nov 2003, 1♀, (FLMNH), (Willmott, K. R.), 5 Nov 2006, 1♀ [FLMNH-MGCL-112410], (FLMNH); *Zamora-Loja* rd., San Francisco, canal subterráneo, [3°58'44"S,79°5'W], 1800 m, (Willmott, K. R.), 27 Jan 2002, 1♂, 1♀, (FLMNH), (Willmott, K. R.), 27 Jan 2002, 1♂ [life history voucher KRW-272], (NHMUK); *Zamora-Loja* rd., San Francisco, canal subterráneo, [3°58'44"S,79°5'W], 1900 m, (Willmott, K. R.), 26 Nov 2003, 1♂, 1♀, (FLMNH).

Other records: **Ecuador:** *Zamora-Chinchi*: km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2000-2100 m, (Willmott, K. R.), 3 Dec 2006, 1♂, 2♀, (W&H), (Willmott, K. R.), 15 Nov 2006, 1♂, 1 individual, (W&H), 2 Nov 2006, 1♂, (W&H), (Willmott, K. R., Aldaz, R.), 12 Nov 2006, 2♂, 1♀, (W&H), 14 Oct 2006, 1♂, (W&H), 31 Oct 2006, 1♂, (W&H); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2050-2100 m, (Aldaz, R.), 18 Oct 2006, 1♀, (W&H); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2100 m, (Willmott, K. R.), 1 Dec 2006, 4♂, (W&H), (Willmott, K. R.), 10 Nov 2006, 1♂, (W&H), 4 Nov 2006, 1♀, (W&H).

Etymology: The name is derived from that of the type locality, San Francisco, and it is treated as a feminine noun in apposition.

Taxonomy and variation: DNA sequence data confirm a close relationship between *P. alida francisca n. ssp.* and *P. alida cosanga n. ssp.* (Fig. 28), the only *P. alida* taxa sampled to date, and *P. alida francisca* is treated as a subspecies of *P. alida* for the same reasons as *P. alida cosanga*. Although the differences between the two east Ecuadorian *P. alida* taxa are relatively slight, they seem to be consistent in the reasonable series of specimens examined and match similar geographic variation in a number of co-mimetic ithomiines, particularly *Pteronymia serrata*, *Godyris hewitsoni* and *Hypomenitis lydia*.

Distribution and natural history: This taxon is known from the eastern Andes of central to southern Ecuador (Morona-Santiago to Zamora-Chinchi) (Fig. 35A), where it occurs in primary cloud forest from 1800-2100 m. The current absence of specimens from Pastaza province, which lies between the distributions of the two east Ecuadorian *P. alida* taxa, might reflect a genuinely disjunct range. Alternatively, the absence of Pastaza specimens could be a result of a lack of easily accessible forest at a suitable elevation in that province, combined with the

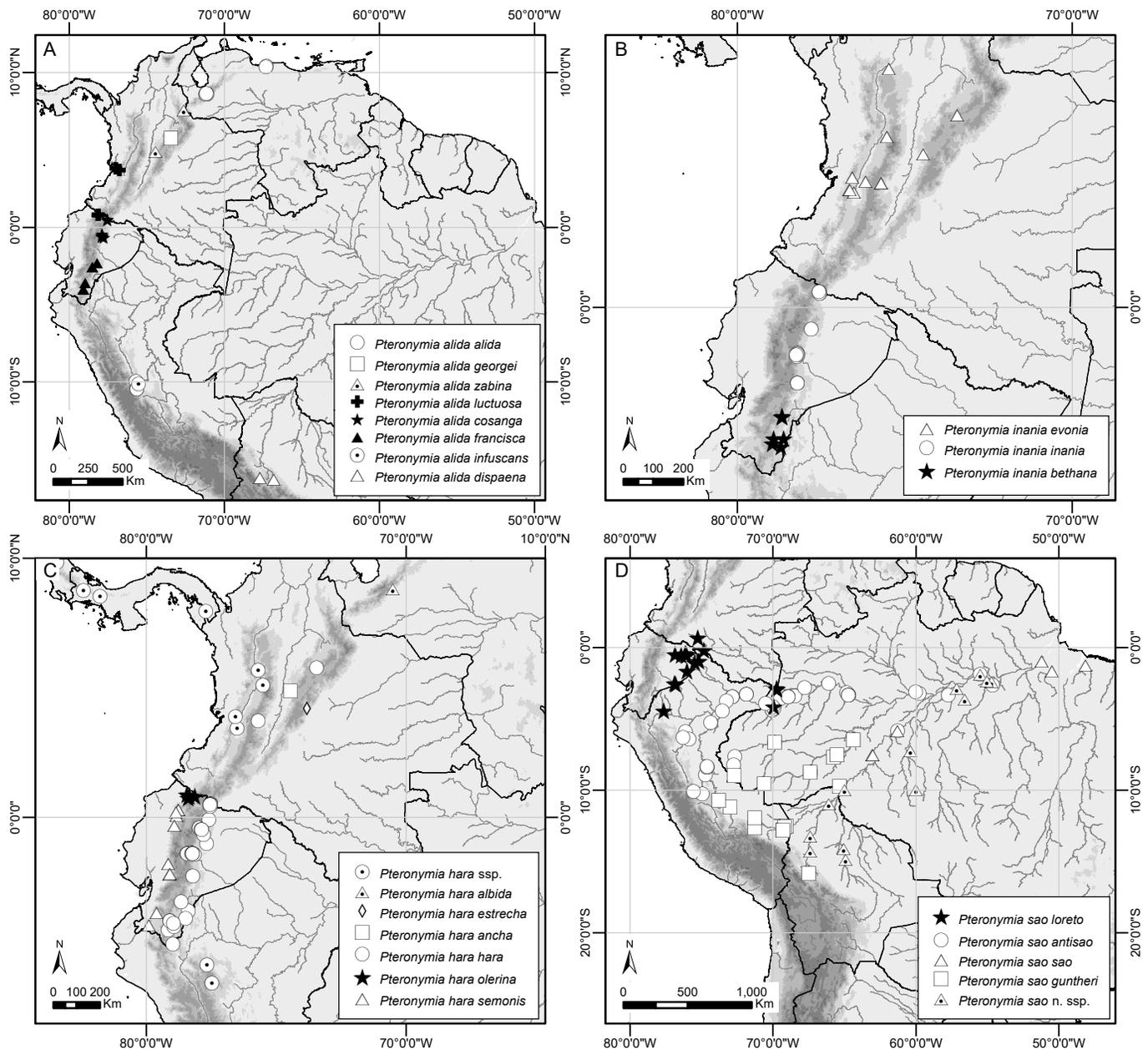


Fig. 35. Distributions of new and related *Pteronymia* taxa: **A**, *Pteronymia alida luctuosa* n. ssp., *Pteronymia alida cosanga* n. ssp., *Pteronymia alida francisca* n. ssp.; **B**, *Pteronymia inania bethana* n. ssp.; **C**, *Pteronymia hara olerina* n. ssp.; **D**, *Pteronymia sao loreto* n. ssp.

behavioral traits of this species, which could be responsible for no Ecuadorian specimens of *P. alida* apparently having been collected prior to 1996. In Ecuador, numerous observations were made of this species at the type locality by Willmott and Elias, using both ground- and rope-based surveys, over a period of several months. The great majority of males were observed from 13:00-16:00 hrs, with most of those seen after 14:00 hrs showing territorial behavior. Males perched in lek sites containing multiple ithomiine species and characterized by tall forest on a relatively shallow slope, near to streams and with a diverse understorey Solanaceae flora. Perching males rested momentarily on leaves, often in sunflecks and small light gaps, but spent more time patrolling areas of c. 5 m in diameter, flying ceaselessly and, for an ithomiine, rapidly. Although a single male was observed perching at 4 m at 12:10

hrs, males later in the afternoon perched higher, from 8-18 m above the ground. Females were observed less frequently but in the same areas as perching males, flying and resting from 1.5-18 m above the ground, again mostly in the afternoon. One female was observed flying 15 m high near a flowering tree at 10:30 hrs, and a female was observed feeding on *Cecropia* Loeffl. (Urticaceae) flower spikes in the canopy on a steep slope at 14:00 hrs. Boyer and Petit found females flying relatively near the ground along a trail up a steep slope through shady primary forest. The taxon is involved in mimicry with numerous sympatric ithomiines, most notably most of those listed in the account of *P. alida cosanga* n. ssp. Two fourth instar larvae were found under leaves of *Solanum nutans* (Solanaceae) in secondary growth near the forest edge, along a wide trail, and reared to adults on that plant. The typically high flight path of

this species, coupled with its tendency to occur only in limited lek sites inside primary forest, have presumably contributed to the rarity of *P. alida* in collections.

Pteronymia inania bethana Willmott & Lamas, **new subspecies**

Figs. 8J,K, 17I-J, 35B

Pteronymia dispaena n. ssp.: Lamas (2004: 187, no. 268e)

Diagnosis and identification: This taxon differs most obviously from the nominate subspecies (Fig. 8L) in the female, which has the translucent area of the HW tinged whitish rather than yellow-brown. The yellow-brown coloring of the VHW margin is more extensive, with the black area reduced to thin rings around the paired white marginal spots. The FW discal cell is only weakly colored, contrasting with the strong yellow-brown tinge of the distal half of the wing, whereas the nominate subspecies has the FW more uniformly colored. Similarly, in the male of *P. inania bethana* n. ssp., the FW discal cell and the HW translucent area are more weakly colored than the yellow-brown distal half of the FW, contrasting with this area.

Description: MALE (Fig. 8J, 17I-J): Forewing mean length 29.5 mm (n=2). *Wings:* as illustrated (Fig. 8J), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head, thorax, abdomen:* as in *Pteronymia alida luctuosa* n. ssp. *Genitalia* (Fig. 17I-J): notable features include broad valvae with symmetrical inner dorsal projections (Fig. 17I,J), aedeagus lightly curving upwards except bent downwards at posterior tip and with flared anterior tip (Fig. 17I).

FEMALE: (Fig. 8K): Forewing length 29 mm (mean 29.5 mm, n=2). *Wings:* as illustrated (Fig. 8K), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♀: **ECUADOR:** *Zamora-Chinchipe:* nr. Paquisha, Chinapintza, [3°55'18"S, 78°36'54"W], 1600 m, (Willmott, K. R.), 29 Sep 1997, (FLMNH, to be deposited in INABIO).

PARATYPES (3♂, 2♀): **Ecuador:** *Morona-Santiago:* km 8.5 Chigiüinda-Gualaquiza rd., El Boliche, [3°15'50"S, 78°39'48"W], 1800 m, (Willmott, K. R.), 10 Oct 2007, 1♂ [FLMNH-MGCL-113492], (FLMNH); km. 9.5 Chigiüinda-Gualaquiza rd., hillside, [3°14'38"S, 78°40'7"W], 1750 m, (Willmott, K. R.), 12 Oct 2007, 1♂ [FLMNH-MGCL-113493]; *Genitalic dissection* KW-21-11], (FLMNH); *Zamora-Chinchipe:* 11 km SW above Zurmi, [4°9'14"S, 78°41'49"W], 1400 m, (Willmott, K. R., J. C. R., J. I. R.), 27 Jun 2014, 1♀ [FLMNH-MGCL-280543], (FLMNH); c. 3 km W Guayguayme Alto, ridge above San Luis, [3°55'14"S, 78°54'49"W], 1470 m, (Willmott, K. R., J. C. R., J. I. R.), 23 Jun 2013, 1♂ [FLMNH-MGCL-157937], (FLMNH); nr. Zamora, Chachacoma, [4°43'30"S, 78°57'36"W], 1600 m, (Willmott, K. R.), 26 Nov 1997, 1♀, (FLMNH).

Etymology: The subspecies name is an anagram of 'thabena', alluding to the close resemblance between the female of this taxon and that of *Pteronymia thabena*.

Taxonomy and variation: This taxon is treated as being conspecific with *P. inania inania* based on the similarly shaped dark FW discocellular bar and paired VHW marginal spots, in addition to the broad, yellow-orange DFW postdiscal band with intense coloring along the basal half of veins M_3 and M_2 in the female, a character unique to *P. inania* and *P. cuneata*. Although the differences in wing pattern between the males are slight, they are striking in the female, and no intermediates are known. Given that the female is the more distinctive sex in this taxon, the holotype is a female specimen.

Lamas (2004) treated this taxon, and others now placed in

P. inania, as conspecific with the Bolivian taxon *Pteronymia (alida) dispaena* (Hewitson, 1876), based on the enlarged white VHW marginal spots, dentate inner edge to the dark HW margin, dark scaling over the FW discocellular veins, and other similarities in wing pattern. However, the absence of other taxa in Peru that plausibly connect Ecuadorian *P. inania* with *P. alida dispaena*, the similarities in male wing shape and venation between *P. alida dispaena* and other *P. alida* taxa (rounded FW, sharply angled HW discocellular veins), and presence in central Peru of other plausible *P. alida* taxa, suggest instead that *dispaena* is best treated as a subspecies of *P. alida*.

Distribution and natural history: This subspecies appears to replace the nominate subspecies (from northern and central Ecuador) in southern Morona-Santiago province (Chigiüinda-Gualaquiza road), and extends south along the east Andean slopes and adjacent Cordillera del Cóndor into Zamora-Chinchipe (Fig. 35B). It has been recorded from 1400-1800 m in selectively logged and old secondary cloud forest, notably on ridge tops. Males were encountered perching with wings closed or half open, from 5-8 m above the ground in tall forest, in sunflecks or small light gaps, on ridge tops and in a diverse ithomiine lek on a steep hillside, from 13:40-15:00 hrs. A female was found flying at the edge of a road and forest on a hillside 2 m above the ground at 13:00 hrs. Females of this taxon are involved in mimicry with the sympatric ithomiines *Pteronymia thabena thabena* and *P. tamina* Haensch, 1909, while the male pattern is less distinctive and perhaps permits a weak mimicry with a number of somewhat similar ithomiine species.

Pteronymia hara olerina Willmott & Lamas, **new subspecies**
Figs. 8M,N, 17K-N, 35C

Pteronymia hara n. ssp.: Lamas (2004: 188, no. 279g)

Diagnosis and identification: *Pteronymia hara olerina* n. ssp. replaces *P. hara semonis* Haensch, 1909 in northwestern Ecuador (Fig. 35C). We have been unable to identify any consistent phenotypic differences between males of these two taxa, but the female of *P. hara olerina* differs from that of *P. hara semonis* (Fig. 8O) by having much broader black margins and FW discocellular bar, more extensive white translucent markings that extend as a continuous postdiscal band on the FW from the costa to cell Cu_2 and fill the HW transparent area, larger white VHW marginal spots, and traces of white marginal spots on the VFW, especially in cell M_2-M_1 . Three subspecies of *P. hara* from northeastern Colombia and western Venezuela are also similar to *P. hara olerina*, but differ as follows: male *P. hara ancha* Neild, 2008, has a yellowish-tinged translucent FW postdiscal band and broader black DFW discocellular bar; male *P. hara estrecha* Neild, 2008, has only a narrow black line of scaling over the DFW discocellular veins; female *P. hara ancha* and *P. hara albida* Neild, 2008, have the HW transparent areas largely colorless (rather than white), and females of all three subspecies have narrower dark wing margins and lack black scaling in the FW apical transparent area.

Pteronymia hara is also very similar to *P. mariannae* Lamas, Willmott & Hall, 2020, but the paired white VHW marginal spots in each cell are a useful identifying character

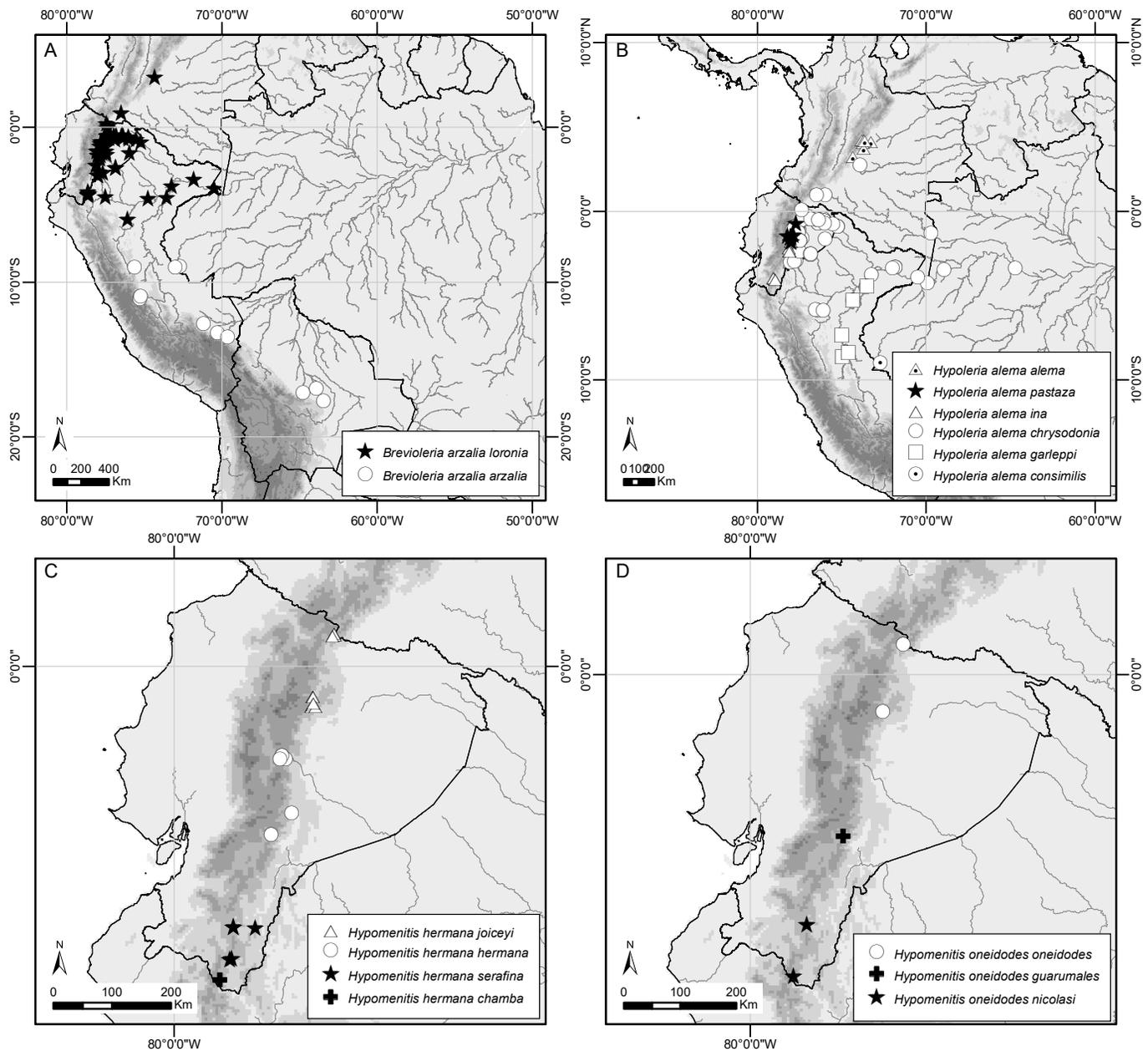


Fig. 36. Distributions of new and related *Brevioleria*, *Hypoleria* and *Hypomenitis* taxa: **A**, *Brevioleria arzalia loronia* n. ssp.; **B**, *Hypoleria alema pastaza* n. ssp.; **C**, *Hypomenitis hermana serafina* n. ssp., *Hypomenitis hermana chamba* n. ssp.; **D**, *Hypomenitis oneidodes guarumales* n. ssp., *Hypomenitis oneidodes nicolasi* n. ssp.

not found in that or most other similar sympatric species (e.g., *Pteronymia zerlina pronuba* (Hewitson, 1870), but see account of *P. alida luctuosa* n. ssp.). The west Colombian species *Pteronymia medellina* Haensch, 1905 is not yet known from western Ecuador but could occur there and would likely also closely resemble *P. hara olerina*; known subspecies of *P. medellina* have the translucent white FW postdiscal band broken in cell Cu_1-M_3 , do not have a uniformly translucent white HW, and have an extra white spot in the VFW apex in cell R_4-R_3 . Similarly, the west Colombian taxon *P. zerlina zerlina* (Hewitson, [1856]) is also very similar and could co-occur with *P. hara olerina*, but can be distinguished by having a single rather than double white VHW marginal spot in Cu_1-M_3 , a white VFW apical spot in R_4-R_3 , and a continuous white translucent

bar in FW cell Cu_2-Cu_1 , rather than two translucent white spots.

Description: MALE (Fig. 8M, 17K-N): Forewing mean length 26.3 mm ($n=4$). **Wings:** as illustrated (Fig. 8M), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. **Head:** eyes brown, bare, with narrow fringe of white scales at base; antennae dark brown; labial palpi white with black terminal segment and black extending slightly laterally onto middle segment, sparse long black hair-like scales ventrally; top of head black with white medial stripe between bases of antennae, two white spots behind eyes, frons black with white lateral stripes. **Thorax:** dorsal surface brown with broad white medial stripe and scattered white lateral scales and long brown hair-like scales, pronotum clothed with long brown hair-like scales with some lateral white long hair-like scales, tegula clothed with long brown hair-like scales becoming white along antero-dorsal edge, ventral surface white except for black where the legs fold, forelegs dark brown with scattered white scales, mid- and hindlegs dark brown with scattered white scales ventrally on femur and dorsally on tibia and tarsus. **Abdomen:** dorsal surface dark brown, ventral surface white.

Genitalia (Fig. 17K-N): notable features include valvae tapering posteriorly with asymmetrical projections in ventral view, strongly asymmetrical inner valva projections with that from right valva forming a double lobe, gnathos narrow and forming two blunt posterior projections (Fig. 17L), aedeagus lightly curving upwards except bent downwards slightly at posterior tip (Fig. 17M) and with strongly flared ('anchor'-like) anterior tip (Fig. 17N).

