# A distinctive new subspecies of *Moschoneura pinthous* (Linnaeus, 1758) (Lepidoptera: Pieridae: Dismorphiinae) from the Orinoco Delta, Venezuela, with comments on the species-level taxonomy

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**Abstract**: A new subspecies of *Moschoneura pinthous* (Linnaeus, 1758), *M. p. carmenae* Neild & Losada, **ssp. nov.**, is described from the Orinoco Delta in north-eastern Venezuela. The adults, male genitalia, and DNA barcode sequences are documented and compared with neighboring *M. p. pinthous* from southern Venezuela and the Guianas, and with *M. pinthous* subspecies from the upper Amazon basin. For the new subspecies, we provide observations and images of its habitat, and discuss flight behavior and possible mimetic associations. Based on the DNA sequence data and observations of analogous pattern variation within co-mimetic butterfly species, we restore the subspecies status of *Moschoneura pinthous ithomia* (Hewitson, 1867), **stat. rev.**

**Resumen**: Se describe una nueva subespecie de *Moschoneura pinthous* (Linnaeus, 1758), *M. p. carmenae* Neild & Losada, **ssp. nov.**, proveniente del Delta del Orinoco, estado Monagas, Venezuela. Se compararon los adultos con los de diferentes subespecies de *M. pinthous* del sur de Venezuela, Guyana y Guayana Francesa, al igual que con las subespecies presentes en la cuenca superior del Amazonas. De igual modo se realizaron comparaciones de las estructuras genitales del macho, y de secuencias de ADN de las diferentes poblaciones, con el fin de clasificar correctamente a la subespecie en estudio. También se hicieron algunas observaciones acerca del comportamiento de la especie y de sus posibles asociaciones miméticas. Con base en las secuencias de ADN y observaciones sobre variaciones análogas dentro de especies de mariposas comiméticas, restauramos el estatus de subespecie de *Moschoneura pinthous ithomia* (Hewitson, 1867), **stat. rev.**

**Key Words**: Batesian mimicry, flooded forest, Dismorphiinae, Müllerian mimicry, Orinoco Delta, Pieridae, Venezuela.

## INTRODUCTION

The Dismorphiinae are a small subfamily within the Pieridae, with the Neotropical region considered to contain a little over 50 species in six genera (Lamas, 2004a). A number of taxa are rare and have only been described comparatively recently (e.g., Lamas, 2004b; Le Crom *et al*., 2004; Llorente *et al.*, 2016), and several Venezuelan subspecies are still awaiting description (Neild & Costa, unpublished).

The small genus *Moschoneura* was the subject of a recent review (Llorente *et al*., 2016), in which four species were recognized: *M. pinthous* (Linnaeus, 1758), *M. ela* (Hewitson, 1877), *M. ithomia* (Hewitson, 1867), and *M. methymna* (Godart, 1819), in contrast to Lamas (2004a) and Freitas *et al*. (2018), who treated *Moschoneura* as monotypic. These species exclusively inhabit continental South America, where they fly low and slowly in the understorey of tropical forests from south-eastern Brazil and the Amazon lowlands to around 1,700 m in the Andean cloud forests. The lowland species are involved in diverse mimicry rings that are dominated by Ithomiini (Danainae; see Beccaloni, 1997). Whether this mimicry is Batesian or Müllerian remains to be tested; Bates (1862) assumed this species to be a palatable mimic, but Srygley & Chai (1990) found that another member of the same tribe, *Dismorphia amphione* (Cramer, 1779), was only moderately palatable to jacamars. The single cloud forest species, *M. ela*, is rare and local, and is not a particularly convincing mimic of any butterfly with which it occurs (KRW, pers. obs.). Remarkably, despite the abundance of the Amazonian species *M. pinthous*, the host plants of the genus appear to be unknown, although they are likely to be within the Leguminosae, as are other dismorphiine genera (Beccaloni *et al*., 2008).

