

A New Subspecies of *Oleria gunilla* (Nymphalidae: Danainae) from North Mato Grosso, Brazil

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A NEW SUBSPECIES OF *OLERIA GUNILLA* (NYMPHALIDAE: DANAINAE)
FROM NORTH MATO GROSSO, BRAZIL

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ABSTRACT. A new subspecies of ithomiine butterfly, *Oleria gunilla lourdes* n. ssp., is described from northern Mato Grosso in central Brazil. The new taxon is confidently assigned to *Oleria gunilla* on the basis of both morphological and molecular evidence. Its wing pattern, with a broad expanse of orange on the dorsal forewing, is typical of the mimetic color patterns found in Ithomiini in the upper Amazon and Andean foothills of Peru, Colombia and Ecuador, very far from the type locality in northern Mato Grosso, where this taxon has no known co-mimics. Future studies are needed to investigate the mimetic relationships of this taxon with other sympatric butterflies.

Additional key words: Amazon, Clearwings, Ithomiini, Mimicry, Oleriina

The genus *Oleria* (Hübner, 1816) is the most species-rich within the tribe Ithomiini, with 49 known species distributed from Mexico to northern Argentina (De-Silva et al. 2016). The genus reaches its highest species richness in the eastern Andes and upper Amazon (Chazot et al. 2016), engages in several different mimicry rings (e.g., Beccaloni 1997) and individual species can present quite different color patterns across their geographic range (De-Silva et al. 2010, Warren et al. 2015). The Amazonian species *Oleria gunilla* (Hewitson, 1858) is a good example; its eight described subspecies are quite different in color pattern, representing at least six different mimicry rings (Chazot et al. 2016; see also Warren et al. 2015).

About a decade ago, the first author received some specimens of butterflies collected in the southwestern Amazon, along the Mureru River, northern Mato Grosso State, central Brazil, including a large sample of ithomiines. Among them were four specimens of an unknown ‘orange-tip’ *Oleria* taxon. In the present paper, we describe this taxon as a new subspecies of *Oleria gunilla*, based on morphological and molecular characters, and discuss its mimetic relationships.

MATERIAL AND METHODS

Specimens of *Oleria* were studied in several field locations in the Neotropics (KRW and AVL) and examined in major public and private collections in Europe, North and South America, including types of all *Oleria gunilla* taxa and names. Distribution data for

examined specimens were compiled in a database to permit study of related taxa and mimicry patterns. In addition, we also examined the Lamas collection of neotropical butterfly type specimen photographs at the MUSM (also available online in Warren et al. 2015), representing all relevant names of *Oleria* (see Lamas, 2004). Morphology was studied using standard techniques, with adult abdomens being soaked in hot 10% KOH for 10–15 minutes, dissected and subsequently stored in glycerin. The following collection acronyms are used in the text: **ZUEC**, Museu de Zoologia da Universidade Estadual de Campinas, Unicamp, Campinas, São Paulo, Brazil; **ZUEC-AVL**, André V. L. Freitas Collection, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil.

Total genomic DNA was isolated from four individuals of the putative new subspecies of *Oleria gunilla* using Invisorb® Spin Tissue Mini Kit (STRATEC Molecular, Germany). The barcode region proposed by Hebert et al. (2003), which is the 5' portion of the mitochondrial DNA (mtDNA) gene cytochrome oxidase subunit I (COI, 658 bp), was sequenced according to published protocols (Wahlberg & Wheat 2008). Sequences were aligned with those of other *Oleria* from the “*amalda*” group (sensu De-Silva et al. 2010) obtained from GenBank (Table 1). The final matrix comprised 50 individuals of the six species of *Oleria* from the “*amalda*” group and one individual of *Oleria vicina* as outgroup. Bayesian analyses (BI) were carried out using the program MrBayes 3.2 (Ronquist &