FEMALE: (Fig. 8N): Forewing length 25 mm (mean 26 mm, n=3). *Wings:* as illustrated (Fig. 8N), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♀: **ECUADOR:** *Carchi:* Reserva Las Golondrinas, N of La Carolina, Santa Rosa, [0°49'38"N,78°7'42"W], 1700 m, (Willmott, K. R., J. I. R., J. C. R.), 16 Jul 2014, [FLMNH-MGCL-280542], (FLMNH, to be deposited in INABIO).

PARATYPES (6♂, 2♀): **Ecuador:** *Carchi:* Lita, ridge east of Río Baboso, [0°53'15"N,78°26'18"W], 850-1000 m, (Hall, J. P. W.), 11 Jul 1994, 1♂ [Genitalic dissection PTERON-4], (FLMNH); *Esmeraldas:* 12 km W Lita, 600 m, (Petit, J.-C.), 23 Nov 2005, 1♂, (JEPE); *Imbabura:* Río Mira, Paramba, [0°49'N,78°21'W], 1110 m, 1♂, (NHMUK); S of Santa Rita de Cachaco, N bank Río Verde, [0°45'19"N,78°22'35"W], 1200 m, (Willmott, K. R.), 4 Aug 1999, 3♂, 2♀, (FLMNH).

Etymology: The name is loosely derived from the generic name *Oleria*, in reference to the similarity of this taxon to locally sympatric *Oleria* species, and it is treated as a feminine noun in apposition.

Taxonomy and variation: *Pteronymia hara olerina n. ssp.* is associated with *P. hara hara* based on both morphology (the male genitalic valvae that are unique among Ithomiini, with tapering posterior tip to the left valva and asymmetrical dorsal inner valva projections) and DNA sequence data. The holotype female from Carchi (LEP-56957) formed a clade with east Ecuadorian *P. hara hara*, showing little differentiation (Fig. 28), whereas *P. hara semonis* from Pichincha formed a distinct clade sister to *P. hara hara*+*P. hara olerina* (De-Silva *et al.*, 2017, as '*P. hara sspnov5*').

Pteronymia hara has had a confused taxonomic history. *Ithomia hara* was described by Hewitson (1877: 88) based on an unspecified number of specimens from "Jima" in southern Ecuador, a general locality for specimens that appear to have been collected on the east Andean slopes along the trail from Cuenca to Gualaquiza. A female syntype is in the NHMUK. Prior to Lamas (2004), the name appears not to have been correctly associated with males, which have generally been treated as '*Pteronymia zabina*' (e.g., D'Abrera, 1984: 252). Haensch (1903: 199) thus described males from central eastern Ecuador (Tungurahua), which differ from Colombian males (where typical *P. alida zabina* occurs) in having the hindwing veins orange brown, as *P. zabina* ab. *brunneata*. Bryk (1937) made this name available (male lectotype in MfN, see Lamas (1994)) and accorded it subspecific rank, but it is in fact a junior subjective synonym (Lamas, 2004) of nominate *P. hara*, which does not show consistent geographic variation throughout eastern Ecuador. As a result of the strong sexual dimorphism and similarity of both sexes to many other ithomiines, a number of taxa have remained undetected or unassociated in collections until recently. Fortunately, however, the unique male genitalia (see above) make *P. hara* taxa readily identifiable on dissection, and the species is now known to range from Costa Rica to southwestern Ecuador, and from Venezuela to Bolivia. Along with a number of undescribed taxa and three recently described Venezuelan subspecies (Neild, 2008), *Pteronymia*

semonis described by Haensch (1905) from southwestern Ecuador (Bolívar, Balzapamba), also proves to be a subspecies of *P. hara* (Willmott & Lamas, unpublished data). The male lectotype of *P. semonis* (in the MfN) is similar to males from throughout western Ecuador, while no females are known from the vicinity of the type locality. Nevertheless, we tentatively assume that females from further north in western Ecuador (southern Imbabura and Pichincha provinces) represent *P. hara semonis*. If they do not, then this female phenotype would at least separate *P. hara olerina n. ssp.* from typical *P. hara semonis* and support the recognition of these as distinct taxa, despite the apparent lack of differences in the male. Given that the female is the distinctive sex, we chose a female specimen as the holotype for this new taxon.

Distribution and natural history: This taxon is known from western Ecuador (Carchi and Esmeraldas to northern Imbabura) (Fig. 35C) from approximately 600-1700 m in primary to secondary cloud forest. The taxon is local and uncommon, and males, and unusually females, were found feeding on white Asteraceae flowers in small, overgrown fields and along forest edges, from 09:30-11:30 hrs. At Santa Rosa, Carchi, a female was found flying with and closely resembling two *Oleria* species, *O. bifurcata* and *O. fumata richardina*, and it is presumably involved in mimicry with these taxa as well as *P. alida luctuosa n. ssp.* Notably, none of these three species is known further south in western Ecuador, where *P. hara semonis* females instead have a simpler, white-banded FW pattern that closely resembles *Pteronymia mariannae*, which occurs only from central Ecuador southwards and is thus not sympatric with *P. hara olerina n. ssp.*

Pteronymia sao loreto Lamas & Willmott, **new subspecies**
Figs. 8P,Q, 17O-P, 35D

Pteronymia sao n. ssp.: Lamas (2004: 188, no. 293d)

Pteronymia obscurata [sic] *lilla:* Piñas (2004: 50, fig. 377), misidentification

Pteronymia sao ssp.: Elias *et al.* (2007: supplementary information)

Pteronymia sao: Chazot *et al.* (2014b)

Pteronymia sao sspnov1: De-Silva *et al.* (2017: Table S1)

Diagnosis and identification: This subspecies is distinguished from the similar *P. sao guntheri* Lamas, 1985 (Fig. 8R) (SE Peru) by the narrower, more elongate and more translucent yellow DFW postdiscal band, and by the translucent yellow on the HW extending less distally. *Pteronymia sao sao* (Hübner, [1813]) and *P. sao antisao* (Bates, 1862) have extensive orange scaling along the DFW medial vein and into the adjacent dark anal margin border, and along the DHW veins and base of DFW vein Cu₁, as well as an orange tinge to the HW translucent areas in cells Cu₂-M₃. The taxon is similar to several other dircennines within its range, particularly *E. arcadia n. sp.* (Fig. 7M,N), but it may be distinguished by its broader, rounder wings and orange scaling at the base of the DFW and (in females) the tornal margin of the DHW, among other more subtle characters.

Description: MALE (Fig. 8P, 17O-P): Forewing length 26 mm (mean 26 mm, n=2). *Wings:* as illustrated (Fig. 8P), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes brown, bare, with fringe of white scales at base; antennae dark brown; labial palpi white except for black terminal segment; top of head with white medial stripe between bases

of antennae, two white spots behind eyes, frons broadly dark brown in middle with white at edges. *Thorax*: dorsal surface dark brown with pale yellowish white medial stripe, sparse pale yellow scaling laterally, tegula pale yellow with sparse black scaling, pronotum dark brown dorsally and yellow laterally, ventral surface between legs white then yellow laterally except for dark brown where legs fold, legs dark brown with scattered white scaling which becomes stronger ventrally. *Abdomen*: dorsal surface dark brown, ventral surface pale yellow. *Genitalia* (Fig. 17O-P): notable features include triangular valvae, gnathos absent, aedeagus with small dorsal 'tooth' at posterior tip, long, curving uncus (Fig. 17O), broad lobed inner dorsal projections of valvae (Fig. 17P), vinculum and valvae somewhat membranous and weakly sclerotized.

FEMALE: (Fig. 8Q): Forewing mean length 24.4 mm (n=5). *Wings*: as illustrated (Fig. 8Q), lacking DHW costal androconial scales. *Head, thorax, abdomen*: similar to male.

Types: HOLOTYPE ♂: **PERU:** Loreto: Castaña, [0°48.22'S, 75°14.40'W], 150 m, (Lamas, G.), 22 Oct 1993, (MUSM).

PARATYPES (59♂, 24♀): **Colombia:** Amazonas: Río Cotuhé, [2°53'S, 69°44'W], Sep, 1♂, (AMNH); Río Tacana, [4°9'37"S, 69°56'11"W], Oct, 1♂, (AMNH); Tarapacá, [2°52'S, 69°44'W], Sep, 1♂, (AMNH); **Caquetá:** Río Ortegua, [0°43'N, 75°16'W], Aug, 7♂, (AMNH); **Putumayo:** lower Río Putumayo, Sep, 4♂, (AMNH); Puerto Leguizamo, Cauca, [0°9'S, 74°49'W], Nov Dec, 24♂, 6♀, (AMNH). **Ecuador:** *Sucumbios:* Río Pañayacu, Laguna de Pañacocha, [0°23'53"S, 76°7'40"W], 250 m, (Willmott, K. R.), 12-14 Oct 1997, 2♂ [Genitalia dissection KW-21-12], 2♀, (FLMNH); *Orellana:* Río Manduro, Río Napo, Yarina, [0°28'14"S, 76°50'W], 300 m, (Gallice, G.), 12 Sep 2010, 1♂ [YL749], (FLMNH); Río Napo, Boca del Río Añangu, [0°31'43"S, 76°23'41"W], 220-300 m, (Willmott, K. R.), 26 Oct 2005, 1♂, (EUIEB), 28 Oct 2005, 1♂, (EUIEB), (Elias, M.), 1 Nov 2005, 1♂, 2♀, (EUIEB), 1♂ [FLMNH-MGCL-ECD-97], 1♂ [FLMNH-MGCL-ECD-98], 1♀ [FLMNH-MGCL-ECD-100], 1♀ [FLMNH-MGCL-ECD-101], 1♀ [FLMNH-MGCL-ECD-102], 1♀ [FLMNH-MGCL-ECD-103], 1♀ [FLMNH-MGCL-ECD-144], 1♀ [FLMNH-MGCL-ECD-145], (FLMNH), 1♀ [FLMNH-MGCL-ECD-99], (INABIO), 18 Nov 2005, 1♂, (EUIEB); Río Napo, Río Yuturi, lodge trail, [0°32'53"S, 76°2'W], 250 m, (Willmott, K. R.), 19 Nov 2003, 1♂, (FLMNH); *Pastaza:* Río Capahuari, Kapawi Lodge, [2°32'30"S, 76°51'32"W], 250 m, (Willmott, K. R., Hall, J. P. W.), 21, 22, 27 Jul 2009, 1♀ [FLMNH-MGCL-144427], (FLMNH); Río Curaray, Lorocachi, [1°37'15"S, 75°59'30"W], 250 m, (Willmott, K. R.), 28 Jul 1998, 2♀, (FLMNH); *Morona-Santiago:* Río Pastaza, Wachirpas airfield, [2°34'20"S, 76°48'12"W], 250 m, (Willmott, K. R., Hall, J. P. W.), 20, 27 Jul 2009, 1♂ [FLMNH-MGCL-144426], (FLMNH). **Peru:** *Amazonas:* Río Santiago, [4°26'S, 77°38'W], Nov Dec, 1♂, 3♀, (AMNH); upper Río Marañón, 1♂, (AMNH); *Loreto:* same data as HT, 30 Oct 1993, 1♀, (MUSM); *Arcadia:* [0°59.37'S, 75°18.55'W], 150 m, (Robbins, R. K.), 31 Oct 1993, 1♂, (MUSM); Río Putumayo, Soplin Vargas, [0°23'S, 74°40'W], 200 m, (Ramírez, J. J., Lequerica, H.), 20 May, Dec 2010, 6♂, (MUSM); Río Napo, Pantoja, [0°58'S, 75°10'W], 190 m, M. Büche Nov 2000, 1♂, (FAVI).

Other records: **Ecuador:** *Sucumbios:* Río Napo, Pañacocha, [0°26'11"S, 76°4'W], 250 m, (Willmott, K. R., Hall, J. P. W.), 15, 16, 20 Oct 1997, (W&H); *Orellana:* Río Napo, Río Yuturi, lodge trail, [0°32'53"S, 76°2'W], 250 m, (Willmott, K. R., Hall, J. P. W.), 17-19 Oct 1997, (sight record) (W&H), 21-22 Jul 1998, (sight record) (W&H); Río Napo, Río Yuturi, Río Manduro trail, [0°33'29"S, 76°2'39"W], 250 m, (Willmott, K. R.), 20 Nov 2003, (sight record) (W&H).

Etymology: This taxon is named for Loreto department in Peru, which occupies a central position in the distribution of this taxon. It is treated as a masculine noun in apposition.

Taxonomy and variation: This taxon is treated as a subspecies of *P. sao* based on its distinctive wing shape (broad and rounded), wing pattern (narrow, tapering translucent yellow DFW postdiscal band, narrow, paired white VHW marginal spots, and variably present orange DHW submarginal line), and yellow ventral abdomen. This combination of characters occurs in no other *Pteronymia*. The genitalia of both sexes are also highly distinctive, with, among other features, absence of male gnathos occurring elsewhere in *Pteronymia* only in *P. latilla* (Hewitson, [1855]), *P. obscuratus* (Fabricius, 1793) and *P. tucuna* (Bates, 1862). DNA sequence data show little

divergence between *P. sao loreto* n. ssp. and *P. sao antisao* (Peru, Ucayali) (Fig. 28; see also De-Silva et al., 2017). There is slight variation in the extent of orange on the dorsal surface of females, which may form a longer orange HW submarginal line than that in the figured specimen, and may extend along the FW medial vein.

Distribution and natural history: This subspecies occupies a restricted region in the western Amazon, in Colombia (Amazonas, Caquetá, Putumayo), Ecuador (Orellana, Pastaza, Morona Santiago, and Sucumbios) and Peru (Amazonas, Loreto) (Fig. 35D). It occurs in relatively undisturbed flat lowland rain forest below 400 m, usually in the vicinity of swamp forest or the edges of large rivers or lakes. Both sexes fly in forest understorey and at the forest edge, typically within 1 m of the ground, from 09:00-15:30 hrs. In Ecuador, caterpillars were found feeding on *Solanum sessile* (Solanaceae) (identified by S. Knapp) growing in secondary growth near the bank of the Río Napo (Willmott & Elias, unpublished data), and on an unidentified *Solanum* species growing in water at the edge of large rivers (Willmott & J. I. Robinson Willmott, unpublished data).

Brevioleria arzalia loria Lamas & Willmott, new subspecies

Figs. 9A,B, 18A-D, 36A

Hypoleria orolina Hewitson: Haensch (1903: 204; 1909-1910: 159, pl. 40, fig. g), misidentification

Brevioleria arzalia n. ssp.: Lamas (2004: 190, no. 332b)

Brevioleria arzalia ssp.: Willmott & Mallet (2004: Appendix A); Elias et al. (2007: supplementary information)

Hypoleria orolina: Piñas (2004: 56, fig. 439, 440)

Brevioleria arzalia ssp. n.: Whinnett et al. (2005, Fig. 2, Table 2)

Brevioleria arzalia: Elias et al. (2008: S1); Chazot et al. (2014b); Brower et al. (2014: Table 1); Willmott et al. (2017)

Brevioleria arzalia sspn: Chazot et al. (2016a)

Diagnosis and identification: This taxon is clearly very distinct from the nominate subspecies (Peru, San Martín, to Bolivia and west Brazil), which has a broad white FW postdiscal band and lacks any dorsal orange coloration. However, it is much more similar to *Brevioleria aelia oncidia* (Bates, 1862) (Fig. 9C) and *B. aelia orolina* (Hewitson, [1861]), as which it is usually misidentified in the literature (e.g., Haensch, 1903) and collections. Both sexes of *B. arzalia loria* n. ssp. can be distinguished from *B. aelia* (Hewitson, 1852) taxa by the following characters: *B. arzalia* (Hewitson, 1876) has slightly more elongate wings, with the HW appearing relatively smaller in comparison with the FW in *B. aelia* than in *B. arzalia*; from its origin, vein Cu₁ on the FW of *B. arzalia* gradually diverges from vein M₃, whereas in *B. aelia* it cuts back sharply towards the tornus; in *B. arzalia*, the translucent white marking in FW cell Cu₂-Cu₁ forms an elongate dash, extending across most of the cell, whereas in *B. aelia* it is reduced to a slightly oval spot in the middle of the cell. *Brevioleria arzalia loria* further differs from *B. aelia oncidia*, with which it is partially sympatric, in having the translucent white on the HW more or less restricted to cell M₃-M₂, whereas in *B. aelia oncidia* it extends as a band across the middle of the transparent area, coloring the medial vein whitish. Male *B. aelia orolina* is similar to *B. aelia oncidia*, but the female of the latter has a broad translucent white discal

band that is absent in the former.

Brevioleria arzalia lronia is also sympatric with a number of other co-mimetic ithomiines, of which *Brevioleria seba oculata* (Haensch, 1903), *Pseudoscada florula aureola* (Bates, 1862) and *Hypoleria alema chrysodonia* (Bates, 1862) are perhaps the most similar. The first two can be distinguished by having translucent white spots between the dark FW discocellular bar and distal orange area, and in the FW tornus, respectively, while the third of these taxa lacks white apical spots on the VFW, among other differences.

Description: MALE (Fig. 9A, 18A-D): Forewing length 23 mm (mean 21.8 mm, n=5). *Wings:* as illustrated (Fig. 9A), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes brown, bare, with narrow fringe of white scales at base; antennae dark brown with scattered white scaling ventrally near base; labial palpi white except for black terminal segment and black continuing ventrally and laterally to middle of palpi; top of head black with white medial dash between bases of antennae, two white spots behind eyes, frons black with white lateral stripes. *Thorax:* dorsal surface dark brown with narrow white medial stripe and scattered white lateral scales, pronotum dark brown dorsally and white laterally, tegula dark brown, ventral surface white except for black where the legs fold, legs dark brown with scattered white scales. *Abdomen:* dorsal surface dark brown, ventral surface white. *Genitalia* (Fig. 18A-D): notable features include broad, 'scoop'-like gnathos, slender, elongate aedeagus (Fig. 18A).

FEMALE: (Fig. 9B): Forewing mean length 22 mm (n=2). *Wings:* as illustrated (Fig. 9B), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **PERU:** Loreto: Arcadia, [0°59.37'S, 75°18.55'W], 150 m, (Lamas, G.), 1 Nov 1993, (MUSM).

PARATYPES (140♂, 103♀): **Colombia:** Putumayo: Villa Garzón, [1°0'N, 76°30'W], 300 m, (Mallet, J.), Sep, 1♂, 1♀, (NHMUK). **Ecuador:** *Sucumbios:* km 10.5 Lumbaqui-Baeza rd., [0°0'15"S, 77°25'W], 700-850 m, (Willmott, K. R., Hall, J. P. W.), 22 Feb 2001, 1♂, (FLMNH); La Bonita-Lumbaqui rd., El Recodo, [0°15'20"N, 77°28'41"W], 600 m, (Aldaz, R.), 18 Dec 2001, 1♂, (FLMNH); *Napo:* Archidona, [0°55'S, 77°48'W], 500 m, (Haensch, R.), 1♂, 2♀, (NHMUK); E Archidona, Mariposa, [0°54'30"S, 77°47'8"W], (Elias, M., Toporov, S., Santaacruz, P.), 2010, 3♂, 1♀, (INABIO), 10 Feb 2010, 1♂, 1♀, (FLMNH), 21 Feb 2010, 5♂, 1♀, (MNHN), 22 Feb 2010, 3♀, (MNHN); km 30 Tena-Puyo rd., Satzayacu, [1°12'35"S, 77°51'38"W], 700 m, (Willmott, K. R., Hall, J. P. W.), 26 Apr 1995, 1♂, (FLMNH); Río Napo, Puerto Napo-Ahuano rd., Jatun Sacha, [1°3'S, 77°35'9"W], 400-450 m, (Murray, D.), Mar 1990, 1♀, (NHMUK); (Beccaloni, G. W., Brachi, J. A.), Jan 1994, 1♂, (NHMUK); (Beccaloni, G. W.), Oct 1991, 1♂, (NHMUK); (Gallice, G.), 25 Aug 2010, 1♂ [JS198], (FLMNH), 26 Aug 2010, 1♂ [JS278], 1♂ [JS281], (INABIO); Río Anzu, [1°04'S, 77°48'W], 700 m, (Velástegui, S. E.), 8, 28 Aug 1969, 1♂, 1♀, (MUSM); Tena-Puyo rd., El Capricho, [1°11'14"S, 77°49'53"W], 800 m, (Hall, J. P. W., Willmott, K. R.), 26 Oct 1996, 1♀, (MUSM); *Orellana:* Coca-Tiguino rd., Río Tiputini, [0°44'3"S, 76°53'31"W], 300 m, (Willmott, K. R., Hall, J. P. W.), 20 Sep 1996, 1♂, (FLMNH); km 52 Coca-Loreto rd., [0°39'41"S, 77°18'35"W], 430 m, (Willmott, K. R., Hall, J. P. W.), 7 Mar 1995, 1♂, (FLMNH); km 52 Coca-Loreto rd., Altamira, [0°39'41"S, 77°18'35"W], 300 m, (Willmott, K. R., Hall, J. P. W.), 7 Mar 1995, 1♂, (FLMNH); Laguna Añangu, Napo Wildlife Center, Napo trail, [0°30'35"S, 76°26'13"W], 250 m, (Willmott, K. R.), 16 Oct 2005, 1♂ [FLMNH-MGCL-ECD-333], (FLMNH), 17 Oct 2005, 1♀ [FLMNH-MGCL-ECD-334], 1♀ [FLMNH-MGCL-ECD-337], (FLMNH), 18 Oct 2005, 1♀, (EUIEB), 20 Oct 2005, 1♂ [FLMNH-MGCL-ECD-335], 1♂ [FLMNH-MGCL-ECD-336], 1♀ [FLMNH-MGCL-ECD-338], (FLMNH); Laguna Añangu, Napo Wildlife Center, Tiputini trail, [0°31'46"S, 76°25'11"W], 250 m, (Willmott, K. R.), 11 Oct 2005, 1♂, (EUIEB); Reserva Biológica del Río Bigal, [0°29'59"S, 77°24'6"W], 543 m, (Radford, J.), 24 Jul 2010, 1♀ [N122], (INABIO) (CULEPEX Expedition, 2010); Reserva Biológica del Río Bigal, [0°31'17"S, 77°25'10"W], 851 m, (Hartley, E.), 22 Jul 2010, 1♀ [N69], (FLMNH) (CULEPEX Expedition, 2010), 1♂ [N68], (INABIO) (CULEPEX Expedition, 2010); Río Manduro, Río Napo, Yarina, [0°28'14"S, 76°50'W], 300 m, (Gallice, G.), 10 Sep 2010, 1♂ [YL687], (INABIO), 15 Sep 2010, 1♀ [YL837], (FLMNH), 1♀ [YL836], (INABIO), 16 Sep 2010, 1♂ [YL852], 1♂ [YL873], (INABIO), 2 Sep 2010, 1♂ [YL465],