While conducting research for the *Butterflies of Venezuela* book project over the past three decades (Neild, 1996, 2008), the first author became increasingly aware that data for the biogeographically important Orinoco Delta were very sparse, coming mostly from the results of commercial collecting in the early 20th century for Eugène Le Moult and concentrating entirely on commercially valuable taxa, such as the nymphalid genera *Morpho* Fabricius, 1807 (Satyrinae) and *Prepona*

Boisduval, 1836 (Charaxinae) (see Le Moult, 1955; Blandin & Neild, 2020). Although a few Venezuelan private collectors and institutions have ventured into this area, the huge cost of such expeditions has limited visits to only a few days. From a scientific viewpoint, the results of these expeditions have been disappointing, presumably because most collecting was effected from boats in the extensively flooded forest, limiting movement and habitat sampling, and because collecting appears to have concentrated on the larger and more attractive species, especially the legendary *Morpho rhetenor augustinae* Le Cerf, 1925. With all this in mind, the first author organized a five day expedition to the Orinoco Delta in April 2014, assisted by the second author, with a view to concentrating on smaller and less colorful taxa, and to explore away from the river systems, if possible inside the forest, although the latter proved very difficult in practice. Nevertheless, a number of interesting taxa were recorded, including a highly distinctive undescribed *Moschoneura* subspecies. The purpose of this paper is therefore to describe this new subspecies, as part of a long term project to document the butterfly fauna of Venezuela (Neild, 1996, 2008).

## METHODS

Sampling was conducted using aerial nets and extendible poles from a fishing launch driven along the numerous river systems of the Delta (see map, Fig. 1B), with limited landings on dry land both inside and outside the forest.

The type specimens of *M. p. carmenae* **ssp. nov.**, were compared with specimens of the nominate *M. p. pinthous* from southern Venezuela (Bolívar state) and the Guianas, as well as with *Moschoneura* taxa from Venezuelan Amazonas state, eastern Colombia, Ecuador, Peru and Brazil in AFEN's personal collection (St. Albans, UK), the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, USA (FLMNH), the Field Museum of Natural History, Chicago, Illinois, USA, the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), and the Yale Peabody Museum of Natural History, Yale University, New Haven, USA (PMNH).

These physical examinations were supplemented with photographs of numerous *Moschoneura* taxa in private and