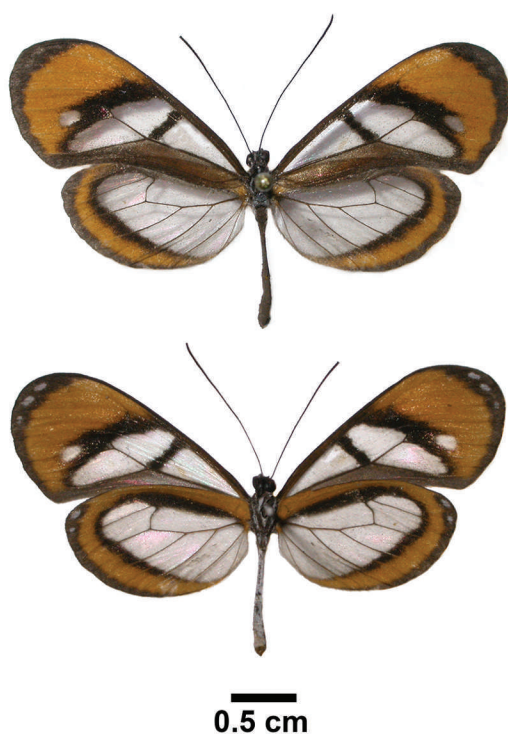


FIG. 1. *Oleria gunilla lourdes* – holotype male. Dorsal above, ventral below.

Huelskenbeck 2003) on the CIPRES portal (Miller et al. 2010). The model-jumping feature of the program was utilized, thereby sampling all possible GTR submodels according to their posterior probability (Ronquist et al. 2012). The gamma parameter was also included to allow site rate variation. Four simultaneous chains were run for 10×10^6 generations for two runs, sampling trees every 1,000 cycles. The first 2,500 trees were discarded as “burn in” based on when the runs had converged and reached equilibrium. The convergence of the likelihood traces of the independent runs was assessed with TRACER v1.5, and the ESS (effective sample size) values were verified to be above 300 for all parameters, which indicates that they were sufficiently sampled to estimate their posterior distributions (Drummond et al. 2006).

***Oleria gunilla lourdes* Freitas, new subspecies**
(Figs. 1, 2)

Description and diagnosis. Male. Antennae entirely black, three quarters length of forewing, with 36–37 antennomeres; club with 10 antennomeres, not conspicuously developed. Thorax black with a thin white dorsal line. Patagium black; Forewing length 19.5–20.0 mm; hind wing length 14.0–14.5 mm ($n = 4$). Wings transparent with pattern virtually identical on dorsal and ventral

surfaces, except by presence of 2–3 small white marginal dots ventrally in apical region of both wings; background transparent; both wings bordered with a marginal black stripe. Forewing with a broad submarginal transverse orange band from costa to vein 2A, this internally bordered with a broad black stripe with a conspicuous transparent patch in CuA_1 – CuA_2 ; a narrow black stripe crossing the discal cell at middle; anal margin rust-brown dorsally, grayish ventrally. Hind wing bordered by a broad orange submarginal band from Rs to 3A dorsally and from humeral region to 3A ventrally, this internally and externally bordered by a black stripe. Male genitalia with saccus as long as tegumen + uncus; uncus somewhat curved, ending in a narrow point; valva with a single point. In dorsal view genitalia asymmetrical, with uncus slightly twisted to right. Tuba analis present and weakly sclerotized. Aedeagus long and straight, with conspicuous cornuti grouped in a single patch of small teeth. Female unknown.

The taxon is distinguished from the most similar subspecies, *Oleria gunilla lubilerda* (Haensch, 1905), from eastern Colombia, by the much broader, and slightly darker, orange borders on both wings, especially on the forewing.

Type material: Holotype male (Fig. 1) from Parque Estadual Igarapés do Juruena, Colniza, Mato Grosso, Brazil, deposited in the Museu de Zoologia da Unicamp (ZUEC), Universidade Estadual de Campinas, Campinas, São Paulo, Brazil, with the following labels (four labels separated by transverse bars): / HOLOTYPE / Parque Estadual Igarapés do Juruena, Colniza, M[A]T[GROSSO], BR[ASIL], 8°55'28"S 59°7'52"W, Rio Mureru, X-XI.2007, Acaccio, G. M. [leg.], DNA Voucher BLU 764 / ZUEC LEP 9780 / Holotypus – *Oleria gunilla lourdes* Freitas det. 2016 /

Paratypes. Two males, same data as holotype (DNA vouchers BLU 764, BLU 765), ZUEC LEP 9781, ZUEC LEP 9782; ZUEC. 1 male, same data as holotype (DNA voucher BAKU-34 and BLU 636); ZUEC-AVLF.

Etymology. This species is dedicated to Maria de Lourdes Retz Lucci (born - 21.II.1923, deceased - 16.XII.2015), grandmother of the first author, who always gave encouragement to his biological endeavors. The name is treated as a feminine noun in apposition.

Taxonomy and variation. All four individuals are very similar, and the only noticeable variation observed was in the size of the transparent patch in CuA_1 – CuA_2 on the forewing.