(FLMNH), 23 Sep 2010, 1♂ [YL1071], (FLMNH), 1♂ [YL1068], (INABIO), 24 Sep 2010, 1♀ [YL1123], (FLMNH), 1♀ [YL1097], (INABIO), 25 Sep 2010, 1♂ [YL1157], (INABIO), 26 Sep 2010, 1♂ [YL1257], (INABIO), 6 Sep 2010, 1♂ [YL550], 1♀ [YL541], (INABIO); Río Napo, Añangu community, [0°29'37"S, 76°25'11"W], 230 m, (Elias, M.), 3 Dec 2005, 1♂, (EUIEB); Río Napo, Boca del Río Añangu, [0°31'43"S, 76°23'41"W], 220-300 m, (Willmott, K. R.), 27 Oct 2005, 1♀, (EUIEB), 6 Dec 2005, 1♂, (EUIEB), (Elias, M.), 18 Nov 2005, 1♂, (EUIEB), 3 Dec 2005, 1♂, (EUIEB); Río Napo, Sacha Lodge, [0°28'14"S, 76°27'33"W], 240 m, (Gallice, G.), 15 Oct 2010, 1♂ [SL1614], (INABIO), 16 Oct 2010, 1♀ [SL1637], (INABIO), 20 Oct 2010, 1♂ [SL1723], 1♂ [SL1744], 1♀ [SL1722], (INABIO), 21 Oct 2010, 1♂ [SL1804], 1♀ [SL1783], (INABIO), 24 Oct 2010, 1♀ [SL1948], (FLMNH), 26 Oct 2010, 1♂ [SL2004], 1♀ [SL2002], (INABIO), 27 Oct 2010, 1♂ [SL2079], (INABIO); Río Tiputini, Tiputini Biodiversity Station, [0°42'12"S, 76°0'30"W], 200-250 m, (Gallice, G.), 9 Dec 2010, 1♂ [TB3362], (INABIO); Río Tiputini, Tiputini Biodiversity Station, [0°42'12"S, 76°0'30"W], 300 m, (Willmott, K. R., Hall, J. P. W.), 12-14 Aug 1999, 1♂, (FLMNH), (Melo, P.), May-Aug 2002, 2♂, (FLMNH); Río Tiputini, via Auca, Estación Científica Yasuni, [0°40'27"S, 76°23'49"W], 220-250 m, (Gallice, G.), 23 Jul 2009, 1♂ [FLMNH-MGCL-153442], (FLMNH), 4 Aug 2009, 1♂ [FLMNH-MGCL-153443], (FLMNH), (Gallice, G.), 28 Nov 2010, 1♂ [YN3034], (INABIO), (Willmott, J. C. R., J. I. R.), 5 Jul 2014 [FLMNH-MGCL-195770], (FLMNH); Estación Científica Yasuni, [0°40'S, 76°24'W], 250 m, (Lamas, G., Vitoria, A., Grados, J.), 2-3 Dec 2004, 24-25 Nov 2005, 9♂, (MUSM); *Pastaza:* 10.5 km SW Palora, [1°45'20"S, 78°1'49"W], 1000 m, (Hall, J. P. W., Willmott, K. R., J. C. R., J. I. R.), 2 Aug 2015, 2♂, (INABIO); Nushiño, [1°14'S, 77°34'30"W], (Simson, A.), 1♀, (NHMUK); Río Bobonaza, Canelos, [1°35'S, 77°45'W], 600-750 m, (Buckley, C.), 1♀, (NHMUK); Río Bobonaza, Canelos, [1°35'S, 77°45'W], 630 m, (Palmer, M. G.), 1♀, (NHMUK); Río Bobonaza, Sarayacu, [1°44'S, 77°29'W], 200 m, (Buckley, C.), 1879, 1♂, (NHMUK); Río Capahuari, Kapawi Lodge, [2°32'30"S, 76°51'32"W], 250 m, (Willmott, K. R., Hall, J. P. W.), 21, 22, 27 Jul 2009, 1♂ [FLMNH-MGCL-144535], 1♂ [FLMNH-MGCL-144536], 1♂ [FLMNH-MGCL-144539], 1♂ [FLMNH-MGCL-144543], 1♀ [FLMNH-MGCL-144530], 1♀ [FLMNH-MGCL-144531], 1♀ [FLMNH-MGCL-144537], 1♀ [FLMNH-MGCL-144540], (FLMNH); Río Curaray, Curaray, [1°29'S, 77°31'W], 250 m, (OUM), (Simson, A.), 1♂, (OUM); Río Pindo Grande, Shell, [1°29'40"S, 78°3'40"W], 1050 m, (Willmott, K. R., Hall, J. P. W.), 2 Oct 1996, 1♂ [Genitalic dissection KW-21-13], (FLMNH). Sarayacu, [1°44'S, 77°29'W], 500-700 m, (Velástegui, S. E.), 13 Feb 1967, 21 Jul 1969, 1♂, 1♀, (MUSM); *Morona-Santiago:* forest nr. San José de Morona, [2°53'17"S, 77°41'52"W], 215 m, (Gallice, G.), 6 Jun 2009, 1♀ [FLMNH-MGCL-153444], (FLMNH); Río Pastaza, playa 2 km W Capitán Chiriboga, [2°33'43"S, 76°51'31"W], 250 m, (Willmott, K. R., Hall, J. P. W.), 22, 23, 25 Jul 2009, 1♀ [FLMNH-MGCL-144533], 1♀ [FLMNH-MGCL-144538], (FLMNH); Río Santiago, Santiago, [3°21'11"S, 78°2'W], 300 m, (Aldaz, R.), 1♂ [FLMNH-MGCL-150907], (FLMNH); 'Sigsig-Gualaquiza trail, Chigüinda' - (error), (Villagomez), 1♀, (NHMUK); Yaupi-Yaapi trail, [2°49'58"S, 77°56'28"W], 320-340 m, (Gallice, G.), 15 Jun 2009, 1♀ [FLMNH-MGCL-153445], (FLMNH); *Zamora-Chinchipe:* lower Río Numpatakaima, c. 3 km S Shaime, [4°21'S, 78°39'28"W], 900 m, (Willmott, K. R., Hall, J. P. W.), 31 Jul 2009, 1♂ [FLMNH-MGCL-144534], 1♂ [FLMNH-MGCL-144542], 1♀ [FLMNH-MGCL-144532], (FLMNH); rd. Zumbi-Yankuam, Quebrada Numbame, [4°9'5"S, 78°38'40"W], (Willmott, K. R., Hall, J. P. W.), 29 Jul 2009, 1♂ [FLMNH-MGCL-144541], (FLMNH); Río Nangaritzta, 4 km S Zurmi, Reserva Maycú, [4°12'45"S, 78°38'36"W], 850 m, (Willmott, K. R., J. C. R., J. I. R.), 28 Jun 2014, 1♂ [FLMNH-MGCL-280546], 1♀ [FLMNH-MGCL-280547], (FLMNH), 7♂, (INABIO); *Not located:* 'Ecuador', 3♂, 6♀, (NHMUK). **Peru:** *Amazonas:* Cordillera del Cóndor, Quebrada Chinganasa (Quebrada Ponce), [3°46'S, 78°20'W], 680 m, (Grados, J., Asenjo, A.), 11 Nov 2003, 1♀, (MUSM); Cordillera del Cóndor, Quebrada Kegkem, [3°38'S, 78°18'W], 700 m, (Grados, J., Asenjo, A.), 19-20 Nov 2003, 2♂, 2♀, (MUSM); Cerro Unki, km 44 Sarameriza-Chiriaco, [4°37'S, 77°40'W], 790 m, (Mallet, J., Eeley, H.), 10 Jun 1986, 2♂, (MUSM); nr. Abra Wawajin, [5°18'S, 78°23'W], 750-850 m, (Chang, F.), 16 Nov 1996, 1♀, (MUSM); *Loreto:* 'Cavallo Cocha' [= Caballicocho], [3°55'S, 70°31'W], 90 m, (Mathan, M. de), 1♂, (NHMUK); Borja, [4°28'S, 77°32'W], 300 m, (Pratt, A. & E.), 1♀, (NHMUK), 210-250 m, (Lamas, G.), 14 Feb 1978, 1♂, (MUSM); Río Tigre, San Jacinto, [2°19'S, 75°52'W], 200 m, (Debinski, D.), 18 Apr 1993, 1♀, (MUSM); Río Marañón, José Olaya, [4°34'S, 73°45'W], 120 m, (Büche, M.), Mar 1993, 4♂, 2♀, (MUSM); Yanamono, 80 km E Iquitos, [3°27'S, 72°51'W], 120 m, 24-27 Jul 1984, (Lamas, G., Mallet, J.), 2♂, 2♀, (MUSM); Río Samiria, Estación Biológica Pithecia,

[5°11'S,74°42'W], 180 m, (Pacheco, V.), 6 Nov 1980, 1♀, (MUSM); km 15 Iquitos-Nauta, [3°57'S,73°22'W], 120 m, (Callegari, C.), 9 Sep 1995, 1♀, (MUSM); Bombonaje Lodge, [3°27'S,72°54'W], 116-120 m, (Quental, T.), 14 Mar 2005, 3♂, (MUSM); Río Momón, San Juan de Poli, [3°37'S,73°25'W], 130 m, (Ramírez, J. J.), 2♂, (MUSM); Picuroyacu, [3°37'S,73°16'W], 115 m, (Lamas, G.), 19 Oct 2015, 2♂, (MUSM); Iquitos, [3°45'S,73°15'W], 100 m, (Mathan, M. de), 2♂, (NHMUK), (Lathy, P.), 4♂, 6♀, (NHMUK); lower Río Napo, 2♀, (NHMUK); Nauta, [4°30'S,73°35'W], 1♀, (OUM); Nauta, [4°30'S,73°35'W], 100 m, 1♀, (NHMUK); Pebas, [3°19'S,71°51'W], 120 m, 1♂, (NHMUK), (Mathan, M. de), 3♂, (NHMUK), 1880, 9♂, 6♀, (NHMUK), Nov 1906, 5♂, 6♀, (NHMUK); Yurimaguas, [5°54'S,76°6'W], 120 m, (Bartlett, E.), 1♂, (NHMUK); same data as HT, 7, 10 Nov 1993, 2♂, (MUSM); Castaña, [0°48.22'S,75°14.40'W], 150 m, (Robbins, R. K.), 150 m, 21 Oct 1993, 1♂, (MUSM); Saramiriza, [4°36'18.01"S,77°21'51.36"W], 141 m, (Pérez, L.), 3 Aug 2018, 1♀, (MUSM); *San Martín*: 'Chambireyacu' [=Río Chambirayacu], [5°54'S,76°14'W], 120 m, (Mathan, M. de), Jun-Aug 1885, 1♂, 5♀, (NHMUK); Tarapoto, [6°29'S,76°22'W], 350 m, 1♀, (MUSM); Achinamiza, [6°25'S,75°51'W], 200 m, (Mallet, J.), 20 Dec 1986, 1♂, (MUSM); Pongo de Aguirre, [6°27'S,75°54'W], 200 m, (Mallet, J.), 21-22 Dec 1986, 3♂, (MUSM); km 7 Pongo del Cainarache-Barranquita, [6°18'S,76°14'W], 250 m, (Joron, M.), 4 Dec 1998, 1♀, (MUSM); Parque Nacional Cordillera Azul, Laguna del Mundo Perdido, 6°45-46'S,75°52'W], 450 m, (Simpson, F.), 11 Sep 2005, 2♀, (MUSM); *Not located*: Río Marañón, 1913, 1♂, 1♀, (NHMUK); 'Río Huallaga', (Bartlett, E.), 1♀, (NHMUK). **Country unknown**: *Not located*: 'Amazón', 1♀ ['Presented 1896 by G. C. Griffiths'], (OUM); 'Amazons', (OUM); no data, 2♂, 1♀, (NHMUK).

Other records: **Ecuador:** *Morona-Santiago*: km 72 Puyo-Macas rd., Río Shangaime, [1°57'15"S,77°51'25"W], 800 m, (Willmott, K. R.), 8 Dec 1996, (sight record) (W&H); nr. Macas, San Luis, [2°23'12"S,78°79'W], 950 m, (Willmott, K. R.), 31 Oct 1996, (sight record) (W&H); *Napo*: Aguano, [1°4'S,77°33'W], 400 m, Jan Apr, (collection unknown) (Haensch, 1903); Archidona, [0°55'S,77°48'W], 550 m, (collection unknown) (Haensch, 1903); E Archidona, Coral, [0°56'11"S,77°45'31"W], (Elias, M., Toporov, S., Santacruz, P.), 20 Feb 2010, 1♀, (sight record) (Elias, M., unpublished data); E Archidona, Mariposa, [0°54'30"S,77°47'8"W], (Elias, M., Toporov, S., Santacruz, P.), 10 Feb 2010, 1♀, (sight record) (Elias, M., unpublished data), 20 Mar 2010, 6♂, 2♀, (sight record) (Elias, M., unpublished data), 21 Feb 2010, 8♂, (sight record) (Elias, M., unpublished data), 23 Feb 2010, 3♀, (sight record) (Elias, M., unpublished data); nr. Misahuallí, Pununo, [1°11'18"S,77°40'12"W], 400 m, (Hall, J. P. W.), 05 May 1994, (sight record) (W&H); Río Hollín, nr. Archidona, 'Hollín2', [0°55'46"S,77°44'24"W], (Elias, M., Toporov, S., Santacruz, P.), 21 Mar 2010, 1♀, (sight record) (Elias, M., unpublished data); Río Misahuallí, Tena, [0°59'28"S,77°49'6"W], 550 m, (Willmott, K. R., Hall, J. P. W.), 02 Aug 1994, (sight record) (W&H); Río Napo, Puerto Napo-Ahuano rd., Jatun Sacha, [1°3'S,77°35'9"W], 400-450 m, (Beccaloni, G. W.), (collection unknown) (Beccaloni, 1996); Río Napo, Puerto Napo-Ahuano rd., Jatun Sacha, [1°3'S,77°35'9"W], 450 m, (Murray, D.), 6 May 1991, 1 specimen [INABIO-TABDP-20354], (INABIO); Tena-Puyo rd., El Capricho, [1°11'14"S,77°49'53"W], 800 m, (Willmott, K. R.), 26 Oct 1996, (sight record) (W&H); *Orellana*: Laguna Añangu, Napo Wildlife Center, Napo trail, [0°30'35"S,76°26'13"W], 250 m, (Elias, M.), 21 Oct 2005, 1♂, (W&H); nr. Coca, [0°28'S,76°59'W], 300 m, (collection unknown) (Haensch, 1903); Río Manduro, Río Napo, Yarina, [0°28'14"S,76°50'W], 300 m, (Gallice, G.), 23 Sep 2010, 1 specimen, (sight record) (Gallice, G., unpublished data), 6 Sep 2010, 1 specimen, (sight record) (Gallice, G., unpublished data); Río Napo, Añangu community, [0°29'37"S,76°25'11"W], 230 m, (Elias, M.), 10 Dec 2005, 1♂, (W&H); Río Napo, Boca del Río Añangu, [0°31'43"S,76°23'41"W], 220-300 m, (Willmott, K. R.), 22 Nov 2005, 1♀, (W&H), 23 Nov 2005, 1♂, (W&H), 26 Oct 2005, 1♂, (W&H), 30 Oct 2005, 1♂, (W&H), 4 Nov 2005, 1♂, (W&H); Río Napo, Río Yuturi, Río Manduro trail, [0°33'29"S,76°23'39"W], 250 m, (Willmott, K. R.), 20 Nov 2003, (sight record) (W&H); Río Napo, Sacha Lodge, [0°28'14"S,76°27'33"W], 200 m, (Hall, J. P. W.), 17,18 Feb 2001, (sight record) (W&H); Río Napo, Sacha Lodge, [0°28'14"S,76°27'33"W], 240 m, (Gallice, G.), 20 Oct 2010, 1 specimen, (sight record) (Gallice, G., unpublished data); Río Napo, Tiputini, [0°45'S,75°32'W], 250 m, (Willmott, K. R.), 21 Oct 1997, (W&H); Río Tiputini, Tiputini Biodiversity Station, [0°42'12"S,76°0'30"W], 200-250 m, (Gallice, G.), 9 Dec 2010, 1 specimen, (sight record) (Gallice, G., unpublished data); Río Tiputini, vía Auca, Estación Científica Yasuní, [0°40'27"S,76°23'49"W], 220-250 m, (Gallice, G.), 29 Nov 2010, 1 specimen, (sight record) (Gallice, G., unpublished data), (Willmott, K. R.), 17-18 Jul 1998, (W&H); *Pastaza*: Puyo-Macas rd., Pitorishca, [1°48'18"S,77°49'15"W], 1000 m, (Willmott, K. R., Hall, J. P. W.), 26 Jul 1998, (sight record) (W&H), 7 Dec

1997, (sight record) (W&H); Río Curaray, Lorocachi, [1°37'15"S,75°59'30"W], 250 m, (Willmott, K. R.), 28 Jul 1998, (W&H); Río Pindo Grande, Shell, [1°29'40"S,78°34'0"W], (Hill, R.), 19 Mar 2010, 1♂ [RH10-267], 1♀ [RH10-261], (RYHI or sight record) (Hill, R., unpublished data); *Sucumbios*: km 15 Lumbaqui-Pto. Libre rd., La Amarilla, [0°5'38"N,77°22'55"W], 600 m, (Willmott, K. R., Hall, J. P. W.), 27 Feb 2001, (sight record) (W&H).

Etymology: The subspecies name is an anagram of *orolina*, the taxon with which this has most often been confused in collections. It is treated as a feminine noun in apposition.

Taxonomy and variation: Morphology (Willmott & Freitas, 2006) and DNA sequence data (Chazot *et al.*, 2016a) show this taxon to be a member of *Brevioleria* Lamas, 2004, within which DNA sequences show that it is closely related to *B. arzalia* (*B. a. arzalia*) and *B. aelia* (*B. aelia plisthenes* (d'Almeida, 1958) and *B. aelia pachiteae* (Tessmann, 1928)) (Fig. 29; see also Chazot *et al.*, 2016a: Suppl. 3). Samples of *B. arzalia loria* **n. ssp.** from NE Ecuador formed a clade, while a specimen from SE Ecuador clustered with a specimen of Peruvian *B. arzalia loria* and one of *B. arzalia arzalia*, but these two *B. arzalia* clusters did not group together, with the latter cluster instead being sister to *B. aelia* (Fig. 29). Nevertheless, branches were extremely short and weakly supported in this clade. Given the sympatry between *B. arzalia loria* and *B. aelia oncidia*, the wing shape and venation characters (discussed above in the diagnosis) that are shared between the former and *B. arzalia arzalia*, and between the latter taxon and other *B. aelia* as treated by Lamas (2004), and the allopatry between *B. arzalia arzalia* and *B. arzalia loria* and their occurrence in east Andean foothills up to 1050 m (*B. aelia* typically occurs only below 300 m), we believe that the taxonomy suggested here is the most parsimonious given current data. Furthermore, in the MUSM there are 1♂ and 2♀ from Perú, San Martín (km 40-41 Tarapoto-Yurimaguas, [6°25'S,76°15'W], 490 m, and Toma del Shilcayo, [6°28'S,76°21'W], 400 m, which we regard as interspecific hybrids of *B. a. arzalia* x *B. arzalia loria*, with typical *B. a. arzalia* known from further west, at 6°25'S,76°19'W, 750 m. Dissections of males of *B. a. aelia*, *B. a. arzalia* and *B. arzalia loria* did not reveal any additional clear characters that might help associate allopatric taxa. Clearly, a comprehensive revision of *Brevioleria*, using both morphology and DNA sequence data, is needed.

Distribution and natural history: This taxon occurs from SE Colombia (Putumayo), throughout eastern Ecuador, to northern Peru (Amazonas, San Martín, Loreto) (Fig. 36A), and it is a widespread and not uncommon taxon in relatively undisturbed rainforest below 1050 m. In Ecuador, both sexes were encountered throughout the day, from 09:00 to 17:30 hrs, flying or resting from 0.3-2 m above the ground in typically shady understorey of tall forest, often within 5-15 m of light gaps. A single male was observed perching on a ridgetop in the forest understorey near a light gap at 0.3 m at 15:20 hrs. Notably, the male was perching with the wings closed and the hindwing androconial hair pencils were concealed, unlike many ithomiines in which the wings are held partly or completely open and the hair pencils exposed. At Boca del Río Añangu in eastern Ecuador, *B. a. loria* eggs were found and reared on a species of woody *Cestrum* L. (Solanaceae) growing in the shady understorey, a hostplant shared with co-mimic *Hypoleria*

alema chrysodonia (Willmott & Elias, unpublished data). Both sexes are involved in mimicry with a number of ithomiines, such as those mentioned above in the diagnosis, and other butterflies (see Beccaloni, 1997).