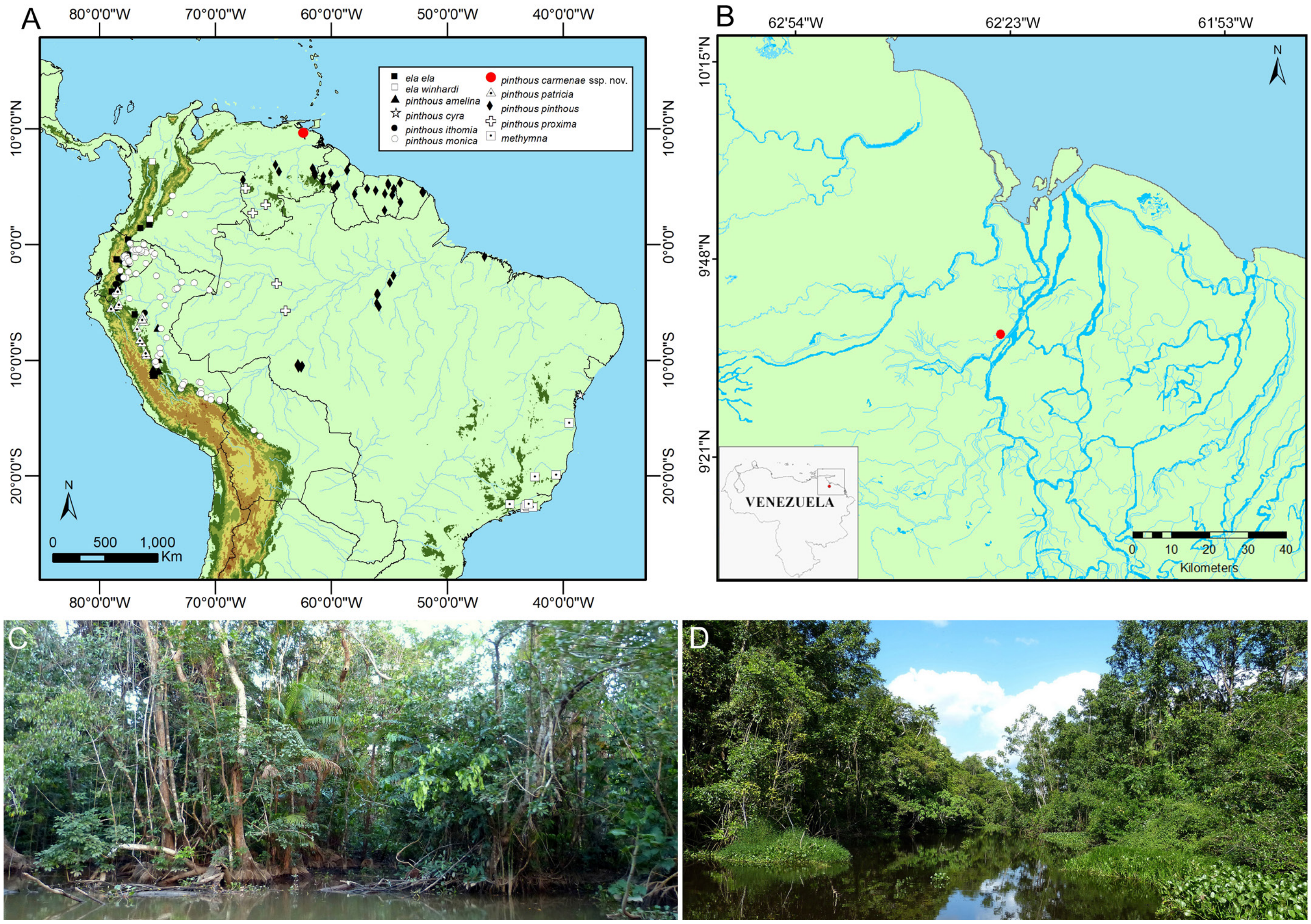

**Fig. 1. A.** Record localities for *Moschoneura*. The data come primarily from museum specimens in the FLMNH (USA), the Natural History Museum (UK), from multiple contributors to the Darwin Andean Butterfly Database of the Tropical Andean Butterfly Diversity Project, from Lamas (2004b), from Freitas *et al.* (2018), and from the unpublished records of K. Willmott and J. Hall. **B.** Map of north-eastern Venezuela, showing the Orinoco Delta and the type locality (red dot). **C.** Vegetation on Caño Culebra, east of Boca de Tigre, on the eastern bank of Caño Manamo near the type locality, showing typical lowland tropical forest habitat frequented by *Moschoneura pinthous carmenae* **ssp. nov. D.** Typical lowland flooded tropical forest habitat on Caño Toro, 5 km SW of Boca de Tigre, south bank of Caño Buja, Orinoco Delta.

**Table 1.** Voucher information and metadata for male *Moschoneura* specimens dissected.

| Dissection | Taxon | Country | State/Province | Location |
|---|---|---|---|---|
| Paratype | *M. pinthous carmenae* **ssp. nov.** | Venezuela | Monagas | Orinoco Delta |
| KW-19-44 | *M. p. pinthous* | Venezuela | Bolívar | Km 82, S. of El Dorado |
| KW-19-53 | *M. pinthous pinthous* | Suriname | Brokopondo | Brownsberg Nature Park |
| KW-19-46 | *M. pinthous monica* | Colombia | Meta | Río Negro |
| KW-19-47 | *M. pinthous monica* | Ecuador | Sucumbíos | Lago Agrio |
| KW-19-50 | *M. pinthous monica* | Peru | Madre de Dios | E slope Cerro Pantiacolla |
| KW-19-48 | *M. pinthous ithomia* | Ecuador | Pastaza | Puyo |
| KW-19-49 | *M. pinthous patricia* | Peru | Huánuco | Tingo María |
| KW-19-51 | *M. pinthous pinthous* | Brazil | Rondônia | 12.5 km S Cacaulândia |
| KW-19-52 | *M. pinthous pinthous* | Brazil | Pará | Curitiba-Santarém km 1294 |
| KW-19-45 | *M. ela winhardi* | Colombia | Huila | Garzón |

**Table 2.** Voucher information and metadata for COI barcode sequences analyzed. Sequences with Genbank voucher numbers beginning with "MT" were newly generated for this study.