Range and habitat. All four known individuals were collected in the same spot, near the banks of the Mureru River in northern Mato Grosso, central Brazil, in dense Amazonian forest.

Phylogenetic relationships. Based on DNA sequences, the four individuals of *Oleria gunilla lourdes* group together with other *Oleria gunilla* individuals from the western Amazon (Fig. 3), validating the description of this taxon as a subspecies of *O. gunilla*.

DISCUSSION

The wing pattern of *O. gunilla lourdes*, with such a broad expanse of orange, resembles the AURELIANA mimicry pattern (Willmott & Mallet 2004), which is typical of the upper Amazon and Andean foothills of Peru, Colombia and Ecuador (Fig. 4). Thus, this taxon appear to be misplaced in terms of its mimicry ring - the type locality in Northern Mato Grosso is more than 600 km distant from any other locality where similarly patterned ithomiines are found (Fig. 4). In addition, in a large sample of more than 25 Ithomiini species from

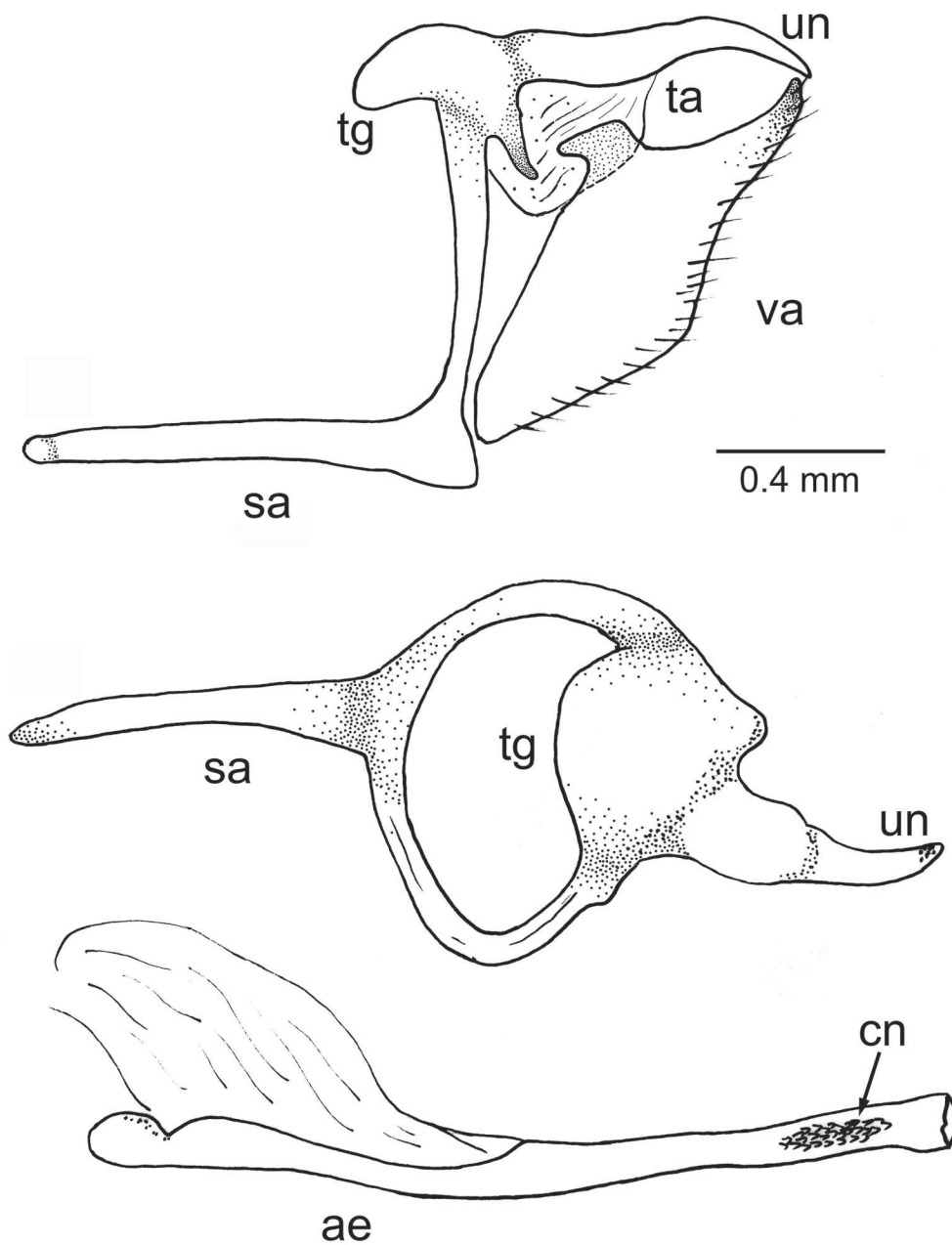


FIG. 2. *Oleria gunilla lourdes* – male genitalia. Lateral on top, dorsal at middle, aedeagus at bottom. Abbreviations: ae - aedeagus; cn - cornutus; sa - saccus; ta - tuba analis; tg - tegumen; un - uncus; va - valva.

TABLE 1 - Species of *Oleria* with code, sampling sites data, and GenBank accession numbers for sequenced genes.

Code	Genus	Species	Subspecies	Country	Locality	Coordinates	Genbank code
-	<i>Oleria</i>	<i>vicina</i>		Costa Rica	Área de Conservación Guanacaste, Guanacaste	-	JQ529731
BLU636	<i>Oleria</i>	<i>gunilla</i>	<i>lourdes</i>	Brazil	Rio Mureru, Pq. Est. Igarapés do Juruena, Colniza, MT	8°55'28"S 59°7'52"W	KX258471
BLU763	<i>Oleria</i>	<i>gunilla</i>	<i>lourdes</i>	Brazil	Rio Mureru, Pq. Est. Igarapés do Juruena, Colniza, MT	8°55'28"S 59°7'52"W	KX258472
BLU764	<i>Oleria</i>	<i>gunilla</i>	<i>lourdes</i>	Brazil	Rio Mureru, Pq. Est. Igarapés do Juruena, Colniza, MT	8°55'28"S 59°7'52"W	KX258473
BLU765	<i>Oleria</i>	<i>gunilla</i>	<i>lourdes</i>	Brazil	Rio Mureru, Pq. Est. Igarapés do Juruena, Colniza, MT	8°55'28"S 59°7'52"W	KX258474
20209	<i>Oleria</i>	<i>gunilla</i>	<i>lota</i>	Ecuador	Río Añangu, Orellana	0°31'24"S 76°23'43"W	EU068916
20641	<i>Oleria</i>	<i>gunilla</i>	<i>lota</i>	Ecuador	Río Añangu, Orellana	0°31'24"S 76°23'43"W	EU068917