Hypoleria alema pastaza Willmott & Lamas, **new subspecies**
Figs. 9D,E, 18C-D, 36B

Hypoleria alema ocniform: Chazot *et al.* (2014b)

Diagnosis and identification: This new subspecies is distinguished from *H. alema ina* (Fig. 9F), which occurs further south in Ecuador, by the yellowish suffusion extending through the translucent HW area from the anal margin to the end of the discal cell, combined with the orange coloration along the anal margin. *Hypoleria alema ina* occurs in three forms, belonging to three different mimicry complexes, including the figured form (Fig. 9F, like the ST of *Ithomia alema ina*), and two with no reddish brown at the HW anal margin, one of which has the HW translucent area tinged white (like the types of the synonyms *Hypoleria ina negrina* Kaye, 1918 and *Hypoleria macasana* Strand, 1916), and one of which has it tinged yellow. *Hypoleria alema alema* (Hewitson, [1857]), which occurs further north in Colombia, has even more extensive yellow on the HW, in addition to yellow throughout the FW translucent areas, a black FW discocellular bar, and less intense orange at the HW anal margin. *Hypoleria alema pastaza n. ssp.* is also similar to several other co-mimetic ithomiines, but can easily be distinguished by the row of small, translucent whitish FW submarginal spots. The neighboring subspecies to the east, *H. alema chrysodonia*, resembles *Brevioleria arzialia loronia n. ssp.* (Fig. 9A,B) and is thus easily distinguished by the broad orange FW subapical band, black FW discocellular bar, and lack of yellow and orange translucence on the HW.

Description: MALE (Fig. 9D, 18C-D): Forewing length 30 mm (mean 29.7 mm, n=3). *Wings:* as illustrated (Fig. 9D), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes brown, bare, with very narrow fringe of white scales at base; antennae brown at very base then becoming pale yellow in middle and orange yellow at club; labial palpi black except for scattered white dorsal scales; top of head black with white medial spot between bases of antennae, two white spots behind eyes, frons black with very thin white lateral stripes. *Thorax:* dorsal surface dark brown with narrow white medial stripe and few scattered white lateral scales, pronotum dark brown dorsally with scattered white scales laterally, tegula dark brown, ventral surface dark brown except for small cluster of scattered white scales forming a spot in middle of meso- and metathorax, legs dark brown except for very sparse scattered white scales. *Abdomen:* entirely dark brown. *Genitalia* (Fig. 18C-D): notable features include broad, 'scoop'-like gnathos, sinuous aedeagus (Fig. 18C), pointed inner projections from valva basal lobes (Fig. 18D).

FEMALE: (Fig. 9E): Forewing mean length 28 mm (n=2). *Wings:* as illustrated (Fig. 9E), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **ECUADOR:** *Pastaza:* Río Pindo Grande, Shell, [1°29'40"S, 78°3'40"W], 1050 m, (Willmott, K. R., Hall, J. P. W.), 7, 8 Feb 1995, [Genitalic dissection KW-21-14], (FLMNH, to be deposited in INABIO).

PARATYPES (3♂, 4♀): **Ecuador:** *Napo:* 'Aguano' - (error), [1°4'S, 77°33'W], (Simson, A.), 1♀, (NHMUK); Tena-Loreto rd., Río Hollin, [0°41'13"S, 77°44'W], (Elias, M., Toporov, S., Santacruz, P.), 14 Mar 2010, 1♂, (MNHN), 22 Mar 2010, 1♂, (FLMNH); *Pastaza:* nr. Shell, Hacienda Moravia, [1°29'S, 78°3'24"W], 1200 m, (Willmott, K. R., Hall, J. P. W.), 9 Feb 1995, 1♀, (FLMNH); Puyo, [1°28'S, 77°59'W], 1000 m, (Boyer, P.), Jun 1996, 1♀, (PIBO); Río Pindo Grande, Shell, [1°29'40"S, 78°3'40"W], 1050 m, (Willmott,

K. R., Hall, J. P. W.), 2 Oct 1996, 1♀, (FLMNH); *Tungurahua:* nr. Río Negro, Santa Inéz, [1°24'44"S, 78°13'43"W], (Simson, A.), 1♂, (NHMUK).

Other records: **Ecuador:** *Pastaza:* N Diez de Agosto, Colonia Mariscal Sucre, [1°23'S, 77°52'W], 1000 m, (Boyer, P.), 13 Jan 2011, 1♀, (PIBO), 22 Jan 2011, 2♀, (PIBO). *Morona-Santiago:* 11 km SW Palora, [1°46'27"S, 78°1'56"W], (Boyer, P.), 17-18 Aug 2011, 22♂, 13♀, (PIBO); 'Macas' (error), [2°19'S, 78°7'W], 1000-1250 m, (Buckley, C.), 1♀, (NHMUK).

Etymology: The subspecies name is derived from that of the province where the holotype and most of the type series were collected. It is treated as a feminine noun in apposition.

Taxonomy and variation: Aside from similar wing shape, venation and male androconial scales, *H. alema pastaza n. ssp.* shares with *H. alema alema* and *H. alema ina* the distinctive row of small, translucent whitish FW submarginal spots and dark brown ventral abdomen (white in other *H. alema* subspecies). Based on this similar coloration, and their occurrence in east Andean middle elevation cloud forest, these three taxa were formerly treated as a species distinct from the lower elevation taxa formerly known as *Hypoleria lavinia* (Hewitson, [1855]) (Lamas, 2004). However, DNA sequence data and additional morphological study resulted in *H. alema* being combined with former east Andean *H. lavinia* taxa (Chazot *et al.*, 2016a; see also Fig. 29), a hypothesis supported by a large series of specimens (> 60) collected by Boyer and Petit at Environs de Santa Rosa, near Palora, in eastern Ecuador, which show numerous variations suggesting intergrading between *H. alema chrysodonia*, *H. alema pastaza* and possibly *H. alema ina*. These specimens are listed above under Other records but not included as paratypes given their likely hybrid origin and the fact that little variation was observed in the small series of *H. alema pastaza* examined from Napo to Tungurahua.

Winhard (2021) described *Hypoleria chrysodonia elegans* Winhard, 2021 based on two males and one female from the Palora region in eastern Ecuador (TL: Morona-Santiago, Río Palora, south of Arapicos) that are typical *H. alema chrysodonia* except for some slight variation that might indicate intergrading to *H. alema pastaza* and/or *H. alema ina*. The holotype male has slightly reduced orange scaling in the opaque border around the FW apex, lining the adjacent scales and extending into M₂-M₁, as well as faint whitish yellow coloring to the HW translucent area, as in *H. alema pastaza* and *H. alema ina*. This specimen fits well within the variation observed in the series collected by Boyer, mentioned above, and we interpret it to represent a hybrid between *H. alema chrysodonia* and *H. alema pastaza/H. alema ina*. As it most closely resembles the first of these three taxa, we treat it as a junior subjective synonym of *Ithomia orolina* var. *chrysodonia* Bates, 1862 (**n. syn.**).

Winhard (2021) also proposed the name *Hypoleria chrysodonia pallida* Winhard, 2021 based on three males and three females from eastern Ecuador (TL: Orellana, Coca). Notwithstanding putative differences in wing pattern discussed in the original description, our examination of more than 350 specimens from western Brazil (including São Paulo de Olivença, the type locality for *Ithomia orolina* var. *chrysodonia*), Colombia, Ecuador (> 150 specimens from > 40 localities in 5 provinces) and northern Peru did not reveal any significant, discrete, geographically restricted variation that we feel merits subspecific recognition. We therefore synonymize *Hypoleria*

chrysodonia pallida with *Ithomia orolina* var. *chrysodonia* (n. syn.).

Distribution and natural history: This taxon has been recorded from the southern slopes of Volcán Sumaco south as far as the north bank of the Río Pastaza (Fig. 36B). Specimens from localities in Morona-Santiago south of the Río Pastaza often show evidence of intergradation with *H. alema chrysodonia* (lowlands of eastern Ecuador) and *H. alema ina* (Morona-Santiago to Zamora-Chinchipec), and the specimen in the NHMUK from ‘Macas’ is likely mislabeled since modern specimens from that area are typical *H. alema ina*. *Hypoleria alema pastaza* n. ssp. occurs in the understorey of relatively undisturbed cloud forest, often near rivers, within a very narrow elevational range (1000-1200 m); the specimen in the NHMUK from ‘Aguano’, a lowland locality where typical *H. alema chrysodonia* occurs, is also presumably mislabeled, and was perhaps collected at higher elevations on the trail from Baeza to Archidona.

Hypomenitis hermana serafina Willmott & Lamas, new subspecies

Figs. 9G,H, 18E-G, 36C

Greta hermana n. ssp.: Lamas (2004: 191, no. 354d)

Greta hermana hewitsoniform: Chazot et al. (2014b)

Diagnosis and identification: This subspecies is distinguished from *H. hermana hermana* (Haensch, 1903) (Fig. 9I) and *H. hermana joiceyi* (Kaye, 1918) (Fig. 9K,L), found further north in Ecuador, by the reduced black over the FW and HW discocellulars, the narrower black HW margin, and smaller white HW marginal spots. It is distinguished further from the first of these by the yellow- rather than white-tinged HW translucent areas, and from the second by the less intense yellow orange scaling in the FW transparent areas. The taxon is also very similar in wing pattern to *Hypomenitis theudelinda zalmunna* (Hewitson, 1869), but both sexes have HW vein M_2 less prominently visible, and the male of *H. hermana* has only a single, rather than double, HW androconial hair pencil, in this respect being similar to *H. enigma* (Haensch, 1905).

Description: MALE (Fig. 9G, 18E-G): Forewing length 32 mm (mean 32.5 mm, n=8). *Wings:* as illustrated (Fig. 9G), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes brown, bare, with narrow fringe of white scales at base; antennae dark brown; labial palpi white except for black terminal segment and black continuing ventrally and laterally to middle of palpi; top of head black with white medial stripe between bases of antennae, two white spots behind eyes, frons black with white lateral stripes. *Thorax:* dorsal surface dark brown with pale yellowish brown medial stripe and similar lateral scales, with sparse long dark hair-like scales, pronotum dark brown dorsally and white laterally, tegula pale yellowish brown with orange tinge ventrally, covered with sparse, long dark hair-like scales, ventral surface white except for black where the legs fold, forelegs dark brown with scattered white scales, mid- and hindlegs dark brown with scattered white scales ventrally on femur and dorsally on tibia and tarsus. *Abdomen:* dorsal surface dark brown, ventral surface white with scattered dark brown scales. *Genitalia* (Fig. 18E-G): notable features include rounded valvae with short dorsal posterior projections, uncus slender and pointed and slightly curving to right (Fig. 18E,F), broad, irregular and short flanges on inner basal edge of valvae (Fig. 18F); vertically directed saccus is presumed to be an artifact.

FEMALE: (Fig. 9H): Forewing length mean 32.8 mm (n=4). *Wings:* as illustrated (Fig. 9H), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: ECUADOR: Zamora-Chinchipec: km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2000 m, (Aldaz, R.), 7 Feb 2002, [Genitalic dissection KW-21-15], (FLMNH, to be deposited in INABIO).

PARATYPES (25♂, 11♀): Ecuador: Zamora-Chinchipec: c. km 26 Yangana-Valladolid rd., Quebrada de los Muertos, [4°28'23"S,79°8'56"W], 2525 m, (Willmott, K. R.), 29 Nov 2005, 1♂ [FLMNH-MGCL-ECD-367], (FLMNH); Cordillera de Nanguipa, Santa Cruz-Nambija, [4°0'S,78°45'46"W], 1600-2000 m, (Boyer, P.), 30 Nov 1998, 2♂, (PIBO), 8 Mar 2001, 1♀, (PIBO); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2000 m, (Aldaz, R.), 7 Feb 2002, 5♂, 2♀, (FLMNH); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2000-2100 m, (Willmott, K. R.), 17 Oct 2006, 1♂ [FLMNH-MGCL-112943], (FLMNH), 2 Nov 2006, 1♂ [FLMNH-MGCL-112941], (INABIO), (Willmott, K. R., Aldaz, R.), 14 Oct 2006, 1♀ [FLMNH-MGCL-112946], (FLMNH), 31 Oct 2006, 1♂ [FLMNH-MGCL-112944], (FLMNH), 6 Nov 2006, 1♂ [FLMNH-MGCL-112942], (FLMNH); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2000-2150 m, (Willmott, K. R.), 4 Feb 2002, 1♀, (NHMUK), (Aldaz, R.), 7 Feb 2002, 1♂, (NHMUK); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2050 m, (Radford, J.), 18 Sep 2007, 1♀ [56B], (JARA); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2100 m, (Willmott, K. R.), 04 Feb 2002, 1♀, (FLMNH), 24 Nov 2003, 1♂, (FLMNH), 25 Nov 2003, 1♂, (FLMNH); Reserva Tapichalaca, Quebrada Honda trail, [4°28'21"S,79°7'18"W], 2000 m, (Willmott, K. R.), 30 Nov 2005, 1♂ [FLMNH-MGCL-ECD-365], (FLMNH); Reserva Tapichalaca, Quebrada Honda trail, [4°28'21"S,79°7'18"W], 2200 m, (Willmott, K. R.), 30 Nov 2005, 1♀ [FLMNH-MGCL-ECD-364], (FLMNH); Reserva Tapichalaca, Quebrada Honda trail, [4°28'21"S,79°7'18"W], 2250 m, (Willmott, K. R.), 30 Nov 2005, 1♂ [FLMNH-MGCL-ECD-366], 1♀ [FLMNH-MGCL-ECD-362], (FLMNH), 1♀ [FLMNH-MGCL-ECD-363], (INABIO); Reserva Tapichalaca, Quebrada Honda trail, [4°28'21"S,79°7'18"W], 2400-2450 m, (Radford, J.), 15 Sep 2007, 1♂ [55A], (JARA). Peru: Amazonas: 2-3 km N P[uesto de] V[igilancia] 3 (Alfonso Ugarte), Cordillera del Cóndor, [3°54'S,78°26'W], 1600-1750 m, (Lamas, G.), 22,25 Jul 1994, 7♂, 1♀, (MUSM).

Etymology (by K. Willmott): This subspecies is named for our good friend Serafín Raúl Aldaz Villafuerte. Raúl accompanied us on many field trips throughout Ecuador, most notably, in the context of this paper, during efforts to find and rear the immature stages of *Ithomiini* in 2001-2002, 2005 and 2006. Raúl's ability to locate and identify Solanaceae, and later Gesneriaceae, based on intuition and a lifetime's knowledge of the natural world, as well as find and rear caterpillars, proved to be remarkable, and his tireless and painstaking dedication in the field has resulted in the discovery of a number of new life histories. The name is treated as a masculine noun in apposition.

Taxonomy and variation: The single DHW androconial hair pencil in the male (an uncommon trait within *Hypomenitis*, found among east Andean congeners only in the sympatric *H. enigma*), distinctive wing pattern elements (black scaling at the FW discocellulars, white VHW marginal spots), and male genitalia (uncus with single point, valvae with short, irregular basal flanges near base of valva in ventral view) support treatment of this taxon as conspecific with *H. hermana hermana*, and DNA sequence data group it with the nominate subspecies as well as *H. hermana joiceyi* (Fig. 30). No notable variation was observed in the series examined.

Distribution and natural history: This subspecies is known from the east Andean slopes of southern Ecuador (Zamora-Chinchipec), from the vicinity of Nambija south to Reserva Tapichalaca, just north of Valladolid, in the headwaters of the Río Chinchipec (Fig. 36C), and in the Cordillera del Cóndor in Amazonas, Peru. The taxon is found in undisturbed cloud forest, where it is rare, and it is typically recorded from 2000-

2525 m, except for one site in the Cordillera del Cóndor at 1600 m. At Reserva Arcoiris, males were found from 11:30-16:30 hrs, typically flying and resting from 4-8 m above the ground in the understorey of tall forest on relatively flat ground near a small stream, in a lek area frequented by multiple ithomiine species. One male was observed by Radford feeding on purple Asteraceae flowers. Both sexes are involved in mimicry with numerous ithomiines, most notably *Napeogenes larilla larilla* (Hewitson, 1877), *Pteronymia serrata amplificata* Kaye, 1918, *Hypomenitis theudelinda zalmunna*, *Hypomenitis oneidodes nicolasi* **n. ssp.**, and *Veladyris pardalis totumbra* (Kaye, 1919).

Hypomenitis hermana chamba Willmott & Lamas, **new subspecies**

Figs. 9J, 18H-J, 36C

Diagnosis and identification: This subspecies differs from all other *H. hermana* taxa by having whitish rather than yellow translucent markings on the FW, more intense orange translucence in the HW tornal area, and orange brown rather than black or black and brown ventral distal margins. The subspecies thus closely resembles *H. ortygia ortygia* and comimics, but is easily distinguished from them by the white VHW marginal spots.

Description: MALE (Fig. 9J, 18H-J): Forewing length 27 mm (n=1). *Wings:* as illustrated (Fig. 9J), single, undivided band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head, thorax, abdomen:* same as *Hypomenitis hermana serafina* **n. ssp.** *Genitalia* (Fig. 18H-J): similar notable features to *H. hermana serafina*.

FEMALE: unknown.

Types: HOLOTYPE ♂: **ECUADOR:** *Zamora-Chinchipe:* km 4.3 San Andrés-Jimbura rd., [4°47'59"S, 79°18'18"W], 2020 m, (Willmott, K. R.), 13 Oct 2010, [FLMNH-MGCL-146844; Genitalic dissection KW-21-16], (FLMNH, to be deposited in INABIO).

Etymology (by K. Willmott): This subspecies is named for Leoncio Chamba, who graciously allowed us to stay at his farm, complete with a fantastic diversity of domestic mammals, birds and fish, while we were collecting at the type locality and other sites along the San Andrés-Jimbura road. The name is treated as a masculine noun in apposition.

Taxonomy and variation: This taxon is treated as a subspecies of *H. hermana* based on the similar wing pattern elements, including white VHW marginal spots, androconia (a single HW androconial hair pencil, rather than double as in most *Hypomenitis*), male genitalia (see characters discussed above under *H. hermana serafina* **n. ssp.**), and DNA barcodes that group it with other Ecuadorian *H. hermana* taxa, including the nominate subspecies. Only a single specimen is known, and therefore it must be considered whether it might represent an aberration of *H. hermana serafina*, which has been recorded only 40 km to the north at the Reserva Tapichalaca above Valladolid. The wing pattern is very similar to that of *H. hermana serafina*, but it seems unlikely that an aberration could result in the change in color from yellow to white in just the FW and apical HW translucent markings, the intensification of the orange-yellow coloration in the HW tornal area, and the increased orange brown coloring in the ventral margins. The fact that these pattern changes in concert result in a wing pattern

that strongly resembles another mimicry complex suggests that they are more likely the result of selection for mimicry driven by faunistic changes between the type locality and the Valladolid area. The occurrence of different subspecies at these two localities is not unprecedented, with, for example, *Perisama oppelii oppelii* (Latreille, [1809]) being present at Valladolid (collected by A. Jasinski, MZUJ) and *P. oppelii eminens* Oberthür, 1881 along the San Andrés-Jimbura road (Willmott & Hall, pers. obs.).

Distribution and natural history: This subspecies is known only from the type locality, at 2020 m on the San Andrés to Jimbura road in southern Zamora-Chinchipe province in southeastern Ecuador (Fig. 36C). The type locality is a road cut across the top of a ridge, with substantial primary forest on all sides. On 13 October 2010, a cloudy but bright day, a number of ithomiines, of both sexes, were observed flying through the road cut from one side of the ridge to the other. These comprised 21 species, including *H. hermana chamba* **n. ssp.**, of which the holotype was flying at 11:45 hrs at 3 m above the ground. Despite repeated visits to the region of the type locality during the last decade, no further specimens have been collected.

Hypomenitis oneidodes guarumales Boyer, Petit & Willmott, **new subspecies**
Figs. 9M,N, 36D

Diagnosis and identification: This subspecies is distinguished from the nominate subspecies (Fig. 9O,R), which occurs further north in Ecuador, by having less intense yellow orange coloring throughout the FW transparent wing area, and by the HW being mostly transparent and colorless with pale grayish translucent submarginal spots, rather than translucent yellow throughout with indistinct translucent yellow submarginal spots. Like other *H. oneidodes* (Kaye, 1918) taxa, this new subspecies can be distinguished from all other *Hypomenitis* by the thin, paired white VHW marginal spots in cells 3A-Cu₂ and Cu₂-Cu₁.

Description: MALE (Fig. 9M): Forewing length 34 mm (n=1). *Wings:* as illustrated (Fig. 9M), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head:* eyes brown, bare, with narrow fringe of white scales at base; antennae dark brown; labial palpi white except for black terminal segment and black continuing ventrally and laterally to middle of palpi; top of head black with white medial stripe between bases of antennae, two white spots behind eyes, frons black with white lateral stripes. *Thorax:* dorsal surface dark brown with white medial stripe and pale yellowish brown lateral scales, with sparse long dark hair-like scales, pronotum dark brown dorsally and white laterally, tegula pale yellowish brown becoming dark brown in anterior-dorsal half, ventral surface white with increasing scattered yellow and orange scales near body except for black where the legs fold, legs dark brown with scattered white scales. *Abdomen:* dorsal surface dark brown, ventral surface white. *Genitalia:* not examined.

FEMALE (Fig. 9N): Forewing length 32 mm (n=1). *Wings:* as illustrated (Fig. 9N), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **ECUADOR:** *Morona-Santiago:* Guarumales/Hidropaute, [2°34'16"S, 78°30'56"W], 2100-2200 m, (Boyer, P.), 11 Nov 2010, (PIBO, to be deposited in PUCE).

PARATYPES (2♂, 2♀): **Ecuador:** *Morona-Santiago:* Guarumales/Hidropaute, [2°34'16"S, 78°30'56"W], 2100 m, (Petit, J.-C.), 12 Nov 2011, 1♀, (JEPE); Guarumales/Hidropaute, [2°34'16"S, 78°30'56"W], 2100-2200 m, (Boyer, P.), 11 Nov 2011, 2♂, (PIBO), 18-20 Jan 2011, 1♀, (PIBO). **Country unknown:** *Not located:* no data, 1♀ [presumably Ecuador], (NHMUK).