| DNA voucher number | Taxon | Locality (decimal latitude and longitude) | Genbank voucher |
|---|---|---|---|
| MFB-00-P234 | *Lieinix nemesis* | Country unknown: Not located: no data | KM046821 |
| LEP-54550 | *M. ela ela* | Ecuador: Napo: Cordillera Galeras (-0.829, -77.537) | MT787484 |
| LEP-08294 | *M. pinthous ithomia* | Ecuador: Morona-Santiago: Río Yungantza (-2.87, -78.366) | MT787477 |
| LEP-08295 | *M. pinthous ithomia* | Ecuador: Morona-Santiago: Río Yungantza (-2.87, -78.366) | MT787478 |
| LEP-00144 | *M. pinthous monica* | Ecuador: Orellana: Napo Wildlife Center, Napo trail (-0.51, -76.437) | MT787475 |
| LEP-00145 | *M. pinthous monica* | Ecuador: Orellana: Napo Wildlife Center, Tiputini trail (-0.529, -76.417) | MT787476 |
| LEP-09481 | *M. pinthous monica* | Ecuador: Pastaza: Kapawi Lodge (-2.542, -76.859) | MT787479 |
| LEP-09482 | *M. pinthous monica* | Ecuador: Zamora-Chinchipe: c. 3 km S Shaime (-4.35, -78.658) | MT787480 |
| LEP-10420 | *M. pinthous monica* | Ecuador: Orellana: Estación Científica Yasuní (-0.674, -76.397) | MT787481 |
| LEP-10424 | *M. pinthous monica* | Ecuador: Orellana: Estación Científica Yasuní (-0.674, -76.397) | MT787482 |
| AFEN-054 | *M. pinthous carmenae* **ssp. nov.** | Venezuela: Monagas: lower Caño Manamo, Caño Corto (9.643°, -62.399°) | MT787474 |
| LEP-64805 | *M. pinthous pinthous* | French Guiana: St-Laurent du Maroni: Moutochi Lodge (5.324, -54.067) | MT787483 |
| MFB-00-P403 | *M. pinthous patricia* | Peru: Huánuco: 9 km S Tingo María | AY870575 |

institutional collections in Venezuela, the USA, and western Europe (see list in Neild, 2008: 20). Photos of the types (and non-types) of all *Moschoneura* taxa taken by Gerardo Lamas and figured on the Butterflies of America web site (Warren *et al*., 2017) were also examined.

The male abdomens of one Venezuelan paratype of *M. p. carmenae* **ssp. nov.** and 10 additional specimens of other *Moschoneura* taxa from Venezuela, Suriname, Colombia, Ecuador, Peru and Brazil were dissected to observe genital structures (Table 1). Adult abdomens were dissected using standard techniques, being soaked in hot 10% KOH for 10-15 minutes, dissected and subsequently stored in glycerin. External morphology and dissections were studied using a stereomicroscope at up to 100x magnification and drawings made using a camera lucida. The terminology for genital and abdominal structures largely conforms to Klots (1970). Nomenclature for wing venation follows the Comstock-Needham system described by Miller (1970), and areas and elements of the wing pattern follow Neild (2008).

We attempted to sequence the DNA barcode region (Hebert *et al*., 2003) for representative *Moschoneura* taxa to help decide on the most appropriate status for the new taxon described here. We extracted genomic DNA from legs removed from dried *Moschoneura* specimens using Qiagen's DNeasy Blood & Tissue Kit following the manufacturer's protocol, incubating samples overnight (24 h) and using a final elution volume of 50 ul. We amplified the first half of the mitochondrial gene *cytochrome oxidase I* (COI) using the primers LCO (forward, GGTCAACAAATCATAAAGATATTGG) and HCO (reverse, TAAACTTCAGGGTGACCAAAAAATCA) (Folmer *et al*., 1994). For samples that were not successfully amplified with this primer pair, we attempted to amplify shorter, partially overlapping fragments of the region, using primer pairs LCO and K699 (reverse, WGGGGGGTAAACTGTTCATCC), and Ron (forward, GGATCACCTGATATAGCATTCCC) and Nancy (reverse, CCTGGTAAAATTAAAATATAAACTTC) (Monteiro & Pierce, 2001; Elias *et al*., 2007). PCR conditions were as described in Willmott *et al.* (2017). Single strands of the PCR products were sequenced by Eurofins Genomics USA using the same primers as in the PCR. Where necessary, fragments were assembled into composite sequences, and all sequences were aligned using BioEdit v. 7.1.3 (Hall, 1999). We also included a sequence from *Lieinix nemesis* (Latreille, [1813]) (Pieridae, Dismorphiinae), obtained from Genbank, to root resulting trees. The final aligned sequences were of length 669 bp. New sequences are deposited in GenBank and details for all sequences used in analyses are listed in Table 2. To examine relationships and test for genetic differences among putative taxa we conducted a neighbor-joining (NJ) analysis using MEGA 7.0 (Kumar *et al*., 2016), with the Kimura 2-parameter substitution model, partial deletion of sites with missing data, 500 bootstrap replicates to estimate branch support, and other default settings. Trees were also inferred with a Bayesian analysis using MrBayes 3.2.7a (Ronquist *et al*., 2012), with the GTR substitution model with gamma-distributed rate variation across sites and a proportion of invariable sites (GTR + I + Γ). The Markov chain Monte Carlo simulation was conducted with two independent runs with four chains, three heated and one cold, calculating diagnostics every 1000 generations, and continued until the standard deviation of split frequencies was below 0.01, as recommended by Ronquist *et al*. (2020). Parameter statistics and trees were summarized with a burn-in fraction of 25%, and the consensus tree and clade credibility values were examined in FigTree 1.4.4 (Rambaut, 2018).