20699	<i>Oleria</i>	<i>gunilla</i>	<i>lota</i>	Ecuador	Río Añangu, Orellana	0°31'24"S 76°23'43"W	EU068918
20249	<i>Oleria</i>	<i>gunilla</i>	<i>lota</i>	Ecuador	Río Añangu, Orellana	0°31'24"S 76°23'43"W	EU069096
LS02-125	<i>Oleria</i>	<i>gunilla</i>	<i>lota</i>	Ecuador	Garza Cocha, Sucumbíos	0°29'52"S 76°22'27"W	EU069097
2-289	<i>Oleria</i>	<i>gunilla</i>	<i>lota</i>	Peru	Km 7.2 Pongo-Barranquita, San Martín	6°17'12"S 76°13'54"W	HM051706
2-1304	<i>Oleria</i>	<i>gunilla</i>	<i>lota</i>	Peru	Km 7.2 Pongo-Barranquita, San Martín	6°17'12"S 76°13'54"W	HM051707
2-1979	<i>Oleria</i>	<i>gunilla</i>	<i>lota</i>	Peru	Km 35 Tarapoto-Yurimaguas, San Martín	6°25'29"S 76°15'02"W	HM051708
2-2118	<i>Oleria</i>	<i>gunilla</i>	<i>lota</i>	Peru	Km 7.2 Pongo-Barranquita, San Martín	6°17'12"S 76°13'54"W	HM051709
4-346	<i>Oleria</i>	<i>gunilla</i>	<i>lota</i>	Peru	Km 7.2 Pongo-Barranquita, San Martín	6°17'12"S 76°13'54"W	HM051710
2-194	<i>Oleria</i>	<i>gunilla</i>	<i>serdolis</i>	Peru	Chumía, San Martín	6°36'57"S 76°11'10"W	HM051711
2-196	<i>Oleria</i>	<i>gunilla</i>	<i>serdolis</i>	Peru	Chumía, San Martín	6°36'57"S 76°11'10"W	HM051712
2-1477	<i>Oleria</i>	<i>gunilla</i>	<i>serdolis</i>	Peru	Chumía, San Martín	6°36'57"S 76°11'10"W	HM051713
2-1981	<i>Oleria</i>	<i>gunilla</i>	<i>serdolis</i>	Peru	Km 35 Tarapoto-Yurimaguas, San Martín	6°25'29"S 76°15'02"W	HM051714
4-508	<i>Oleria</i>	<i>gunilla</i>	<i>serdolis</i>	Peru	Km 22, Nuevo Lima - La Perla del Ponacillo, San Martín	7°10'04"S 76°20'42"W	HM051715
4-509	<i>Oleria</i>	<i>gunilla</i>	<i>serdolis</i>	Peru	Km 22, Nuevo Lima - La Perla del Ponacillo, San Martín	7°10'04"S 76°20'42"W	HM051716
5-436	<i>Oleria</i>	<i>gunilla</i>	<i>serdolis</i>	Peru	Cerro Mira Culo, Loreto	7°27'12"S 75°50'16"W	HM051717
5-870	<i>Oleria</i>	<i>gunilla</i>	<i>serdolis</i>	Peru	Caño Negro, Río Biabo, PNCAZ	7°45'10"S 76°20'03"W	HM051718
5-922	<i>Oleria</i>	<i>gunilla</i>	<i>serdolis</i>	Peru	Quebrada Machaco, Cachatigre, Río Biabo, PNCAZ, San Martín	7°43'05"S 76°20'51"W	HM051719
5-923	<i>Oleria</i>	<i>gunilla</i>	<i>serdolis</i>	Peru	Quebrada Machaco, Cachatigre, Río Biabo, PNCAZ, San Martín	7°43'05"S 76°20'51"W	HM051720
4-470	<i>Oleria</i>	<i>gunilla</i>	<i>serdolis</i>	Peru	Km 22, Nuevo Lima, Selva Andina, San Martín	7°11'36"S 76°20'06"W	EU069098