Etymology: The subspecies name is derived from that of the type locality.

Taxonomy and variation: *Hypomenitis oneidodes* is a very rare species that was known from only a handful of historical specimens, in the NHMUK, prior to its collection in Ecuador in the last couple of decades. Kaye (1918) described *Hymenitis oneidodes* from a single female (Fig. 9R) from 'Ecuador', now in the NHMUK, and mentioned the paired white VHW marginal spots that are diagnostic of the species. The holotype lacks precise locality data but bears the same small, white handwritten label 'Ecdr' found on three males of *Hypomenitis hermana joiceyi* (described in the same paper as *H. oneidodes*) and specimens of *Oleria baizana baizana* in the NHMUK. The last two taxa are restricted to NE Ecuador, with the only accessible area within their known range at the time of collection being the vicinity of Baeza, on the trail from Quito to Archidona, where C. Buckley collected at the site of Yanayacu. This area therefore seems the likely source for the holotype of *H. oneidodes*, which indeed matches specimens collected by us in the same region in 2006 and 2010. The highly distinctive wing pattern, including the deeply dentate dark HW margin, paired white VHW marginal spots and dark scaling over the FW discocellulars, all support the conspecificity of the two new taxa described here with *H. oneidodes*.

Distribution and natural history: This subspecies is known only from the Guarumales area in the upper Río Paute valley of Morona-Santiago province, eastern Ecuador (Fig. 36D). However, an evidently old female specimen with no data in the NHMUK was likely collected either in the upper Río Pastaza valley, Tungurahua, or in the Chigüinda area, Morona-Santiago, south of the type locality, since likely co-mimics, discussed below, are known from both areas. At the type locality, both sexes were found along a steeply ascending trail through primary cloud forest from 2100-2200 m. This subspecies is presumably involved in mimicry with a number of other similar sympatric ithomiines that have an intense yellow subspecies in NE Ecuador, a clear hindwing subspecies in central Ecuador, and a more muted yellow subspecies in southern Ecuador, including: *Napeogenes larilla*, *Pteronymia serrata*, *Veladyris pardalis* (Salvin, 1869), *Velamysta pupilla* (Hewitson, 1874) (not known from SE Ecuador), *Hypomenitis theudelinda* (Hewitson, [1861]) and *Hypomenitis hermana*.

Hypomenitis oneidodes nicolasi Willmott & Lamas, new subspecies

Figs. 9P,Q, 18K-M, 36D

Greta oneidodes n. ssp.: Lamas (2004: 191, no. 361b)

Greta oneidodes hewitsoniform: Chazot et al. (2014b)

Diagnosis and identification: This subspecies is distinguished from *H. oneidodes guarumales* n. ssp. (Fig. 9M,N), which replaces it to the north, by the yellowish tinge to the HW transparent areas and translucent submarginal markings. In this respect it more closely resembles the nominate subspecies (Fig. 9O,R) from NE Ecuador, but that subspecies may be distinguished by having even more intense yellow translucence, such that the translucent yellow submarginal markings on the

FW are less distinct, and by having the FW veins Cu₂, Cu₁, M₃, M₂ and M₁ more strongly lined with orange scaling. These characters were also used to determine to which population the name *oneidodes* should apply, in the absence of a precise type locality. Like *H. oneidodes guarumales* and *H. o. oneidodes*, *H. oneidodes nicolasi* n. ssp. is distinguished from a number of similar godryidines by the paired white VHW marginal spots.

Description: MALE (Fig. 9P, 18K-M): Forewing length 34 mm (mean 33 mm, n=3). *Wings:* as illustrated (Fig. 9P), band of androconial hair-like scales in anterior edge of DHW discal cell, and associated modified wing scales in DHW costal region, as in nominate subspecies. *Head, thorax, abdomen:* same as in *Hypomenitis oneidodes guarumales* n. ssp. *Genitalia* (Fig. 18K-M): notable features include vertically elongate valvae with long dorsal and ventral posterior projections (Fig. 18K,M), uncus broad and bluntly bifurcate (Fig. 18L).

FEMALE: (Fig. 9Q): Forewing mean length 32 mm (n=3). *Wings:* as illustrated (Fig. 9Q), lacking DHW costal androconial scales. *Head, thorax, abdomen:* similar to male.

Types: HOLOTYPE ♂: **ECUADOR:** *Zamora-Chinchipe:* km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2000-2100 m, (Willmott, K. R.), 22 Oct 2006, [FLMNH-MGCL-112939; Genitalic dissection KW-20-14], (FLMNH, to be deposited in INABIO).

PARATYPES (5♂, 4♀): **Ecuador:** *Zamora-Chinchipe:* km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2000 m, (Aldaz, R.), 07 Feb 2002, 2♀, (FLMNH); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2000-2100 m, (Willmott, K. R.), 17 Oct 2006, 1♂ [FLMNH-MGCL-112938], (FLMNH), 21 Sep 2007, 1♀ [FLMNH-MGCL-113528], (FLMNH), (Willmott, K. R., Aldaz, R.), 15 Oct 2006, 1♀ [FLMNH-MGCL-112937], (FLMNH); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2050 m, (Radford, J.), 17 Sep 2007, 1♂ [55B], (FLMNH); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2100 m, (Willmott, K. R.), 26 Oct 2006, 1♂ [FLMNH-MGCL-112940], (FLMNH); km 5.3 San Andrés-Jimbura rd., Finca San Carlos, [4°47'53"S,79°18'34"W], 2050 m, (Willmott, K. R., J. C. R., J. I. R.), 20 Jun 2014, 1♂ [FLMNH-MGCL-280555], (FLMNH); N of Valladolid, 2200 m, (Petit, J.-C.), 3 Jan 2004, 1♂, (JEPE).

Etymology (by K. Willmott): This rare subspecies is named for Nicolas Chazot, in gratitude for allowing us to stay in his wonderful apartment in Paris in 2014, and in recognition of his extraordinary contributions to knowledge of the evolution, ecology and conservation of ithomiines. The name is treated as a Latinized masculine noun in the genitive case.

Taxonomy and variation: We treat this taxon as a subspecies of *H. oneidodes* for the same reasons as discussed above under *H. oneidodes guarumales* n. ssp. In addition, the male genitalia are similar to those of *H. oneidodes oneidodes* (NHMUK, Ecuador, 'Chigüinda' [presumably mislabeled and actually from Yanayacu, Napo, area], Genitalic dissection BM-6464), with the combination of features discussed above in the description unique to this species and the otherwise much less similar *Hypomenitis jamesiana* Willmott, Lamas & Hall (2020) (see Willmott et al., 2020), which is sympatric with *H. oneidodes nicolasi* n. ssp. at the type locality. Finally, DNA barcodes group this new taxon with the nominate subspecies (Fig. 30).

Distribution and natural history: This subspecies is known from the east Andean slopes of southern Ecuador (Zamora-Chinchipe), from the upper Río Zamora south to the San Andrés to Jimbura road near the border with Peru (Fig. 36D). It occurs in undisturbed cloud forest from 2000-2100 m, where it is very rare. Males were observed from 12:10 to 15:20 hrs, flying and resting 0.5-4 m above the ground, in shady forest understorey and sunflecks in tall forest on a shallow slope near a stream,

in an area where there were numerous lekking ithomiines. Females were observed flying from 0.4-2 m above the ground in the same areas, from 12:10 to 13:20 hrs. This subspecies is involved in mimicry with numerous ithomiines, including those mentioned above under *H. oneidodes guarumales* n. ssp., as well as most of those listed under the account for *Pteronymia alida francisca* n. ssp.

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Appendix 1. Voucher information and metadata for COI barcode sequences analyzed. Sequences with GenBank voucher numbers starting “OK...” are newly published in this study.

Taxon	DNA voucher number	Locality (decimal latitude and longitude)	Genbank voucher
Brevioleria aelia oncidia	LEP-10335	Ecuador: Orellana: Estación Científica Yasuni (-0.674, -76.397)	OK065766
Brevioleria aelia pachiteae	05-112	Peru: San Martín: Puente Serranoyacu above Rioja (-5.672, -77.676)	KX362056.1
Brevioleria aelia pachiteae	5-561	Peru: San Martín: Quebrada Huacaní	EU069024.1
Brevioleria arzalia arzalia	02-3431	Peru: Cuzco: Pilcopata to Santa Rosa de Huacaria	KX362083.1
Brevioleria arzalia arzalia	2-1200	Peru: 'Peru'	HM051790.1
Brevioleria arzalia arzalia	2-1769	Peru: 'Peru'	HM051791.1
Brevioleria arzalia loria	264	Ecuador: Pastaza: Comunidad Shuar Mirador	KX362077.1
Brevioleria arzalia loria	20212	Ecuador: Orellana: Napo Wildlife Center, Tiputini trail (-0.529, -76.417)	EU068768.1
Brevioleria arzalia loria	20259	Ecuador: Orellana: Napo Wildlife Center, Napo trail (-0.51, -76.437)	EU068769.1
Brevioleria arzalia loria	20670	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068770.1
Brevioleria arzalia loria	20709	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068956.1
Brevioleria arzalia loria	E-44-4	Ecuador: Sucumbios: El Recodo (0.256, -77.478)	DQ157477.1
Brevioleria arzalia loria	LS02-14	Ecuador: Sucumbios: Lake Garzacocho	EU068977.1
Brevioleria arzalia loria	ME10-205	Ecuador: Napo: Mariposa (-0.908, -77.786)	KX362012.1
Brevioleria arzalia loria	ME10-206	Ecuador: Napo: Mariposa (-0.908, -77.786)	KX362040.1
Brevioleria arzalia ssp	2-2108	Peru: 'Peru'	HM051788.1
Brevioleria arzalia ssp	05-874	Peru: San Martín: Caño Negro, Río Biabo	KX362039.1
Brevioleria coenina	ME10-359	Ecuador: Napo: Cocodrilo (-0.649, -77.791)	JX573755.1
Brevioleria n. sp.	G128	Peru: Cuzco: Quebrada Quitacalzón (-13.022, -71.493)	KX362023.1
Brevioleria plisthenes plisthenes	BAKU-45	Brazil: São Paulo: Monte Alegre do Sul	KX362028.1
Brevioleria seba oculata	20458	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU069025.1
Brevioleria seba oculata	ME10-212	Ecuador: Napo: Mariposa (-0.908, -77.786)	KX362087.1
Elzunia humboldt albomaculata	LEP-00104	Ecuador: Tungurahua: Río Machay (-1.389, -78.28)	OK065729
Elzunia humboldt cassandrina	LEP-00105	Ecuador: Morona-Santiago: Río Abanico (-2.254, -78.202)	OK065730
Elzunia humboldt cassandrina	LEP-06870	Ecuador: Morona-Santiago: Guarumales/Hidropaute (-2.576, -78.513)	KF268430.1
Elzunia humboldt cassandrina	LEP-06874	Ecuador: Morona-Santiago: Río Bomboiza (-2.649, -78.464)	OK065755
Elzunia humboldt golondrina	LEP-00103	Ecuador: Carchi: Santa Rosa (0.827, -78.128)	OK065728
Elzunia pavonii	LEP-01457	Ecuador: Loja: Santuario San Vicente, Quebrada El Sauce (-3.948, -79.448)	OK065734
Elzunia pavonii	LEP-54950	Ecuador: Zamora-Chinchipec: km 30 Zumba-Chito rd. (-4.945, -79.072)	OK065781
Episcada apuleia apuleia	21020	Ecuador: Zamora-Chinchipec: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573759.1
Episcada apuleia apuleia	E-29-3	Ecuador: Loja: no specific locality	DQ157487.1
Episcada arcadia arcadia	20347	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068779.1
Episcada arcadia arcadia	20398	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068780.1
Episcada arcadia arcadia	20454	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU069035.1
Episcada arcadia arcadia	LS07-441	Ecuador: Sucumbios: Lake Garzacocho	EU069036.1
Episcada clausina bomboiza	LEP-01525	Ecuador: Morona-Santiago: Yakunk-Cutucú trail, lower ridge (-2.761, -78.161)	MG210107.1
Episcada clausina clausina	02-3173	Peru: Cuzco: Palma Real	MG210073.1
Episcada hemixanthe	03-104	Brazil: Bahia: Serra Bonita (-15.39, -39.56)	MG210087.1
Episcada hemixanthe	03-105	Brazil: Bahia: Serra Bonita (-15.39, -39.56)	MG210063.1
Episcada hymen n. ssp. [1]	2-1456	Peru: San Martín: Chumia (-6.6, -76.15)	EU068781.1
Episcada hymenaea hymenaea	BAKU-41	Brazil: São Paulo: Monte Alegre do Sul	MG210112.1
Episcada hymenaea hymenaea	MACN-Bar-Lep-ct 02044	Argentina: Misiones: Departamento de Iguazú, Parque Nacional Iguazú, Seccional Yacui (-25.675, -54.169)	MF546229.1
Episcada mira	ME10-471	Ecuador: Pastaza: nr. trailhead to Río Anzu (-1.42, -78.05)	JX573760.1
Episcada mira	ME11-59	Ecuador: Zamora-Chinchipec: Quebrada de Chorillos (-4.042, -78.991)	MG210069.1
Episcada philoclea	BAKU-3	Brazil: Minas Gerais: Parque Nacional do Caparaó (-20.5, -41.667)	MG210062.1
Episcada philoclea	BLU591	Country unknown: no data	MK330658.1
Episcada polita flava	LEP-01526	Ecuador: Morona-Santiago: Loma Kilamo (-2.305, -78.145)	MG210108.1
Episcada polita pichincha	LEP-08697	Ecuador: Pichincha: 12 km SW Las Tolas (0.051, -78.838)	MG210101.1
Episcada polita pichincha	LEP-08701	Ecuador: Pichincha: Tandayapa Bird Lodge (0.002, -78.678)	MG210100.1
Episcada polita pichincha	LEP-08703	Ecuador: Carchi: Finca San Francisco (0.803, -78.171)	MG210099.1
Episcada salvinia salvinia	8042	Panama: Chiriquí: Finca Café Durán, near Santa Clara (8.836, -82.709)	MG210075.1
Episcada striposis	03-134	Brazil: Bahia: Serra Bonita (-15.39, -39.56)	MG210061.1
Episcada striposis	BAKU-19	Brazil: Minas Gerais: Parque Nacional do Caparaó (-20.5, -41.667)	MG210098.1
Episcada sylvo	B-17-1	Brazil: São Paulo: Atibaia (-23.136, -46.567)	DQ157489.1
Episcada sylvo	MACN-Bar-Lep-ct 02039	Argentina: Misiones: Departamento de Iguazú, Parque Nacional Iguazú, Seccional Yacui (-25.675, -54.169)	MF546229.1
Episcada tucidella tucidella	21037	Ecuador: Zamora-Chinchipec: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573761.1
Episcada tucidella tucidella	21555	Ecuador: Zamora-Chinchipec: San Francisco, casa de Arcoiris (-3.986, -79.09)	MG210084.1
Episcada trapezula	G113	Peru: Cuzco: El Mirador (-13.067, -71.55)	MG210056.1
Episcada vitrea	BAKU-2	Brazil: Minas Gerais: Parque Nacional do Caparaó (-20.5, -41.667)	MG210085.1
Episcada vitrea	BLU375	Brazil: Minas Gerais: Parque Nacional do Caparaó (-20.5, -41.667)	MG210060.1
Hyaliris antea achuar	KW-071204-10	Ecuador: Morona-Santiago: km. 9.5 Chigüinda-Gualaquiza rd., hillside (-3.244, -78.669)	MH893351.1
Hyaliris antea achuar	LEP-54908	Ecuador: Morona-Santiago: km 14 Chigüinda-Gualaquiza rd. (-3.262, -78.651)	OK065776
Hyaliris antea achuar	LEP-54909	Ecuador: Morona-Santiago: km 14 Chigüinda-Gualaquiza rd. (-3.262, -78.651)	OK065777
Hyaliris antea amarilla	E-30-4	Ecuador: Zamora-Chinchipec: Quebrada de Chorillos (-4.042, -78.991)	DQ069237.1
Hyaliris antea amarilla	KW-071204-18	Ecuador: Zamora-Chinchipec: km 8 Valladolíd-Tapala rd. (-4.539, -79.106)	MH893355.1
Hyaliris antea amarilla	LEP-54906	Ecuador: Zamora-Chinchipec: Quebrada Huanchunangui (-4.92, -79.165)	OK065774
Hyaliris antea amarilla	LEP-54907	Ecuador: Zamora-Chinchipec: Quebrada Huanchunangui (-4.92, -79.165)	OK065775
Hyaliris antea amarilla	LEP-56933	Ecuador: Zamora-Chinchipec: 11 km SW above Zurmi (-4.154, -78.697)	OK065803
Hyaliris antea antea	ME10-521	Ecuador: Napo: Río Hollín (-0.687, -77.733)	OK065818
Hyaliris antea atagalpa	PE-10-14	Peru: Cuzco: Quebrada Chaupimayo (-12.95, -72.667)	DQ157502.1
Hyaliris antea lalimba	LEP-06820	Ecuador: Zamora-Chinchipec: Quebrada Huanchunangui (-4.92, -79.165)	OK065751
Hyaliris antea lalimba	LEP-56936	Ecuador: Zamora-Chinchipec: km 2.6 El Pite-Río Mayo rd. (-4.866, -79.094)	OK065805
Hyaliris antea lalimba	LEP-56937	Ecuador: Zamora-Chinchipec: km 2.6 El Pite-Río Mayo rd. (-4.866, -79.094)	OK065806
Hyaliris antea lalimba	LEP-56943	Ecuador: Zamora-Chinchipec: Río Mayo (-4.879, -79.091)	OK065807
Hyaliris coeno angustior	M2836	Colombia: Casanare: Sacama, Río Casanare	MH893290.1
Hyaliris coeno florida	M1100	Colombia: Caquetá: Paraíso, km 7 Caraño	MH893291.1
Hyaliris coeno florida	M1369	Colombia: Caquetá: Paraíso, km 7 Caraño	MH893292.1
Hyaliris coeno norellana	KW-071204-01	Ecuador: Napo: Río Achiyacu (-1.012, -77.905)	MH893354.1
Hyaliris coeno norellana	KW-071204-02	Ecuador: Sucumbios: Quebrada El Copal (0.39, -77.522)	MH893363.1
Hyaliris coeno norellana	LEP-57382	Ecuador: Sucumbios: Cerro Lumbaqui Norte rd., 3rd bridge (0.024, -77.319)	OK065815
Hyaliris excelsa decumana	8001	Panama: Chiriquí: Fortuna, Quebrada Hornito Trail (9.155, -82.224)	MH893294.1
Hyaliris excelsa decumana	8431	Panama: Chiriquí: Fortuna, Quebrada Hornito Trail (9.155, -82.224)	MH893295.1
Hyaliris excelsa robertus	KW-071204-04	Ecuador: Esmeraldas: Río Chuchuví (0.881, -78.515)	MH893297.1
Hyaliris juninensis juninensis	4-290	Peru: Ucayali: Bosque Nacional von Humboldt, INIA (-8.825, -75.055)	MH893298.1
Hyaliris juninensis juninensis	NapK15	Brazil: Acre: Alto Rio Acre	KJ566620.1
Hyaliris lactea crocata	LEP-56930	Ecuador: Zamora-Chinchipec: km 29 Zumba-Los Sungas rd. (-4.951, -79.211)	MT790706.1
Hyaliris lactea crocata	LEP-56931	Ecuador: Zamora-Chinchipec: km 29 Zumba-Los Sungas rd. (-4.951, -79.211)	MT790707.1
Hyaliris lactea lactea	KW-071204-06	Ecuador: Sucumbios: Cascada de San Rafael (-0.097, -77.582)	KF020563.1
Hyaliris latilimbata	G108	Peru: Amazonas: San Antonio (-5.783, -77.4)	MH893252.1
Hyaliris latilimbata	LEP-06824	Ecuador: Zamora-Chinchipec: Quebrada Huanchunangui (-4.92, -79.165)	OK065752
Hyaliris mestra mestra	KW-071204-05	Ecuador: Zamora-Chinchipec: Quebrada Limones (-4.075, -78.974)	KF020564.1
Hyaliris mestra mestra	KW-071204-08	Ecuador: Zamora-Chinchipec: Quebrada Limones (-4.075, -78.974)	MH893361.1
Hyaliris mestra mestra	LEP-06554	Ecuador: Zamora-Chinchipec: San José (-4.075, -78.727)	OK065742
Hyaliris mestra mestra	LEP-54912	Ecuador: Zamora-Chinchipec: Río Ismanchi (-4.828, -79.262)	OK065779
Hyaliris mestra mestra	LEP-56934	Ecuador: Zamora-Chinchipec: km 29 Zumba-Los Sungas rd. (-4.951, -79.211)	OK065804
Hyaliris mestra personata	9153	Ecuador: Morona-Santiago: Río Abanico (-2.253, -78.201)	MH893301.1
Hyaliris mestra personata	KW-071204-12	Ecuador: Morona-Santiago: Río Abanico (-2.254, -78.202)	MH893356.1
Hyaliris mestra personata	LEP-56648	Ecuador: Morona-Santiago: Río Abanico (-2.254, -78.202)	OK065799
Hyaliris oca equatoria	KW-071204-03	Ecuador: Sucumbios: Quebrada El Copal (0.39, -77.522)	MH893303.1

Appendix 1. Voucher information and metadata for COI barcode sequences analyzed, continued.