**Fig. 2.** *Moschoneura pinthous carmenae* **ssp. nov.**: male holotype (top row, dorsal/ventral) and female paratype (bottom row, dorsal/ventral) (scale bar = 10 mm).

## RESULTS

### *Moschoneura pinthous carmenae* Neild & Losada, **ssp. nov.** **(Figs. 2, 3)**

**Description and diagnosis**

**Male.** The ground colour of both wing surfaces is creamy white, with no hint of the yellow typical of other *M. pinthous* subspecies (*sensu* Llorente *et al*., 2016). Compared with the nominate subspecies (south-central and south-eastern Venezuela, and the Guianas), *M. p. monica* Lamas, 2004 (eastern Bolivia to eastern Colombia, and western Brazil - see Le Crom, 2004: 56-57) and *M. p. proxima* (Röber, 1924) (south-western Venezuela and western Brazil), the heavy black bands of both wing surfaces are significantly reduced in width and number, as follows: dorsally the forewing wide subapical black band is entirely missing, as is the black band extending from the base to the submarginal area of the outer margin; the transverse black postdiscal band is much thinner (approximately 1.0-1.25 mm along the disco-cellular veins), fainter, and more brownish than black, and extends in equal width to space $M_3$-$Cu_1$ where it terminates, not reaching the outer margin. The dorsal hindwing is mostly devoid of black, this being restricted to a narrow marginal band at the apex, widening to 1 mm in $M_1$-$M_2$, beyond which it becomes narrower and gradually more diffuse and brownish, and disappears entirely before the tornus; in addition, the orange submarginal band is only faintly visible on the dorsal wing surface. Ventrally, the same differences are notable, except that the hindwing orange submarginal band is well-defined and about 0.8-1.0 mm wide, and the hindwing subcostal band is present, but fainter, more diffuse, and pale brown, and disappears entirely near the subapex where it meets the submarginal orange band.

**Female.** The female is similar to the male, but with the black outer margin of both wings approximately 30-50% wider (difficult to define precisely due to rather diffuse edges); in addition, the dark subapical band seen in other *Moschoneura* subspecies is present, but narrow (< 1.0 mm), pale, and distally diffuse, while the dark postdiscal transverse band is similar to that of the male in width but continues almost to the outer margin, where it becomes very diffuse and enters an extended suffused area of the greyish-brown tornal margin. Ventrally, the female is much closer in appearance to the male, with only a hint of the dark subapical forewing band, while the postdiscal band extends only slightly further than the male, reaching almost to vein $Cu_1$; the white, straight marginal forewing dashes are replaced by a distinctive white triangle in $M_3$-$Cu_1$, and a white relatively less pointed chevron in both interspaces between $M_1$ and $M_3$, in this respect differing from the male and from the other two subspecies compared above; on the hindwing the subcostal band is a little wider, and there is a diffuse but narrow submarginal brownish-grey band on the basal edge of the orange submarginal band, widest at the anal margin and tapering to a point in space $M_2$-$M_3$.