TABLE 1 - Continued.

Code	Genus	Species	Subspecies	Country	Locality	Coordinates	Genbank code
8369	<i>Oleria</i>	<i>rubescens</i>		Panamá	Quebrada Hornito, Chiriquí	8°69'28"N 82°22'45"W	DQ085460
8404	<i>Oleria</i>	<i>rubescens</i>		Panamá	Continental Divide Trail, Fortuna, Chiriquí	8°78'53"N 82°21'43"W	FN646327
CJ8093	<i>Oleria</i>	<i>rubescens</i>		Panamá	Quebrada Alemán, Fortuna, Chiriquí	8°76'70"N 82°23'26"W	FN646328
CJ8094	<i>Oleria</i>	<i>zelica</i>	<i>pagasa</i>	Panamá	Quebrada Alemán, Fortuna, Chiriquí	8°76'70"N 82°23'26"W	FN646344
8396	<i>Oleria</i>	<i>zelica</i>	<i>pagasa</i>	Panamá	Continental Divide Trail, Fortuna, Chiriquí	8°78'53"N 82°21'43"W	FN646345
CJ8398	<i>Oleria</i>	<i>zelica</i>	<i>pagasa</i>	Panamá	Continental Divide Trail, Fortuna, Chiriquí	8°78'53"N 82°21'43"W	FN646346
CJ8433	<i>Oleria</i>	<i>zelica</i>	<i>pagasa</i>	Panamá	Quebrada Hornito trail, Fortuna, Chiriquí	8°69'28"N 82°22'45"W	FN646347
CJ8473	<i>Oleria</i>	<i>zelica</i>	<i>pagasa</i>	Panamá	Cerro Campana, Panamá	8°68'74"N 79°91'97"W	FN646348
F17-7	<i>Oleria</i>	<i>zelica</i>	<i>zelica</i>	Ecuador	Lita, Carchi	-	FN646349
EC94	<i>Oleria</i>	<i>amalda</i>	<i>modesta</i>	Ecuador	Km 106.5 from Mindo, Pichincha	-	FN646262
EC135	<i>Oleria</i>	<i>amalda</i>	<i>modesta</i>	Ecuador	near Hotel Tinalandia, Alluriquín, Pichincha	-	FN646263
KW10	<i>Oleria</i>	<i>amalda</i>	<i>faunula</i>	Ecuador	Río Chuchuví, Km 12.5 Lita-San Lorenzo rd., Esmeraldas	0°52'85"N 78°30'90"W	FN651609
8474	<i>Oleria</i>	<i>paula</i>		Panamá	Cerro Campana, Panamá	08°68'74"N 79°91'97"W	FN646319
CJ8824	<i>Oleria</i>	<i>paula</i>		Panamá	Caná, near runway, Darién	07°75'68"N 77°68'41"W	FN646320
CJ8089	<i>Oleria</i>	<i>paula</i>		Panamá	Bocas del Toro, 9.5 Km Chiriquí Grande-Almirante, Chiriquí	08°98'10"N 82°24'00"W	FN646321
CJ9026	<i>Oleria</i>	<i>paula</i>		Panamá	Río Pi-as Campsite, Darién	07°63'62"N 78°18'97"W	FN646322
MAL-04156	<i>Oleria</i>	<i>paula</i>		México	Res. de la Biosfera de Calakmul, Zona K, Dos Naciones, Campeche	17°58'19"N 89°21'28"W	GU658907
-	<i>Oleria</i>	<i>paula</i>		Costa Rica	Área de Conservación Guanacaste, Sector Cacao, Estacion Cacao, Guanacaste	10°55'36"N 85°28'5"W	JN807066
-	<i>Oleria</i>	<i>paula</i>		Costa Rica	Área de Conservación Guanacaste, Sector Pitilla, Pasmompa, Guanacaste	11° 1'8"N 85°24'36"W	JQ542174
-	<i>Oleria</i>	<i>paula</i>		Costa Rica	Área de Conservación Guanacaste, Sector Pitilla, Pasmompa, Guanacaste	11° 1'8"N 85°24'36"W	JQ542175
-	<i>Oleria</i>	<i>paula</i>		Costa Rica	Área de Conservación Guanacaste, Rincon Rainforest, Montanya Figueres, Guanacaste	10°53'2"N 85°17'27"W	JQ543493
-	<i>Oleria</i>	<i>paula</i>		Costa Rica	Área de Conservación Guanacaste, Sector Pitilla, Coneja, Guanacaste	11°0'54"N 85°23'52"W	JQ548213
-	<i>Oleria</i>	<i>paula</i>		Costa Rica	Área de Conservación Guanacaste, Sector Pitilla, Pasmompa, Guanacaste	11° 1'8"N 85°24'36"W	JQ548220
4-400	<i>Oleria</i>	<i>estella</i>	<i>estella</i>	Peru	La Antena, Km 16 Tarapoto - Yurimaguas, San Martín	06°27'18"S 76°17'54"W	FN646295
2-406	<i>Oleria</i>	<i>estella</i>	<i>estella</i>	Peru	La Antena, Km 16 Tarapoto - Yurimaguas, San Martín	06°27'18"S 76°17'54"W	FN646296