Taxon	DNA voucher number	Locality (decimal latitude and longitude)	Genbank voucher
Hyaliris ocna equatoria	LEP-55436	Ecuador: Orellana: Reserva Biológica del Río Bigal, main campsite (-0.525, -77.418)	OK065788
Hyaliris ocna equatoria	LEP-57300	Ecuador: Napo: Río Chalayacu (-0.718, -77.682)	OK065814
Hyaliris ocna ocna	M2837	Colombia: Cundinamarca: Chirajara (4.204, -73.792)	KF020565.1
Hyaliris praxilla abscondita	LEP-55900	Ecuador: Zamora-Chinchi: Refugio de Vida Silvestre Bosque Protector El Zarza (-3.818, -78.569)	OK065789
Hyaliris praxilla leuca	KW-071204-09	Ecuador: Zamora-Chinchi: Quebrada Limones (-4.075, -78.974)	MH893358.1
Hyaliris praxilla leuca	LEP-06544	Ecuador: Zamora-Chinchi: San José (-4.075, -78.727)	OK065741
Hyaliris praxilla leuca	LEP-55986	Ecuador: Zamora-Chinchi: Quebrada San Vicente (-4.503, -79.02)	OK065790
Hyaliris praxilla leuca	ME11-7	Ecuador: Zamora-Chinchi: Quebrada de Chorillos (-4.042, -78.991)	JX573784.1
Hyaliris praxilla praxilla	9151	Ecuador: Morona-Santiago: Río Abanico (-2.253, -78.201)	MH893306.1
Hyaliris praxilla praxilla	9152	Ecuador: Morona-Santiago: Río Abanico (-2.253, -78.201)	MH893307.1
Hyaliris praxilla praxilla	KW-071204-11	Ecuador: Morona-Santiago: km. 9.5 Chigüinda-Gualaquiza rd., river (-3.244, -78.671)	MH893366.1
Hyaliris praxilla praxilla	LEP-06827	Ecuador: Morona-Santiago: 'Sopladora ridge' (-2.598, -78.456)	OK065753
Hyaliris praxilla praxilla	LEP-54910	Ecuador: Morona-Santiago: km 14 Chigüinda-Gualaquiza rd. (-3.262, -78.651)	OK065778
Hyaliris praxilla praxilla	LEP-56649	Ecuador: Morona-Santiago: Río Abanico (-2.254, -78.202)	OK065800
Hyaliris yasanina	20275	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068793.1
Hyaliris yasanina	20320	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068794.1
Hypoleria alema chrysonodia	20220	Ecuador: Orellana: Napo Wildlife Center, Napo trail (-0.51, -76.437)	EU068796.1
Hypoleria alema chrysonodia	20328	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068797.1
Hypoleria alema chrysonodia	20657	Ecuador: Orellana: Añangu community (-0.494, -76.42)	EU069045.1
Hypoleria alema chrysonodia	20673	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068798.1
Hypoleria alema chrysonodia	LS02-98	Ecuador: Sucumbios: Lake Garzacocho	EU068985.1
Hypoleria alema chrysonodia	ME10-215	Ecuador: Napo: Mariposa (-0.908, -77.786)	XX362109.1
Hypoleria alema oreas	BAKU-52	Brazil: Alagoas: Usina Serra Grande (-8.967, -36.05)	XX362059.1
Hypoleria alema oreas	BAKU-53	Brazil: Alagoas: Usina Serra Grande (-8.967, -36.05)	XX362060.1
Hypoleria alema pastaza	ME10-517	Ecuador: Napo: Río Hollin (-0.687, -77.733)	JX573785.1
Hypoleria alema proxima	B-16-8	Brazil: São Paulo: Jundiá (-23.174, -46.522)	DQ157504.1
Hypoleria alema proxima	BAKU-44	Brazil: São Paulo: Monte Alegre do Sul	XX362047.1
Hypoleria asellia	RB358	Brazil: Rondônia: Ariquemes (-9.933, -63.05)	DQ157503.1
Hypoleria aureliana	02-679	Peru: San Martín: Tarapoto-Yurimaguas, km 19 (-6.455, -76.286)	XX362048.1
Hypoleria aureliana	MJ07-264	Peru: San Martín: km 5 Shapaja-Chasuta (-6.593, -76.219)	XX362092.1
Hypoleria lavinia cassotis	00-SRNP-06	Costa Rica: Alajuela: Área de Conservación Guanacaste, Sector San Cristóbal, Potrero Argentina (10.887, -85.386)	GU334028.1
Hypoleria lavinia cassotis	06-SRNP-34820	Costa Rica: Guanacaste: Sector Pitilla, Sendero Memos (10.976, -85.423)	JQ544098.1
Hypoleria lavinia lavinia	LEP-00092	Ecuador: Manabí: Cerro Prieto, S Santa Lucía, km 20 Jipijapa-Guayaquil rd. (-1.511, -80.507)	XX362120.1
Hypoleria lavinia lavinia	LEP-00093	Ecuador: Pichincha: Río Silanche (-0.145, -79.141)	XX362121.1
Hypoleria lavinia libera	YB-BC122499	Panama: Panama: Wheeler2	KP849010.1
Hypoleria lavinia libera	YB-BC163973	Panama: Panama: Armour1 (9.153, -79.842)	KP849011.1
Hypoleria lavinia vanilla	LEP-11339	Colombia: Antioquia: Finca Jacaranda (5.674, -75.701)	XX362069.1
Hypoleria ocalea gephira	LEP-11332	Colombia: Antioquia: Finca Jacaranda (5.674, -75.701)	XX362124.1
Hypoleria ocalea ocalea	BMC-1631	Colombia: Antioquia: Porce (6.738, -75.093)	XX362070.1
Hypoleria xenophis	05-624	Peru: San Martín: Robashca, Puesto de Control 11 (-6.706, -76.033)	XX362050.1
Hypoleria xenophis	G127	Peru: San Martín: Quebrada Yacuisa	XX362061.1
Hypomenitis alphasiboea	259	Country unknown: no data	XX362125.1
Hypomenitis alphasiboea	05-1012	Peru: San Martín: Jorge Chávez (-5.683, -77.667)	JX573766.1
Hypomenitis candida	13361	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	XX362114.1
Hypomenitis candida	MJ07-704	Peru: Cuzco: San Pedro Lodge	XX362032.1
Hypomenitis depauperata umbrosa	LEP-06790	Ecuador: Loja: Centro Admin. PN Colambo-Yacuri, km 16.5 Jimbura-San Andrés rd. (-4.712, -79.44)	XX362062.1
Hypomenitis decretis decretis	21040	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573769.1
Hypomenitis decretis n. ssp.	02-2144	Peru: San Martín: La Antena (-6.452, -76.289)	XX362102.1
Hypomenitis enigma pseudortygia	21074	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573770.1
Hypomenitis enigma pseudortygia	21292	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	XX362112.1
Hypomenitis esula esula	KW-120728-13	Colombia: 'Colombia'	XX362017.1
Hypomenitis gardneri devriesi	21121	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573772.1
Hypomenitis gardneri devriesi	21282	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	XX362113.1
Hypomenitis hermana chamba	LEP-04535	Ecuador: Zamora-Chinchi: km 4.3 San Andrés-Jimbura rd. (-4.8, -79.305)	OK065738
Hypomenitis hermana hermana	LEP-06787	Ecuador: Morona-Santiago: Guarumales/Hidropaute (-2.571, -78.516)	OK065749
Hypomenitis hermana joiceyi	400	Ecuador: Napo: Estación Científica Yanayacu (-0.59, -77.883)	XX362105.1
Hypomenitis hermana joiceyi	E-39-46	Ecuador: Sucumbios: Quebrada El Garrapatal (0.488, -77.553)	DQ069236.1
Hypomenitis hermana serafina	21145	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573773.1
Hypomenitis hermana serafina	21341	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	XX362117.1
Hypomenitis hermana serafina	21493	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	XX362096.1
Hypomenitis jamesiana	21002	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573771.1
Hypomenitis libethris libethris	21579	Peru: Cuzco: San Pedro Lodge	XX362116.1
Hypomenitis lojana	21291	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	XX362111.1
Hypomenitis lojana	21468	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	XX362107.1
Hypomenitis lydia	21122	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573776.1
Hypomenitis lydia	21272	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	XX362079.1
Hypomenitis ochretis ochretis	LEP-08656	Ecuador: Carchi: Maldonado-Tulcán rd. (0.889, -78.08)	XX632147.1
Hypomenitis ochretis ochretis	LEP-15324	Ecuador: Pichincha: Sachatamia (-0.022, -78.76)	OK065768
Hypomenitis oneidodes nicolasi	21476	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573777.1
Hypomenitis oneidodes nicolasi	21535	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	XX362052.1
Hypomenitis oneidodes oneidodes	ME10-20	Ecuador: Napo: Estación Científica Yanayacu (-0.59, -77.883)	OK065817
Hypomenitis ortygia ortygia	21203	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573778.1
Hypomenitis ortygia ortygia	21233	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	XX362097.1
Hypomenitis ortygia pyrzi	02-1693	Peru: San Martín: 'Alto Río Nieva' [= Alto Nieva] (-5.683, -77.783)	XX362027.1
Hypomenitis polissena polissena	LEP-08648	Ecuador: Pichincha: 12 km SW Las Tolas (0.051, -78.838)	OK065757
Hypomenitis polissena polissena	LEP-56634	Ecuador: Imbabura: Santa Rita de Cachaco, ridge to S (0.773, -78.371)	OK065798
Hypomenitis polissena umbrana	02-SRNP-628	Costa Rica: Alajuela: Área de Conservación Guanacaste, Sector San Cristóbal, Sitio San Gerónimo (10.87, -85.375)	GU333968.1
Hypomenitis polissena umbrana	02-SRNP-629	Costa Rica: Alajuela: Área de Conservación Guanacaste, Sector San Cristóbal, Sitio San Gerónimo (10.87, -85.375)	GU333967.1
Hypomenitis theudelinda zalmunna	21000	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573779.1
Hypomenitis theudelinda zalmunna	E-28-4	Ecuador: Loja: El Guarango (-4.2, -79.183)	DQ157499.1
Hyoscada anchiala ecuadorina	20312	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068801.1
Hyoscada anchiala ecuadorina	20639	Ecuador: Orellana: Napo Wildlife Center, Napo trail (-0.51, -76.437)	EU068802.1
Hyoscada anchiala interrupta	2-2105	Peru: San Martín: km 7.2 Pongo-Barranquita (-6.285, -76.221)	HM051794.1
Hyoscada anchiala interrupta	2-512	Peru: San Martín: km 7.2 Pongo-Barranquita (-6.285, -76.221)	HM051793.1
Hyoscada anchiala mendax	2-1602	Peru: San Martín: La Antena (-6.452, -76.289)	HM051797.1
Hyoscada anchiala mendax	2-716	Peru: San Martín: Puente Serranoyacu above Rioja (-5.672, -77.676)	HM051796.1
Hyoscada illinissa aesion	C18807	Panama: Darién: Cana, near runway (7.757, -77.687)	FN646221.1
Hyoscada illinissa aesion	LEP-57275	Ecuador: Esmeraldas: Reserva de Tigrillo, Peñon del Santo trail (0.851, -78.778)	OK065813
Hyoscada illinissa brisotis	5-187	Peru: Loreto: Boca de Ushpayacu (-7.09, -75.855)	FN646223.1
Hyoscada illinissa brisotis	5-871	Peru: San Martín: Caño Negro, Río Biabo	FN646225.1
Hyoscada illinissa dolabella	2-3347	Peru: Cuzco: Pilcopata (-12.917, -71.4)	FN646226.1
Hyoscada illinissa dolabella	2-3424	Peru: Cuzco: Pilcopata to Santa Rosa de Huacaria	EU069047.1
Hyoscada illinissa ida	LEP-56601	Ecuador: Pastaza: 10.5 km SW Palora (-1.756, -78.03)	OK065796
Hyoscada illinissa ida	LS02-191	Ecuador: Sucumbios: Lake Garzacocho	EU069048.1
Hyoscada illinissa margarita	2-55	Peru: San Martín: Tarapoto-Yurimaguas, km 30 (-6.406, -76.303)	FN646231.1
Hyoscada illinissa margarita	2-121	Peru: San Martín: Quebrada Pucayaquillo	FN646233.1
Hyoscada illinissa morona	LEP-56602	Ecuador: Morona-Santiago: 2.5 km N Puerto Morona (-2.902, -77.742)	OK065797
Hyoscada illinissa morona	LEP-56919	Ecuador: Morona-Santiago: km 3 Puerto Morona-San José de Morona (-2.912, -77.707)	OK065802
Hyoscada illinissa tundayme	LEP-56962	Ecuador: Zamora-Chinchi: 2 km SW above Zurmi (-4.11, -78.689)	OK065809

Appendix 1. Voucher information and metadata for COI barcode sequences analyzed, continued.

Taxon	DNA voucher number	Locality (decimal latitude and longitude)	Genbank voucher
<i>Hyposcada illinissa tundayme</i>	LEP-56963	Ecuador: Zamora-Chinchi: Reserva Maycú (-4.212, -78.642)	OK065810
<i>Hyposcada kena flexibilis</i>	2-197	Peru: San Martín: Chumia (-6.6, -76.15)	HM051732.1
<i>Hyposcada kena flexibilis</i>	5-872	Peru: San Martín: Parque Nacional Cordillera Azul	EU069050.1
<i>Hyposcada kena kena</i>	EC458	Ecuador: Napo: Jatun Sacha (-1.05, -77.586)	FN646238.1
<i>Hyposcada kena kena</i>	LS07-6	Ecuador: Sucumbios: Lake Garzacocho	EU069051.1
<i>Hyposcada schausi lactea</i>	K5	Ecuador: Esmeraldas: Río Chuchuví (0.881, -78.515)	FN646240.1
<i>Hyposcada schausi lactea</i>	LEP-00111	Ecuador: Esmeraldas: Río Chuchuví (0.881, -78.515)	OK065732
<i>Hyposcada schausi lactea</i>	LEP-00114	Ecuador: Esmeraldas: Río Chuchuví (0.881, -78.515)	OK065733
<i>Hyposcada sinilia napoensis</i>	21740	Ecuador: no specific locality but presumed Ecuador	FN646230.1
<i>Hyposcada sinilia napoensis</i>	LEP-56599	Ecuador: Orellana: Río Cocaya cabañas (-0.918, -75.254)	OK065794
<i>Hyposcada sinilia napoensis</i>	LEP-56600	Ecuador: Orellana: Río Cocaya cabañas (-0.918, -75.254)	OK065795
<i>Hyposcada taliata laetitia</i>	21482	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	FN651607.1
<i>Hyposcada taliata n. ssp.</i>	5-1023	Peru: San Martín: Limite San Martín-Amazonas, km 387 (-5.658, -77.752)	FN646244.1
<i>Hyposcada taliata taliata</i>	6-11	Peru: Junín: 1.5 km N Mina Pichita (-11.091, -75.42)	FN651608.1
<i>Hyposcada virginiana adelphina</i>	CJ8833	Panama: Darién: Cerro Pirre (8, -77.667)	FN646245.1
<i>Hyposcada virginiana evanides</i>	8000	Panama: Chiriquí: Fortuna, Quebrada Hornito Trail (9.155, -82.224)	FN646246.1
<i>Hyposcada virginiana evanides</i>	8339	Panama: Chiriquí: Fortuna, Quebrada Hornito Trail (9.155, -82.224)	FN646247.1
<i>Hyposcada zarepha bonplandi</i>	LEP-01285	Venezuela: 'Venezuela'	MH893237.1
<i>Hypothesis anastasia acreana</i>	2-3263	Peru: Cuzco: Pilcopata (-12.917, -71.4)	EU068807.1
<i>Hypothesis anastasia anastasia</i>	2-275	Peru: San Martín: Pongo (-6.317, -76.283)	EU068808.1
<i>Hypothesis anastasia bicolora</i>	ME10-501	Ecuador: Napo: 'Hollin2' (-0.929, -77.74)	JX573787.1
<i>Hypothesis anastasia honesta</i>	20327	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068811.1
<i>Hypothesis anastasia honesta</i>	LEP-56586	Ecuador: Orellana: Tambococho (-0.978, -75.426)	OK065791
<i>Hypothesis anastasia porsenna</i>	LEP-56837	Ecuador: Morona-Santiago: Isla de las Conchas (-3.036, -77.975)	OK065801
<i>Hypothesis cantobrica cantobrica</i>	02-3266	Peru: Cuzco: Pilcopata (-12.917, -71.4)	MH893310.1
<i>Hypothesis cantobrica nundina</i>	RB360	Brazil: Rondônia: Ariquemes (-9.933, -63.05)	DQ157506.1
<i>Hypothesis cantobrica schunkeae</i>	4-68	Peru: Huánuco: Tingo María (-9.3, -76)	MH893313.1
<i>Hypothesis cantobrica schunkeae</i>	5-799	Peru: San Martín: Quebrada Yanayacu to Camp 2 on trail to Laguna del Mundo Perdido, Camp 1 (-6.742, -75.937)	MH893315.1
<i>Hypothesis cantobrica zamorita</i>	LEP-16716	Ecuador: Zamora-Chinchi: km 6 Los Encuentros-El Pangui (-3.731, -78.609)	OK065769
<i>Hypothesis cantobrica zamorita</i>	LEP-16717	Ecuador: Zamora-Chinchi: km 6 Los Encuentros-El Pangui (-3.731, -78.609)	OK065770
<i>Hypothesis daphnis daphnis</i>	03-28	Brazil: Mato Grosso: Cristalino Jungle Lodge (-8, -57.5)	MH893316.1
<i>Hypothesis daphnis ssp</i>	RB237	Brazil: Rondônia: Ariquemes (-9.933, -63.05)	DQ157507.1
<i>Hypothesis euclea intermedia</i>	20689	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068815.1
<i>Hypothesis euclea intermedia</i>	LS02-151	Ecuador: Sucumbios: Lake Garzacocho	EU068988.1
<i>Hypothesis euclea micheneri</i>	LEP-00109	Ecuador: Esmeraldas: San Francisco ridge (1.107, -78.699)	OK065731
<i>Hypothesis euclea micheneri</i>	LEP-08709	Ecuador: Esmeraldas: Angostura (0.888, -78.848)	OK065762
<i>Hypothesis euclea ssp</i>	LEPAR773-11	Argentina: Misiones: Departamento de Iguazú, Parque Nacional Iguazú, Seccional Yacui (-25.675, -54.169)	MF546050
<i>Hypothesis euclea ssp</i>	LEPIG151-11	Argentina: Misiones: Departamento de Iguazú, Parque Nacional Iguazú, Seccional Yacui (-25.675, -54.169)	MF547030
<i>Hypothesis euclea valora</i>	YB-BC12731	Panama: Panamá: no specific locality	HM416500.1
<i>Hypothesis euclea valora</i>	YB-BC14501	Panama: Panamá: no specific locality	HM416515.1
<i>Hypothesis fluonia berna</i>	LEP-06615	Ecuador: Pastaza: Kapawi Lodge (-2.542, -76.859)	OK065743
<i>Hypothesis fluonia berna</i>	LEP-06617	Ecuador: Pastaza: Kapawi village (-2.538, -76.836)	OK065744
<i>Hypothesis fluonia pardalina</i>	2-279	Peru: San Martín: Pongo (-6.317, -76.283)	EU068819.1
<i>Hypothesis fluonia seminigra</i>	2-3275	Peru: Cuzco: Pilcopata (-12.917, -71.4)	EU068820.1
<i>Hypothesis fluonia seminigra</i>	02-3276	Peru: Cuzco: Pilcopata (-12.917, -71.4)	MH893321.1
<i>Hypothesis leprieuri ssp</i>	Nap4	Brazil: Acre: Alto Rio Juruá	KJ56625.1
<i>Hypothesis lycaste ssp</i>	YB-BC1170417	Panama: Panamá: Barro Colorado Is, Zetek1 (9.153, -79.842)	MT357667.1
<i>Hypothesis lycaste ssp</i>	YB-BC1170455	Panama: Panamá: Barro Colorado Is, Zetek2 (9.153, -79.842)	MT357876.1
<i>Hypothesis moebiusi moebiusi</i>	20299	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU069060.1
<i>Hypothesis moebiusi moebiusi</i>	LS07-624	Ecuador: Sucumbios: Lake Garzacocho	EU069063.1
<i>Hypothesis ninonia amica</i>	LEP-06842	Ecuador: Morona-Santiago: Chupianza Grande (-2.741, -78.335)	OK065754
<i>Hypothesis ninonia amica</i>	LEP-54903	Ecuador: Zamora-Chinchi: km 6 Los Encuentros-El Pangui (-3.731, -78.609)	OK065773
<i>Hypothesis ninonia mamerus</i>	20806	Ecuador: Orellana: Añangu community (-0.494, -76.42)	EU068823.1
<i>Hypothesis ninonia mamerus</i>	LS02-51	Ecuador: Sucumbios: Sani Lodge (-0.442, -76.309)	EU068989.1
<i>Hypothesis ninonia mansuetus</i>	02-3357	Peru: Cuzco: Chontachaca (-13.033, -71.467)	MH893324.1
<i>Hypothesis ninonia mansuetus</i>	02-3401	Peru: Cuzco: Chontachaca (-13.033, -71.467)	MH893325.1
<i>Hypothesis ninonia meterus</i>	MJ05-258	Peru: San Martín: Tarapoto (-6.483, -76.367)	EU068824.1
<i>Hypothesis ninonia meterus</i>	MJ05-259	Peru: San Martín: Tarapoto (-6.483, -76.367)	EU068825.1
<i>Hypothesis semifulva pallisteri</i>	5-53	Peru: Loreto: Río Pauya	MH893339.1
<i>Hypothesis semifulva pallisteri</i>	2-1185	Peru: San Martín: Tarapoto-Yurimaguas, km 28 (-6.406, -76.307)	MH893333.1
<i>Hypothesis semifulva putumayoensis</i>	LEP-56587	Ecuador: Orellana: Río Cocaya cabañas (-0.918, -75.254)	OK065792
<i>Hypothesis semifulva satura</i>	20307	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068829.1
<i>Hypothesis semifulva satura</i>	LEP-06625	Ecuador: Pastaza: Kapawi Lodge (-2.542, -76.859)	OK065745
<i>Hypothesis semifulva semifulva</i>	350	Ecuador: Pastaza: Comunidad Shuar Mirador	MH893329.1
<i>Hypothesis semifulva semifulva</i>	LEP-55163	Ecuador: Zamora-Chinchi: 2 km SW above Zumi (-4.11, -78.689)	OK065786
<i>Hypothesis thea theatina</i>	03-31	Brazil: Mato Grosso: Cristalino Jungle Lodge (-8, -57.5)	MH893362.1
<i>Ithomia adelinda peruana</i>	2-1454	Peru: 'Peru'	HM051903.1
<i>Ithomia adelinda peruana</i>	MJ11-3400	Country unknown: no data	MH893238.1
<i>Ithomia agnosia agnosia</i>	20311	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068833.1
<i>Ithomia agnosia agnosia</i>	2-1651	Peru: San Martín: Puente Serranoyacu above Rioja (-5.672, -77.676)	EU068832.1
<i>Ithomia agnosia agnosia</i>	LEP-06629	Ecuador: Zamora-Chinchi: km 3 Guayzimi-San José (-4.06, -78.699)	OK065746
<i>Ithomia agnosia zumba</i>	LEP-01458	Ecuador: Zamora-Chinchi: Progreso, c. km 10 Zumba-Valladolid rd. (-4.834, -79.102)	OK065735
<i>Ithomia agnosia zumba</i>	LEP-54901	Ecuador: Zamora-Chinchi: km 8 Zumba-Chito rd. (-4.891, -79.115)	OK065771
<i>Ithomia agnosia zumba</i>	LEP-54902	Ecuador: Zamora-Chinchi: km 30 Zumba-Chito rd. (-4.945, -79.072)	OK065772
<i>Ithomia amarilla</i>	20222	Ecuador: Orellana: Napo Wildlife Center, Napo trail (-0.51, -76.437)	EU068835.1
<i>Ithomia amarilla</i>	LS02-123	Ecuador: Sucumbios: Lake Garzacocho	EU068991.1
<i>Ithomia arduinna ardua</i>	LEP-06801	Ecuador: Morona-Santiago: Río Yungantza (-2.87, -78.366)	OK065750
<i>Ithomia avella epona</i>	21466	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573790.1
<i>Ithomia avella epona</i>	E-35-5	Ecuador: Sucumbios: El Higuierón (0.515, -77.537)	DQ157508.1
<i>Ithomia cleora</i>	LEP-55114	Ecuador: Esmeraldas: Tundaloma Lodge (1.178, -78.748)	OK065782
<i>Ithomia diasia hippocrenis</i>	00-SRNP-11796	Costa Rica: Alajuela: Área de Conservación Guanacaste, Dos Ríos, Encanto (10.958, -85.355)	GU334032.1
<i>Ithomia diasia hippocrenis</i>	06-SRNP-33827	Costa Rica: Guanacaste: Sendero Laguna (10.987, -85.421)	JQ543483.1
<i>Ithomia drymo</i>	B-16-5	Brazil: São Paulo: Jundiá (-23.174, -46.522)	DQ069238.1
<i>Ithomia heraldica ssp</i>	03-SRNP-6461	Costa Rica: Alajuela: Área de Conservación Guanacaste, Sector San Cristóbal, Quebrada Cementerio (10.869, -85.386)	GU334030.1
<i>Ithomia heraldica ssp</i>	03-SRNP-7758	Costa Rica: Alajuela: Área de Conservación Guanacaste, Sector San Cristóbal, Sendero Corredor (10.874, -85.387)	GU334031.1
<i>Ithomia iphianassa ethilla</i>	LEP-08722	Ecuador: Esmeraldas: Tundaloma Lodge (1.178, -78.748)	OK065763
<i>Ithomia iphianassa ethilla</i>	LEP-08728	Ecuador: Esmeraldas: Angostura (0.888, -78.848)	OK065764
<i>Ithomia iphianassa occidentissa</i>	LEP-10860	Ecuador: Pichincha: km 20 Pacto-Guayabillas rd. (0.193, -78.858)	OK065767
<i>Ithomia iphianassa occidentissa</i>	LEP-56596	Ecuador: Pichincha: Reserva Mangaloma (0.121, -78.994)	OK065793
<i>Ithomia leila</i>	KW13-3b	Country unknown: no data	MH893240.1
<i>Ithomia salapia aquinia</i>	4-51	Peru: Huánuco: Tingo María, Castillo Grande, Villa Jennifer (-9.269, -76.005)	FN646350.1
<i>Ithomia salapia aquinia</i>	2-1445	Peru: San Martín: Chumia (-6.6, -76.15)	EU068838.1
<i>Ithomia salapia derasa</i>	E-44-2	Ecuador: Sucumbios: El Recodo (0.256, -77.478)	DQ157509.1
<i>Ithomia salapia salapia</i>	20246	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068840.1
<i>Ithomia salapia salapia</i>	20713	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068841.1
<i>Ithomia salapia salapia</i>	LS02-5	Ecuador: Sucumbios: Lake Garzacocho	EU069069.1
<i>Ithomia terra terra</i>	21470	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573791
<i>Ithomia terra terrana</i>	E-15-2	Ecuador: Pichincha: Tandapi (-0.45, -78.767)	DQ157510.1
<i>Ithomia terra terrana</i>	LEP-08734	Ecuador: Imbabura: Chontal Alto (0.297, -78.701)	OK065765