**Forewing length (wingspan in brackets).** ♂ holotype 23 mm (43 mm), ♂ paratype 21.5 mm (41 mm), ♀ paratype 20.5 mm (40 mm).

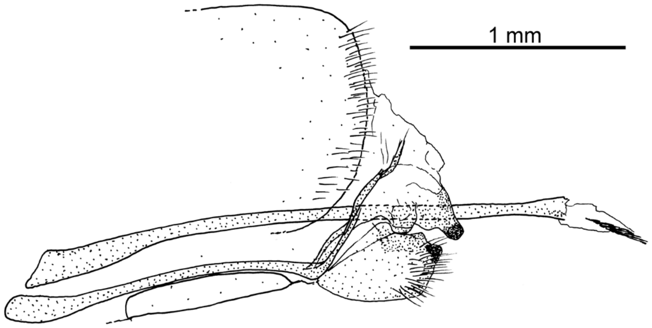

**Fig. 3.** *Moschoneura pinthous carmenae* **ssp. nov.**: lateral view of genitalia of paratype ♂.

**Types.** HOLOTYPE ♂ (as written on label): Caño Corto 9°38'35.73"N, 62°23'58.00"W / Lower Caño Manamo, Monagas, NE Venezuela. 12 April 2014, 13 m elevation. A. Neild & M. E. Losada *leg*. (Andrew Neild collection, St Albans, UK; to be deposited in the Museo del Instituto de Zoología Agrícola, Maracay, Venezuela [MIZA]).
PARATYPES: 1♂, 1♀ same data as holotype (Andrew Neild collection, St Albans, UK).

**Etymology.** The second author (ML) dedicates this beautiful butterfly to her mother, Carmen de Losada, as a gesture of her love and deep thanks for always being there as a model of strength, dedication and perseverance. This subspecies name is treated as a Latinized female noun in the genitive case derived from the modern Spanish name Carmen.

**Etimología.** La subespecie ha sido nombrada como *carmenae*, forma latinizada del nombre Carmen, en honor a la madre de la segunda autora como un gesto de profundo amor y agradecimiento por ser ella siempre un modelo de fortaleza, dedicación y perseverancia.

**Genitalia (Fig. 3).** The genitalia of the dissected male paratype resemble those of other *Moschoneura* taxa (e.g., Llorente *et al.*, 2016). Although some slight variation was apparent among dissected individuals in the broad shape of the valva, no taxonomically or geographically consistent differences were found.

## DNA Barcoding analysis

Both NJ and Bayesian analyses (Figs. 4A,B) recovered a strongly supported clade (100% bootstrap support and clade credibility of 1, respectively) containing all included *Moschoneura* taxa except for *M. ela ela.* Both analyses also found the single included sample of *M. p. carmenae* **ssp. nov.** to be sister to the single included sample of *M. pinthous pinthous* from the Guianas. The NJ analysis recovered remaining *Moschoneura* taxa as a clade, but with weak bootstrap support (50%), while the Bayesian analysis recovered these taxa as a paraphyletic grade, but also with weak support (0.69, 0.8). Neither analysis provided any support for the monophyly of either *M. p. ithomia* (*sensu* Lamas, 2004) or *M. p. monica*.

## Behavior and habitat (Figs. 1C,D)

In April 2014 the first two authors spent five days in the Orinoco Delta in eastern Venezuela, visiting numerous tributaries of two major rivers (caños) east of San José de Buja - specifically Caño Buja and the larger river it feeds into, Caño Manamo (the largest river in the north-western Delta, which flows out to the sea in the south-eastern Delta and is itself a distributary of the Orinoco river) (see Fig. 1B). Butterflies were sampled and observed from the fishing launch at numerous sites along the riverside vegetation (see Figs. 1C,D), while on three occasions exploratory excursions were undertaken into the forest, although finding suitable landing sites proved difficult. On all the land sorties very few butterflies were seen, and only the second visit resulted in a significant discovery. This second excursion took place on 12 April 2014, between approximately 14:00 and 15:00, in a site with relatively clear understorey, with a maze of roots under foot, just above the high water line (the area is tidal), in low-canopy, occasionally flooded forest within 25 m of the bank of Caño Corto (see Figs. 1C,D). According to Google Earth, the elevation is 13 m above sea level. The mouth of Caño Corto is located 9 km north of the junction of Caño Manamo with Caño Buja.