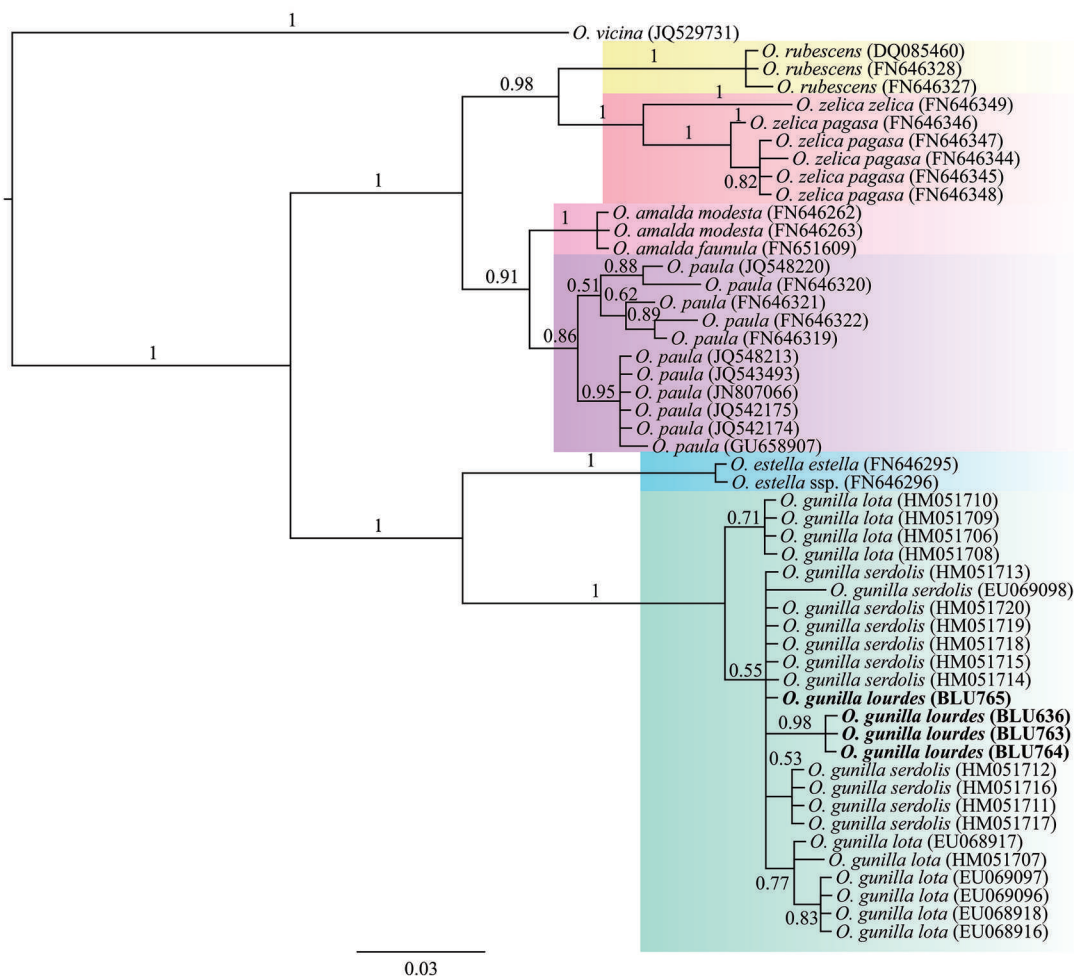


FIG. 3. Bayesian Inference tree for the "amalda" species group of *Oleria*, including the four specimens of *Oleria gunilla lourdes* **new ssp.** Posterior probabilities of nodes are presented below the nodes.

the same locality, not a single species with a similar mimetic pattern was observed, an unexpected fact considering that local convergence in mimetic patterns has been long known for aposematic butterflies (Müller 1879). Most strikingly, the extent of orange wing markings in this subspecies is one of the largest within the whole tribe, mirrored in very few other ithomiines (Warren et al. 2015). Although no other local Ithomiini converge in mimicry pattern with *O. gunilla lourdes*, candidate co-mimic butterflies not reported in the type locality could include some Riodinidae, such as species of *Stalachtis* Hübner, 1818, or classical mimetic Pieridae such as *Dismorphia theucharila* (E. Doubleday, 1848). This atypical situation surely deserves further investigation in depth, including

additional fieldwork to uncover possible sympatric mimetic species of *O. gunilla lourdes*.

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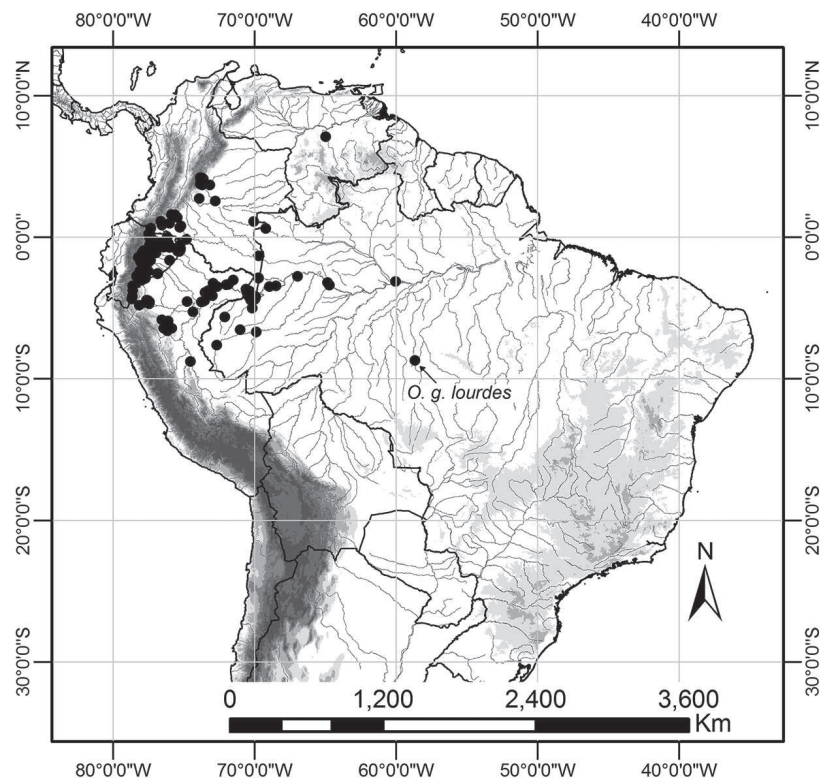


FIG. 4. Distribution of the ithomiine species belonging to the AURELIANA mimicry pattern in the Neotropics (solid circles). The location of the type locality of *O. gunilla lourdes* is indicated.