Appendix 1. Voucher information and metadata for COI barcode sequences analyzed, continued.

Taxon	DNA voucher number	Locality (decimal latitude and longitude)	Genbank voucher
Ithomia terra vulcana	INB0004101760	Costa Rica: Limón: entre Laguna Dabagri y Laguna Sacabico (9.617, -83.284)	ASAR02316-12
Ithomia terra vulcana	INB0004101761	Costa Rica: Limón: entre Laguna Dabagri y Laguna Sacabico (9.617, -83.284)	ASAR02314-12
Mcclungia cymo salonina	BAKU-42	Brazil: São Paulo: Monte Alegre do Sul	KX362035.1
Mcclungia cymo ssp	MACN-Bar-Lep-ct 01938	Argentina: Misiones: Departamento de Iguazú, Parque Nacional Iguazú, Seccional Yacui (-25.675, -54.169)	MF547301.1
Mcclungia cymo subtilis	06-205	Peru: San Martín: Achinamiza (-6.417, -75.85)	KX362063.1
Megoleria orestilla orestilla	EC402	Ecuador: Napo: Estación Científica Yanayacu (-0.59, -77.883)	FN646250.1
Megoleria orestilla orestilla	LEP-54920	Ecuador: Zamora-Chinchipe: Quebrada Troya (-4.792, -79.312)	OK065780
Methona confusa confusa	2-105	Peru: San Martín: Quebrada Pucayaquillo	EU068881.1
Methona confusa confusa	LS02-157A	Ecuador: Sucumbios: Lake Garzacocho	EU069080.1
Methona confusa psamathe	LEP-06464	Ecuador: Pastaza: Kapawi Lodge (-2.542, -76.859)	OK065739
Methona confusa psamathe	LEP-08634	Ecuador: Pichincha: km 20 Pacto-Guayabillas rd. (0.193, -78.858)	OK065756
Methona curvifascia	BAKU-57	Brasil: Pará: Parque Nacional da Amazonia	MH893262.1
Methona curvifascia	BAKU-58	Brasil: Pará: Parque Nacional da Amazonia	MH893263.1
Methona curvifascia	LS02-162	Ecuador: Sucumbios: Lake Garzacocho	EU069004.1
Methona curvifascia	MJ02-1094	Peru: San Martín: Tarapoto (-6.483, -76.367)	EU068884.1
Methona grandior batesi	20849	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU069082.1
Methona grandior batesi	20876	Ecuador: Orellana: Napo Wildlife Center, Napo trail (-0.51, -76.437)	EU068885.1
Methona grandior batesi	21734	Ecuador: Orellana: Pañacocho (-0.436, -76.067)	EU068886.1
Methona grandior batesi	21806	Ecuador: Orellana: Yarina (-0.471, -76.833)	EU068957.1
Methona grandior batesi	L-322-2005	Ecuador: Sucumbios: Lake Garzacocho	EU069083.1
Methona grandior batesi	LEP-06467	Ecuador: Pastaza: Kapawi village (-2.538, -76.836)	OK065740
Methona grandior batesi	LEP-55124	Ecuador: Orellana: Estación Científica Yasuni, camino torre (-0.679, -76.4)	OK065783
Methona grandior incana	LEP-57658	Ecuador: Pastaza: Mera (-1.467, -78.1)	OK065816
Methona maxima nigerrima	G101	Peru: Cuzco: Quebrada Morro Leguia (-13.117, -71.57)	MH893256.1
Methona singularis	BAKU-35	Brazil: Ceará: Palestina, Serra da Meruoca	MH893247.1
Methona singularis	BAKU-51	Brazil: Alagoas: Usina Serra Grande (-8.967, -36.05)	MH893235.1
Methona themisto ssp	LEPPA701-13	Argentina: Corrientes: Departamento Concepción, Ea. El Transito (-28.42, -57.692)	MF546881
Methona themisto themisto	B-20-1	Brazil: São Paulo: Mogi-Guaçu (-22.367, -46.933)	DQ157519.1
Oleria aegle n. ssp.	3-20	Brazil: Mato Grosso: Cristalino Jungle Lodge (-8, -57.5)	FN646257.1
Oleria agarista agarista	2-1307	Peru: San Martín: km 7.2 Pongo-Barranquita (-6.285, -76.221)	FN646258.1
Oleria agarista agarista	2-293	Peru: San Martín: km 7.2 Pongo-Barranquita (-6.285, -76.221)	EU069092.1
Oleria agarista agarista	L-359-2005	Ecuador: Sucumbios: Lake Garzacocho	EU069094.1
Oleria amalda faunula	KW10	Ecuador: Esmeraldas: Río Chuchuvi (0.881, -78.515)	FN651609.1
Oleria amalda modesta	EC94	Ecuador: Pichincha: 106.5 km from Mindo	FN646262.1
Oleria amalda modesta	LEP-08676	Ecuador: Esmeraldas: Estero Tachina (0.9, -79.565)	OK065760
Oleria antaxis antaxis	BAKU-55	Brasil: Pará: Parque Nacional da Amazonia	MH893264.1
Oleria antaxis antaxis	BAKU-56	Brasil: Pará: Parque Nacional da Amazonia	MH893265.1
Oleria assimilis assimilis	20278	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068912.1
Oleria assimilis assimilis	5-615	Peru: San Martín: Robashca, Puesto de Control 11 (-6.706, -76.033)	FN646266.1
Oleria assimilis assimilis	LS07-4	Ecuador: Sucumbios: Lake Garzacocho	EU069095.1
Oleria astrea astrea	BAKU28	Brazil: Bahia: Camamu	MH893283.1
Oleria astrea astrea	BAKU-54	Brazil: Alagoas: Usina Serra Grande (-8.967, -36.05)	MH893266.1
Oleria athalina banjana	EC414	Ecuador: Napo: Estación Científica Yanayacu (-0.59, -77.883)	FN646269.1
Oleria athalina banjana	LEP-55171	Ecuador: Loja: Quebrada Angashcola (-4.565, -79.369)	OK065787
Oleria attalia tabera	21176	Ecuador: Zamora-Chinchipe: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573797.1
Oleria attalia tabera	21234	Ecuador: Zamora-Chinchipe: San Francisco, casa de Arcoiris (-3.988, -79.095)	FN646277.1
Oleria baizana baizana	EC382	Ecuador: Napo: Estación Científica Yanayacu (-0.59, -77.883)	FN646278.1
Oleria baizana baizana	EC413	Ecuador: Napo: Estación Científica Yanayacu (-0.59, -77.883)	FN646281.1
Oleria bifurcata	LEP-56952	Ecuador: Carchi: Santa Rosa (0.827, -78.128)	MT790704.1
Oleria bifurcata	LEP-56953	Ecuador: Carchi: Santa Rosa (0.827, -78.128)	MT790705.1
Oleria bioculata tapio	2-750	Peru: San Martín: Puente Serranoyacu above Rioja (-5.672, -77.676)	FN646282.1
Oleria bioculata tapio	2-879	Peru: San Martín: Puente Aguas Verdes (-5.683, -77.65)	FN646283.1
Oleria boyeri	LEP-01270	Venezuela: 'Venezuela'	MH893377.1
Oleria cyrene solida	21475	Ecuador: Zamora-Chinchipe: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573798.1
Oleria cyrene solida	EC394	Ecuador: Napo: Estación Científica Yanayacu (-0.59, -77.883)	FN646287.1
Oleria cyrene susianoides	KW05	Ecuador: Napo: Estación Científica Yanayacu (-0.59, -77.883)	FN651616.1
Oleria didymaea didymaea	2-3370	Peru: Cuzco: Chontachaca (-13.033, -71.467)	FN646259.1
Oleria didymaea didymaea	2-3613	Peru: Cuzco: no specific locality	FN646260.1
Oleria didymaea ramona	6-54	Peru: Junín: Camino a Catarata del Tiro (-11.138, -75.34)	FN646291.1
Oleria didymaea ramona	6-55	Peru: Junín: Camino a Catarata del Tiro (-11.138, -75.34)	FN646292.1
Oleria didymaea ramona	5-255	Peru: Loreto: Pongo del Río Paywua	FN646289.1
Oleria didymaea ramona	5-635	Peru: San Martín: Robashca, Puesto de Control 11 (-6.706, -76.033)	FN646290.1
Oleria estella estella	2-406	Peru: San Martín: La Antena (-6.452, -76.289)	FN646296.1
Oleria estella estella	4-400	Peru: San Martín: La Antena (-6.452, -76.289)	FN646295.1
Oleria fasciata fasciata	21114	Ecuador: Zamora-Chinchipe: San Francisco, casa de Arcoiris (-3.988, -79.095)	FN646298.1
Oleria fasciata fasciata	2001-2002-9-2	Ecuador: Sucumbios: Río Sucio (0.475, -77.555)	FN646297.1
Oleria flora flora	NapK17	Brazil: Pará: Dom Eliseu	KJ566622.1
Oleria fumata fumata	K15	Colombia: Antioquia: El Socorro-Amagá (6.251, -75.687)	FN651622.1
Oleria fumata fumata	OF30	Colombia: Antioquia: Jardín, Finca Montenegro	FN646300.1
Oleria fumata richardina	LEP-55129	Ecuador: Carchi: Santa Rosa (0.827, -78.128)	OK065784
Oleria fumata richardina	LEP-55130	Ecuador: Carchi: Santa Rosa (0.827, -78.128)	OK065785
Oleria gunilla lota	20699	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068918.1
Oleria gunilla lota	2-2118	Peru: San Martín: km 7.2 Pongo-Barranquita (-6.285, -76.221)	HM051709.1
Oleria gunilla serdolis	4-470	Peru: San Martín: Parque Nacional Cordillera Azul	EU069098.1
Oleria gunilla serdolis	5-923	Peru: 'Peru'	HM051720.1
Oleria ileridina lerida	20438	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU069099.1
Oleria ileridina lerida	2-2023	Peru: Loreto: Yurimaguas-Tarapoto, km 26 (-5.993, -76.238)	FN646306.1
Oleria ileridina lerida	EC446	Ecuador: Napo: Jatun Sacha (-1.05, -77.586)	FN646301.1
Oleria makrena caucana	OM21	Colombia: Antioquia: Jardín, Finca El Vergel (5.606, -75.838)	FN646302.1
Oleria makrena makrena	21165	Venezuela: Aragua: Rancho Grande (10.343, -67.684)	JX573800.1
Oleria makrena makrena	21166	Venezuela: Aragua: Rancho Grande (10.343, -67.684)	FN651625.1
Oleria makrena makrenita	21115	Ecuador: Zamora-Chinchipe: San Francisco, casa de Arcoiris (-3.988, -79.095)	FN651624.1
Oleria makrena makrenita	EC409	Ecuador: Napo: Estación Científica Yanayacu (-0.59, -77.883)	FN646305.1
Oleria onega astigara	20227	Ecuador: Orellana: Napo Wildlife Center, Napo trail (-0.51, -76.437)	EU068922.1
Oleria onega astigara	20235	Ecuador: Orellana: Napo Wildlife Center (-0.524, -76.441)	EU068970.1
Oleria onega astigara	20677	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068923.1
Oleria onega astigara	CI20204	Ecuador: Orellana: Napo Wildlife Center, Tiputini trail (-0.529, -76.417)	FN646330.1
Oleria onega astigara	LS02-110	Ecuador: Sucumbios: Lake Garzacocho	EU069013.1
Oleria onega astigara	LS02-7	Ecuador: Sucumbios: Lake Garzacocho	EU069014.1
Oleria onega janarilla	2-1165	Peru: San Martín: km 5 Shapaja-Chasuta (-6.593, -76.219)	EU068924.1
Oleria onega janarilla	2-515	Peru: San Martín: km 7.2 Pongo-Barranquita (-6.285, -76.221)	HM051918.1
Oleria onega n. ssp. [4]	2-1674	Peru: San Martín: Puente Serranoyacu above Rioja (-5.672, -77.676)	HM051987.1
Oleria onega n. ssp. [4]	2-835	Peru: San Martín: Puente Serranoyacu above Rioja (-5.672, -77.676)	HM051973.1
Oleria padilla cajamarcensis	5-1025	Peru: San Martín: Limite San Martín-Amazons, km 387 (-5.658, -77.752)	FN646317.1
Oleria padilla cajamarcensis	5-1169	Peru: San Martín: Venceremos + 4 km (Segundo Baden) (-5.668, -77.751)	FN646318.1
Oleria padilla gorkyi	6-75	Peru: Junín: Puente Pan de Azúcar, S San Ramón (-11.172, -75.45)	FN651612.1
Oleria padilla gorkyi	6-14	Peru: Junín: 1.5 km N Mina Pichita (-11.091, -75.42)	FN651610.1
Oleria padilla gorkyi	6-15	Peru: Junín: 1.5 km N Mina Pichita (-11.091, -75.42)	MH893273.1
Oleria padilla padilla	LEP-08667	Ecuador: Pichincha: Tandayapa Bird Lodge (0.002, -78.678)	OK065758

Appendix 1. Voucher information and metadata for COI barcode sequences analyzed, continued.