At this site, three specimens were captured of a predominantly white dismorphiine that was immediately recognized as an undescribed taxon, but it was so distinctive that it was not initially identified as a subspecies of *M. pinthous*. These individuals appeared within an approximately half hour period, reflecting a typical frequency of encounter with this species elsewhere in SE Venezuela (Bolívar state), where it is locally relatively common in the understorey of tropical lowland forest and can usually be found as single individuals, although occasionally as many as a half dozen may be seen (pers. obs.; Mauro Costa, pers. comm.).

Like the adults of its southern neighbor *M. p. pinthous*, the flight pattern of *M. p. carmenae* **ssp. nov.** is slow and low to the ground, generally below 1 m. However, this new subspecies differs in one notable respect from all other *M. pinthous* subspecies - its ground colour is white, not yellow, and in flight it is therefore remarkably similar to that of other common white pierids that fly low in shaded forest habitat in tropical lowland forest elsewhere in Venezuela (and probably in much of the Orinoco Delta too), specifically females of *Eurema albula* (Cramer, 1775), and males of *Perrhybris pamela* (Stoll, 1780) and especially *Itaballia demophile* (Linnaeus, 1763), with which it was initially confused when seen at a distance. Another white pierid of similar size and shape, *Enantia aloikea* Brévignon, 1993 (a new record for Venezuela, A. Neild, unpublished data), was sampled on several nearby rivers, but its much faster flight, outside the forest interior, makes confusion (and therefore possible mimetic association) with *M. pinthous carmenae* **ssp. nov.** less probable.

As mentioned above, the white coloration of this new subspecies is most unusual; other *M. pinthous* subspecies have a yellow wing coloration and participate in Batesian (or possibly Müllerian) mimicry complexes, whose distasteful models are local "yellow transparent complex" ithomiines such as *Aeria* Hübner, 1816, *Episcada* Godman & Salvin, 1879, *Ithomia* Hübner, 1816, *Pteronymia* Butler & H. Druce, 1872, and

*Scada* Kirby, 1871 (see Beccaloni, 1997, and further references therein). The fact that this new subspecies lacks any yellow coloration may reflect the absence of any suitable ithomiine models in the region where it is found (pers. obs. by the first author in the field and in major Venezuelan and non-Venezuelan collections; see Neild, 2008), and it is therefore possible that the white phenotype of *M. p. carmenae* **ssp. nov.** represents an ancestral non-mimetic state. An alternative hypothesis is that the ancestral color pattern of this subspecies was yellow and mimetic of ithomiines, but with a lack of appropriate models/co-mimics in the Orinoco Delta to educate predators (e.g., Pfennig *et al*., 2001, 2007), the coloration of *M. p. carmenae* **ssp. nov.** evolved to be white, perhaps due to selection against a more conspicuous yellow-and-black aposematic pattern (Prudic & Oliver, 2008). The latter hypothesis is more consistent with the phylogenetic relationships inferred from COI barcode data, with this taxon nested among other black and yellow taxa, although more comprehensive sampling and data are needed to test this idea further. Another possibility is that the new subspecies is a Batesian or Müllerian mimic of one or more species of pierids, which may fly in the same microhabitat as *M. p. carmenae* **ssp. nov.**, despite the fact that we did not observe these species in the immediate area during our very short visit. Anecdotal and empirical studies suggest that a number of pierid species and genera are distasteful and aposematic (pers. obs.; Carpenter, 1942; DeVries, 1987; Corbet & Pendlebury, 1992; Parsons, 1998; Larsen, 2005; Braby & Trueman, 2006), enjoying a degree of protection from substances such as carotenoids and mustard oil glycosides (Rothschild, 1972; Braby & Trueman, 2006). For example, in the Neotropics such protection has been demonstrated for live *Perrhybris* Hübner, [1819] individuals which were found to be repeatedly rejected by avian predators (Chai, 1986). In the absence of any knowledge about the host plants of *Moschoneura* (Beccaloni *et al*., 2008) it is not possible to speculate whether or not *M. pinthous* is chemically defended, but relatives in the Dismorphiinae feed almost exclusively on Mimosoideae (Leguminosae), a plant clade not known to confer any biochemical protection.