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REFERENCES

- BECCALONI, G. W. 1997. Ecology, natural history and behaviour of ithomiine butterflies and their mimics in Ecuador (Lepidoptera: Nymphalidae: Ithomiinae). *Trop. Lepid.* 8:103–124.
- CHAZOT, N., K. R. WILLMOTT, A. V. L. FREITAS, D. L. DE SILVA, R. PELLENS & M. ELIAS. 2016. Patterns of Species, Phylogenetic and Mimicry Diversity of Clearwing Butterflies in the Neotropics, pp. 333–353. In Pellens, R. & P. Grandcolas (eds.), *Biodiversity Conservation and Phylogenetic Systematics. Preserving our evolutionary heritage in an extinction crisis. Topics in Biodiversity and Conservation*, 14. Springer Open.
- DE-SILVA, D. L., J. J. DAY, M. ELIAS, K. WILLMOTT, A. WHINNETT & J. MALLETT. 2010. Molecular phylogenetics of the neotropical butterfly subtribe Oleriina (Nymphalidae: Danainae: Ithomiini). *Mol. Phylogenet. Evol.* 55:1032–1041.
- DE-SILVA, D. L., M. ELIAS, K. WILLMOTT, J. MALLETT & J. J. DAY. 2016. Diversification of clearwing butterflies with the rise of the Andes. *J. Biogeography* 43:44–58.
- DRUMMOND, A. J., S. Y. W. HO, M. J. PHILLIPS & A. RAMBAUT. 2006. Relaxed phylogenetics and dating with confidence. *PLoS Biology* 4: 0699–0710.
- HEBERT, P. D. N., A. CYWINSKA, S. L. BALL, & J. R. DEWAARD. 2003. Biological identifications through DNA barcodes. *Proc. R. Soc. Lond. [Biol.]* 270:313–321.
- LAMAS, G. 2004. Ithomiinae. *Atlas of Neotropical Lepidoptera. Checklist: Part 4A Hesperioidea – Papilionoidea* (ed. by J.B. Heppner), pp. 172–191. Association of Tropical Lepidoptera, Scientific Publishers, Gainesville, FL.
- MILLER, M. A., M. T. HOLDER, R. VOS, P. E. MIDFORD, T. LIEBOWITZ, L. CHAN, P. HOOVER, AND T. WARNOW. 2010. The CIPRES Portals. CIPRES. Website http://www.phylo.org/sub_sections/portal [accessed 18 February 2016].
- MÜLLER, F. 1879. *Ituna* and *Thyridia*: a remarkable case of mimicry in butterflies. *Proc. Entomol. Soc. Lond.* 1879, xx–xxix.
- RONQUIST, F. & J. P. HUELSENBECK. 2003. MrBayes 3: Bayesian phylogeny inference under mixed models. *Bioinformatics* 19:1572–1574.
- RONQUIST, F., M. TESLENKO, P. VAN DER MARK, D. L. AYRES, A. DARLING, S. HÖHNA, B. LARGET, L. LIU, M. A. SUCHARD & J. P. HUELSENBECK. 2012. Mrbayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 61: 539–542.
- WAHLBERG, N. & C. W. WHEAT. 2008. Genomic outposts serve the phylogenomic pioneers: designing novel nuclear markers for genomic DNA extractions of Lepidoptera. *Syst. Biol.* 57:231–242.
- WARREN, A. D., K. J. DAVIS, E. M. STANGELAND, J. P. PELHAM & N. V. GRISHIN. 2015. Illustrated Lists of American Butterflies. Available from: <http://www.butterfliesofamerica.com/> (17 May 2016).
- WILLMOTT, K. R. & J. MALLETT. 2004. Correlations between adult mimicry and larval host plants in ithomiine butterflies. *Proc. R. Soc. Lond. [Biol.]* 271: S266–S269.

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