Taxon	DNA voucher number	Locality (decimal latitude and longitude)	Genbank voucher
Oleria padilla padilla	LEP-08669	Ecuador: Pichincha: Tandayapa Bird Lodge (0.002, -78.678)	OK065759
Oleria paula paula	06-SRNP-30324	Costa Rica: Guanacaste: Pasmompa (11.018, -85.406)	JQ542174.1
Oleria paula paula	MAL-04156	MEXICO: Campeche: Reserva de la Biosfera de Calakmul (18.184, 88.248)	GU658907.1
Oleria phenomoe phenomoe	21167	Venezuela: Aragua: Rancho Grande (10.343, -67.684)	FN651627.1
Oleria phenomoe phenomoe	MC2	Venezuela: Aragua: Colonia Tovar (10.417, -67.267)	FN651626.1
Oleria quintina	6-72	Peru: Junin: Puente Pan de Azúcar, S San Ramón (-11.172, -75.45)	FN646324.1
Oleria quintina	6-77	Peru: Junin: Puente Pan de Azúcar, S San Ramón (-11.172, -75.45)	FN646325.1
Oleria radina bonita	2001-2002-11-2	Ecuador: Sucumbios: Old rd. to La Alegría (0.558, -77.528)	FN646326.1
Oleria rubescens	8369	Panama: Chiriquí: Fortuna, Quebrada Hornito Trail (9.155, -82.224)	DO085460.2
Oleria rubescens	8404	Panama: Chiriquí: Fortuna, Continental Divide Trail (8.809, -82.224)	FN646327.1
Oleria santineza reducida	2001-2002-3-2	Ecuador: Sucumbios: Río Sucio (0.475, -77.555)	EU068928.1
Oleria santineza reducida	KW13	Ecuador: Sucumbios: Río Palmar, trail above S. bank (0.423, -77.54)	FN651628.1
Oleria santineza santineza	21484	Ecuador: Zamora-Chinchipec: San Francisco, casa de Arcoiris (-3.988, -79.095)	FN651629.1
Oleria santineza santineza	21497	Ecuador: Zamora-Chinchipec: San Francisco, casa de Arcoiris (-3.988, -79.095)	FN651630.1
Oleria sexmaculata sexmaculata	20253	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU069100.1
Oleria sexmaculata sexmaculata	20469	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068930.1
Oleria similigena n. ssp. [1]	napk20	Brazil: 'Brazil'	KT225387.1
Oleria tigilla n. ssp. [3]	PE18-24	Peru: Madre de Dios: Reserva de Tambopata [= Explorer's Inn] (-12.833, -69.283)	FN651619.1
Oleria tigilla raya	LEP-56964	Ecuador: Zamora-Chinchipec: Reserva Maycú (-4.212, -78.642)	OK065811
Oleria tigilla raya	LEP-56965	Ecuador: Zamora-Chinchipec: Reserva Maycú (-4.212, -78.642)	OK065812
Oleria tigilla tigilla	ME10-282	Ecuador: Napo: Mariposa (-0.908, -77.786)	JX573802.1
Oleria tremona benigna	21196	Ecuador: Zamora-Chinchipec: San Francisco, casa de Arcoiris (-3.988, -79.095)	FN651631.1
Oleria tremona benigna	21241	Ecuador: Zamora-Chinchipec: San Francisco, casa de Arcoiris (-3.988, -79.095)	FN651632.1
Oleria tremona benigna	LEP-06747	Ecuador: Zamora-Chinchipec: km 4.3 San Andrés-Jimbura rd. (-4.8, -79.305)	OK065747
Oleria tremona benigna	LEP-06748	Ecuador: Zamora-Chinchipec: km 4.3 San Andrés-Jimbura rd. (-4.8, -79.305)	OK065748
Oleria tremona tremona	2001-2002-6-4	Ecuador: Sucumbios: km 8 La Bonita-Tulcán rd. (0.515, -77.525)	FN646333.1
Oleria tremona tremona	EC407	Ecuador: Napo: Estación Científica Yanayacu (-0.59, -77.883)	FN646304.1
Oleria vicina	2987	Panama: Chiriquí: Fortuna, Continental Divide Trail (8.809, -82.224)	FN646334.1
Oleria vicina	CJ8485	Panama: Chiriquí: Boquete, Los Quetzales Trail, Bajo Mono	FN646337.1
Oleria victorine sarilis	4-262	Peru: Ucayali: Bosque Nacional von Humboldt, INIA (-8.825, -75.055)	FN646340.1
Oleria victorine sarilis	MJ05-351	Peru: San Martín: Tarapoto (-6.483, -76.367)	EU068932.1
Oleria victorine victorine	2-3066	Peru: Cuzco: no specific locality	FN646341.1
Oleria victorine victorine	2-3339	Peru: Cuzco: Pilcopata (-12.917, -71.4)	EU068931.1
Oleria zelica pagasa	CJ8094	Panama: Chiriquí: Fortuna, Quebrada Aleman (8.807, -82.221)	FN646344.1
Oleria zelica pagasa	CJ8433	Panama: Chiriquí: Fortuna, Quebrada Hornito Trail (9.155, -82.224)	FN646347.1
Oleria zelica zelica	F17-7	Ecuador: Carchi: Lita (0.87, -78.451)	FN646349.1
Ollantaya aegineta inelegans	21126	Ecuador: Zamora-Chinchipec: San Francisco, casa de Arcoiris (-3.988, -79.095)	FN646251.1
Ollantaya aegineta inelegans	21300	Ecuador: Zamora-Chinchipec: San Francisco, casa de Arcoiris (-3.988, -79.095)	FN646252.1
Ollantaya canilla	6-41	Peru: Junin: 0-1 km E Mina Pichita (-11.087, -75.417)	FN651615.1
Ollantaya canilla	6-13	Peru: Junin: 1.5 km N Mina Pichita (-11.091, -75.42)	FN651614.1
Ollantaya canilla	5-1174	Peru: San Martín: Venceremos + 4 km (Segundo Baden) (-5.668, -77.751)	FN646253.1
Ollantaya canilla	5-1175	Peru: San Martín: Venceremos + 4 km (Segundo Baden) (-5.668, -77.751)	FN646254.1
Ollantaya olerioides baeza	21217	Ecuador: Zamora-Chinchipec: San Francisco, casa de Arcoiris (-3.988, -79.095)	FN646255.1
Ollantaya olerioides baeza	21283	Ecuador: Zamora-Chinchipec: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573805.1
Pigritina sarepta famina	21693	Ecuador: Orellana: Pañacocha (-0.436, -76.067)	OK362021.1
Pteronymia aletta lilla	20059	Ecuador: Esmeraldas: Esmeraldas (0.967, -79.654)	KY750031.1
Pteronymia aletta lilla	LEP-08681	Ecuador: Esmeraldas: km 11-12 Lagarto-Anchayacu rd. (1.007, -79.211)	OK065761
Pteronymia alida cosanga	MJ07-626	Ecuador: Napo: Estación Científica Yanayacu (-0.59, -77.883)	KY750035.1
Pteronymia alida francisca	21025	Ecuador: Zamora-Chinchipec: San Francisco, casa de Arcoiris (-3.988, -79.095)	KY750033.1
Pteronymia alida francisca	21093	Ecuador: Zamora-Chinchipec: San Francisco, casa de Arcoiris (-3.988, -79.095)	KY750034.1
Pteronymia alida francisca	21185	Ecuador: Zamora-Chinchipec: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573812.1
Pteronymia alina machay	20056	Ecuador: Zamora-Chinchipec: Quebrada San Ramón, power station (-3.97, -79.062)	KY750108.1
Pteronymia alina machay	21224	Ecuador: Zamora-Chinchipec: San Francisco, casa de Arcoiris (-3.988, -79.095)	KY750109.1
Pteronymia alissa alissa	LEP-08684	Ecuador: Carchi: Río Chorro Blanco (0.805, -78.145)	KY750029.1
Pteronymia andreas andreas	21323	Ecuador: Zamora-Chinchipec: San Francisco, casa de Arcoiris (-3.988, -79.095)	KY750038.1
Pteronymia andreas andreas	21607	Peru: Cuzco: San Pedro (-13.053, -71.541)	KY750039.1
Pteronymia artena afrania	21565	Peru: Cuzco: San Pedro (-13.053, -71.541)	KY750043.1
Pteronymia artena afrania	ME10-370	Ecuador: Napo: Cocodrilo (-0.649, -77.791)	KY750044.1
Pteronymia asopo	21169	Venezuela: Aragua: Rancho Grande Biological Station (10.343, -67.684)	KY750046.1
Pteronymia carlia	BAKU-18	Brazil: Minas Gerais: Alto Caparaó, Parque Nacional do Caparaó, Base alto Caparaó	KY750047.1
Pteronymia carlia	MACN-Bar-Lep-ct 02781	Argentina: Formosa: Departamento de Pilcomayo, Parque Nacional Río Pilcomayo, Seccional Estero Poi (-25.119, -58.17)	MF546236.1
Pteronymia cottyto cottyto	MJ07-626	Nicaragua: Matagalpa: Matagalpa-Jinotega, km 146 (13.022, -85.921)	KY750028.1
Pteronymia cottyto ssp	MAL-04151	Mexico: Campeche: Calakmul, Reserva de la Biosfera de Calakmul, 24 km N X-Pujil, Entrada a 'El Papagayo' (18.725, -89.39)	GU658910.1
Pteronymia cuneata	20071	Ecuador: Sucumbios: Río Palmar (0.418, -77.537)	KY750050.1
Pteronymia cuneata	ME10-322	Ecuador: Napo: Estación Científica Yanayacu (-0.59, -77.883)	JX573816.1
Pteronymia dispas	LEP-11330	Colombia: Antioquia: Finca Jacaranda (5.674, -75.701)	KY750027.1
Pteronymia dispas	PT033	Colombia: Antioquia: Fredonia - 'San Cayetano' F1	KY750054.1
Pteronymia donella donata	MJ07-629	Panama: Darién: Cana (7.933, -77.717)	KY750024.1
Pteronymia donella donata	MJ07-630	Panama: Darién: Cana (7.933, -77.717)	KY750026.1
Pteronymia donella donella	MJ07-632	Colombia: Cundinamarca: 23.6 km W Wileta (5.017, -74.483)	KY750023.1
Pteronymia donella donella	PT001	Colombia: Antioquia: Amalfi, Porcé, El Caimán	KY750055.1
Pteronymia donella donella	PT025	Colombia: Antioquia: Amalfi, Porcé, El Encanto	KY750005.1
Pteronymia euritea	BAKU-1	Brazil: Minas Gerais: Alto Caparaó, Parque Nacional do Caparaó, Base alto Caparaó	KY750219.1
Pteronymia forsteri	02-1429	Peru: San Martín: km 14 Shapaja-Chasuta	KF268429.1
Pteronymia forsteri	BAKU-10	Brazil: Acre: Marechal Thaumaturgo, Reserva Extrativista Alto Rio Jurua, Colocação Pedra Pintada	KY750059.1
Pteronymia fulvimargo	04-SRNP-48111	Costa Rica: Guanacaste: Quebrada Otilio (10.887, -85.475)	GU157530.1
Pteronymia fulvimargo	99-SRNP-4473	Costa Rica: Alajuela: Área de Conservación Guanacaste, Sector San Cristóbal, Sendero Corredor (10.874, -85.387)	GU334305.1
Pteronymia gertschi gertschi	20072	Ecuador: Morona-Santiago: Yakunk-Cutucú trail, river camp (-2.752, -78.182)	KY750060.1
Pteronymia granica granica	165	Ecuador: Loja: Vilcabamba Ecolodge, Ruinas Lodge to Rumi Wilco	KY750061.1
Pteronymia granica granica	LEP-01505	Ecuador: Loja: Santuario San Vicente, Quebrada El Sauce (-3.948, -79.448)	KY750062.1
Pteronymia hara hara	20035	Ecuador: Zamora-Chinchipec: San Francisco, casa de Arcoiris (-3.988, -79.095)	KY750063.1
Pteronymia hara hara	21135	Ecuador: Zamora-Chinchipec: San Francisco, casa de Arcoiris (-3.988, -79.095)	KY750065.1
Pteronymia hara hara	E-39-43	Ecuador: Sucumbios: La Bonita (0.478, -77.545)	DO157538.1
Pteronymia hara hara	ME10-371	Ecuador: Napo: Cocodrilo (-0.649, -77.791)	KY750218.1
Pteronymia hara hara	LEP-56957	Ecuador: Carchi: Santa Rosa (0.827, -78.128)	OK065808
Pteronymia hara seimonis	LEP-04484	Ecuador: Pichincha: km 20 Pacto-Guayabillas rd. (0.193, -78.858)	KY750019.1
Pteronymia hara seimonis	LEP-04485	Ecuador: Pichincha: 12 km SW Las Tolas (0.051, -78.838)	KY750020.1
Pteronymia inania inania	20070	Ecuador: 'Ecuador'	KY750067.1
Pteronymia inania inania	ME10-178	Ecuador: Napo: Cocodrilo (-0.649, -77.791)	JX573818.1
Pteronymia inania inania	ME10-385	Ecuador: Napo: Cocodrilo (-0.649, -77.791)	KY750066.1
Pteronymia latilla barilla	LEP-01514	Ecuador: Manabí: ridge c. 7.5 km SE Ayampe (-1.704, -80.784)	OK065736
Pteronymia latilla fulvescens	04-SRNP-48109	Costa Rica: Guanacaste: Quebrada Otilio (10.887, -85.475)	JQ535560.1
Pteronymia latilla fulvescens	04-SRNP-48112	Costa Rica: Guanacaste: Quebrada Otilio (10.887, -85.475)	JQ535561.1
Pteronymia latilla nigricans	LEP-11341	Colombia: Antioquia: Finca Jacaranda (5.674, -75.701)	KY750018.1
Pteronymia latilla nigricans	PT007	Colombia: Antioquia: El Socorro-Amagá (6.251, -75.687)	KY750070.1
Pteronymia laura	HW6	Colombia: Cundinamarca: Gruadas	KY750221.1
Pteronymia linzera linzera	20081	Ecuador: Sucumbios: Old rd. to La Alegría (0.558, -77.528)	KY750104.1
Pteronymia linzera linzera	20083	Ecuador: Loja: Yangana (-4.357, -79.167)	KY750214.1
Pteronymia linzera linzera	E-43-16	Ecuador: no specific locality but presumed Ecuador	DO069242.1

Appendix 1. Voucher information and metadata for COI barcode sequences analyzed, continued.

Taxon	DNA voucher number	Locality (decimal latitude and longitude)	Genbank voucher
<i>Pteronymia linzera linzera</i>	ME10-453	Ecuador: Napo: Cocrodrilo (-0.649, -77.791)	KY750105.1
<i>Pteronymia lonera</i>	2983	Panama: Chiriquí: Fortuna, Continental Divide Trail	KY750072.1
<i>Pteronymia lonera</i>	8327	Panama: Chiriquí: Fortuna, Quebrada Hornito Trail (9.155, -82.224)	KY750073.1
<i>Pteronymia luisa</i>	LEP-04481	Ecuador: Pichincha: Bellavista Lodge ridge road (0.017, -78.689)	OK065737
<i>Pteronymia luisa</i>	LEP-06893	Ecuador: Carchi: E of Maldonado (0.887, -78.096)	KY750008.1
<i>Pteronymia mariannae mariannae</i>	164	Ecuador: Loja: Vilcabamba Ecologde, Ruinas Lodge to Rumi Wilco	KY750049.1
<i>Pteronymia mariannae mariannae</i>	21336	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	KY750051.1
<i>Pteronymia medellina medellina</i>	BMC2203	Colombia: Cauca: Cajibío, Bellavista	KY750074.1
<i>Pteronymia medellina medellina</i>	PT005	Colombia: Antioquia: Ciudad Bolívar, Las Acacias	KY750217.1
<i>Pteronymia obscuratus</i>	8978	Panama: Darién: Río Pi-as Campsite (7.64, -78.193)	KY750075.1
<i>Pteronymia olimba olimba</i>	MJ07-655	Bolivia: La Paz: Caranavi (-15.833, -67.573)	KY750017.1
<i>Pteronymia oneida oneida</i>	20036	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	KY750076.1
<i>Pteronymia oneida oneida</i>	ME10-347	Ecuador: Napo: Estación Científica Yanayacu (-0.59, -77.883)	KY750079.1
<i>Pteronymia ozia ozia</i>	20049	Ecuador: Morona-Santiago: Yakunk-Cutucú trail, lower ridge (-2.761, -78.161)	KY750080.1
<i>Pteronymia ozia ozia</i>	21024	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573820.1
<i>Pteronymia ozia tanampaya</i>	21599	Peru: Cuzco: San Pedro (-13.053, -71.541)	KY750081.1
<i>Pteronymia parva</i>	00-SRNP-1047	Costa Rica: Alajuela: Área de Conservación Guanacaste, Sector San Cristóbal, Melina Bufalo (10.884, -85.385)	GU334307.1
<i>Pteronymia parva</i>	06-SRNP-9373	Costa Rica: Guanacaste: Área de Conservación Guanacaste, Sector San Cristóbal, Camino Brasilia (10.924, -85.37)	JQ548397.1
<i>Pteronymia picta notilla</i>	8342	Panama: Chiriquí: Fortuna, Quebrada Hornito Trail (9.155, -82.224)	KY750082.1
<i>Pteronymia picta notilla</i>	8846	Panama: Darién: Cana (7.933, -77.717)	KY750083.1
<i>Pteronymia picta picta</i>	PT013	Colombia: Antioquia: Amalfí, Porcé, La Hacienda	KY750216.1
<i>Pteronymia picta picta</i>	PT016	Colombia: Antioquia: Amalfí, Porcé, La Hacienda	KY750085.1
<i>Pteronymia primula primula</i>	20213	Ecuador: Orellana: Napo Wildlife Center, Tiputini trail (-0.529, -76.417)	EU069103.1
<i>Pteronymia primula primula</i>	20255	Ecuador: Orellana: Napo Wildlife Center, Napo trail (-0.51, -76.437)	EU069104.1
<i>Pteronymia rufocincta</i>	MJ07-659	Mexico: Michoacan: La Nuéz	KY750015.1
<i>Pteronymia rufocincta</i>	MJ07-660	Mexico: Michoacan: La Nuéz	KY750016.1
<i>Pteronymia sao antisao</i>	2-560	Peru: San Martín: Convento (-6.283, -76.283)	EU068943.1
<i>Pteronymia sao antisao</i>	4-169	Peru: Ucayali: Pucallpa, Lago Yarinacocha, Caño Tushmo	KY750088.1
<i>Pteronymia sao antisao</i>	4-170	Peru: Ucayali: Pucallpa, Lago Yarinacocha, Caño Tushmo	KY750089.1
<i>Pteronymia sao loreto</i>	20045	Ecuador: Orellana: Río Yuturi, lodge trail (-0.548, -76.033)	KY750090.1
<i>Pteronymia sao loreto</i>	20274	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068944.1
<i>Pteronymia sao loreto</i>	20286	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU069105.1
<i>Pteronymia sao loreto</i>	20520	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068945.1
<i>Pteronymia sao loreto</i>	20522	Ecuador: Orellana: Boca del Río Añangu (-0.529, -76.395)	EU068946.1
<i>Pteronymia serrata amplificata</i>	20033	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	KY750091.1
<i>Pteronymia serrata amplificata</i>	21516	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	KY750092.1
<i>Pteronymia sexpunctata sexpunctata</i>	MJ07-663	Peru: Amazonas: Quebrada Gebil (-6.467, -77.4)	KY750013.1
<i>Pteronymia sexpunctata sexpunctata</i>	MJ07-666	Peru: Cuzco: San Pedro (-13.053, -71.541)	KY750014.1
<i>Pteronymia simplex simplex</i>	8407	Panama: Chiriquí: Fortuna, Café Vista Hermosa	KY750093.1
<i>Pteronymia tamina</i>	21474	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573822.1
<i>Pteronymia tamina</i>	21479	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	KY750094.1
<i>Pteronymia teresita</i>	LEP-04482	Ecuador: Pichincha: 12 km SW Las Tolas (0.051, -78.838)	KY750012.1
<i>Pteronymia teresita</i>	LEP-04483	Ecuador: Pichincha: 7 km SW Las Tolas (0.057, -78.818)	KY750111.1
<i>Pteronymia thabena denticulata</i>	21606	Peru: Cuzco: San Pedro (-13.053, -71.541)	KY750213.1
<i>Pteronymia thabena denticulata</i>	2-797	Peru: San Martín: Puente Serranoyacu above Rioja (-5.672, -77.676)	KY750095.1
<i>Pteronymia thabena thabena</i>	20057	Ecuador: Morona-Santiago: km 14 Limón-Gualaceo rd. (-3.01, -78.5)	KY750215.1
<i>Pteronymia thabena thabena</i>	21480	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573823.1
<i>Pteronymia thabena thabena</i>	ME10-386	Ecuador: Napo: Cocrodrilo (-0.649, -77.791)	KY750116.1
<i>Pteronymia tícida tícida</i>	21263	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	JX573824.1
<i>Pteronymia tícida tícida</i>	E-39-34	Ecuador: Sucumbios: La Bonita (0.478, -77.545)	DQ157541.1
<i>Pteronymia tícida yungava</i>	21592	Peru: Cuzco: San Pedro (-13.053, -71.541)	KY750101.1
<i>Pteronymia tucuna</i>	2-3168	Peru: Cuzco: Palma Real	KY750102.1
<i>Pteronymia tucuna</i>	5-1372	Peru: San Martín: Bocatoma Río Shilcayo	KY750103.1
<i>Pteronymia vestilla sparsa</i>	20270	Ecuador: Orellana: nr. Coca (-0.467, -76.983)	EU069106.1
<i>Pteronymia vestilla sparsa</i>	20272	Ecuador: Orellana: Napo Wildlife Center, Napo trail (-0.51, -76.437)	EU068947.1
<i>Pteronymia zerlina pronuba</i>	LEP-08685	Ecuador: Carchi: Río Chorro Blanco (0.805, -78.145)	KY750006.1
<i>Pteronymia zerlina pronuba</i>	LEP-08686	Ecuador: Pichincha: km 9 Pacto-Guayabillas rd. (0.155, -78.821)	KY750007.1
<i>Scada karschina delicata</i>	BPU40	Brazil: Alagoas: Quebrangulo	MTS12664.1
<i>Scada karschina delicata</i>	BPU41	Brazil: Alagoas: Quebrangulo	MTS12665.1
<i>Scada karschina karschina</i>	BAKU-22	Brazil: Rio de Janeiro: Reserva Ecologica de Guapiacu, Cachoeiras de Macacu	MH893270.1
<i>Scada karschina karschina</i>	BPU62	Brazil: Bahia: Reserva Biológica de Una (-15.173, -39.103)	MTS12666.1
<i>Scada karschina karschina</i>	G130	Peru: Cajamarca: Quebrada El Platano (-6.836, -79.17)	MH893251.1
<i>Scada kusa</i>	LEP-06866	Ecuador: Zamora-Chinchi: Río Palanda, km 14 Valladolid-Zumba rd. (-4.631, -79.138)	MTS24278.1
<i>Scada reckia ethica</i>	2-1621	Peru: 'Peru'	HM051908.1
<i>Scada reckia junina</i>	05-688	Peru: San Martín: Robashca, Puesto de Control 11 (-6.706, -76.033)	MH893274.1
<i>Scada reckia junina</i>	4-289	Peru: 'Peru'	HM051905.1
<i>Scada reckia ortygia</i>	PE-10-15	Peru: Cuzco: Quebrada Chaupimayo (-12.95, -72.667)	DQ157544.1
<i>Scada reckia reckia</i>	BPU155	Brazil: Pernambuco: Areia	MTS12671.1
<i>Scada reckia reckia</i>	BPU160	Brazil: Alagoas: Quebrangulo	MTS12672.1
<i>Scada reckia ruiza</i>	LEP-06868	Ecuador: Zamora-Chinchi: km 22 Zumba-Loja rd. (-4.769, -79.118)	MTS24281.1
<i>Scada reckia ruiza</i>	LEP-55157	Ecuador: Zamora-Chinchi: km 2.6 El Pite-Río Mayo rd. (-4.866, -79.094)	MTS24282.1
<i>Scada reckia theaphia</i>	BPU125	Brazil: Mato Grosso: Alta Floresta	MTS12675.1
<i>Scada reckia theaphia</i>	BPU58	Brazil: Acre: Marechal Thaumaturgo (-8.942, -72.787)	MTS12674.1
<i>Scada zemira</i>	LEP-01499	Ecuador: Loja: Reserva Jorupe, W Macará (-4.379, -79.904)	MH893277.1
<i>Scada zibia batesi</i>	20266	Ecuador: Orellana: Napo Wildlife Center, Napo trail (-0.51, -76.437)	EU068951.1
<i>Scada zibia batesi</i>	BPU151	Brazil: Acre: Marechal Thaumaturgo (-8.942, -72.787)	MTS12676.1
<i>Scada zibia xanthina</i>	8296	Panama: Colón: Santa Rita ridge (9.357, -79.723)	EU068949.1
<i>Scada zibia zeroca</i>	LEP-06892	Ecuador: Esmeraldas: Río Chuchuvi (0.881, -78.515)	MTS24283.1
<i>Scada zibia zeroca</i>	LEP-56652	Ecuador: Esmeraldas: Río Chuchuvi (0.881, -78.515)	MTS24284.1
<i>Scada zibia zibia</i>	LEP-11342	Colombia: Antioquia: Finca Jacaranda (5.674, -75.701)	MH893268.1



Pteronymia sao loreto n. ssp., eastern Ecuador



Brevioleria arzalia loronia n. ssp., eastern Ecuador