## DISCUSSION

A number of new *Moschoneura* taxa have recently been described and the taxonomy of the genus continues to evolve, suggesting further work is needed to establish a firm understanding of the true species diversity (e.g., Lamas, 2004a,b; Llorente *et al*., 2016). Recognition of the distinctive,

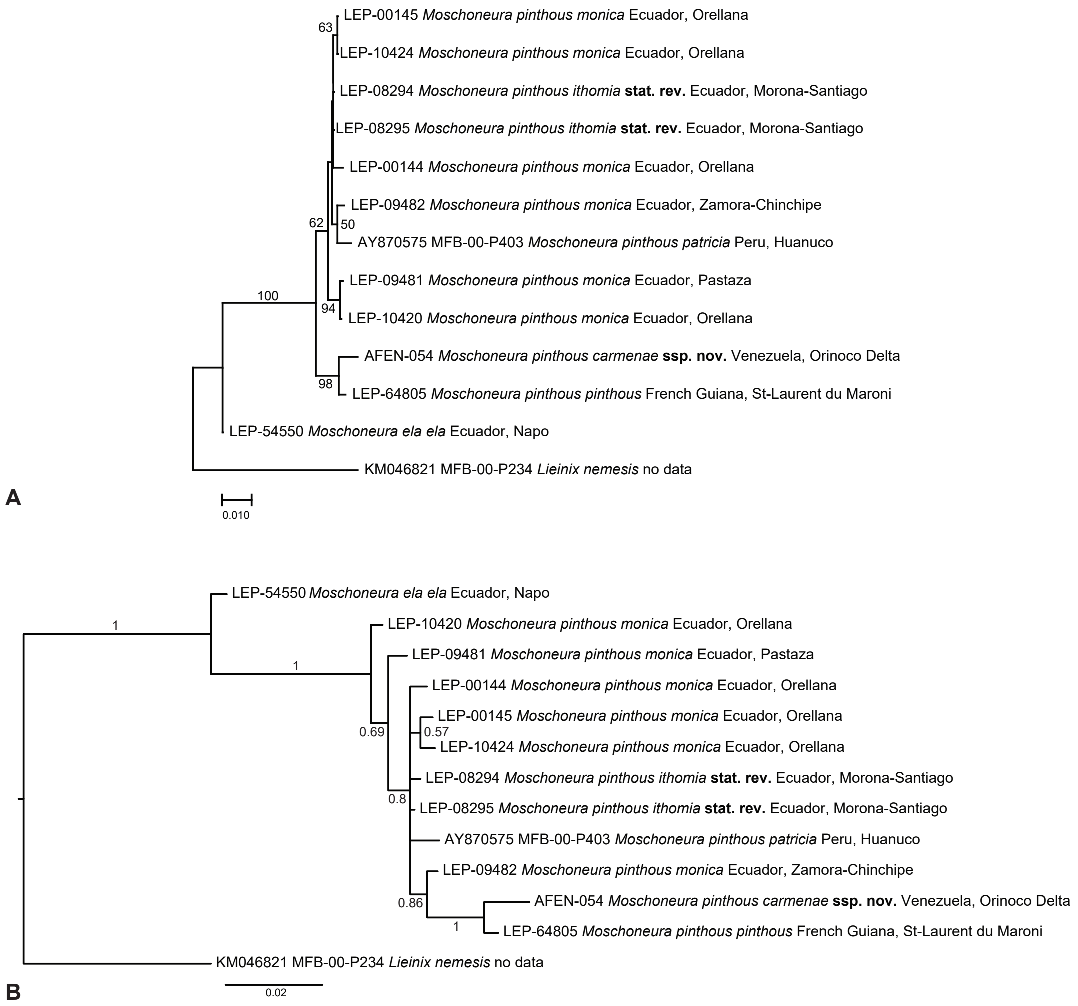

**Fig. 4. A.** Tree resulting from Neighbor-joining analysis (Kimura 2-parameter) for *Moschoneura* based on analysis of 669 bp of COI (barcode region). Bootstrap values (%) greater than 50 are shown by branches. **B.** Tree resulting from Bayesian analysis for *Moschoneura* based on same dataset as A. Clade credibility values are shown by branches.

larger cloud forest species *M. ela* (see Le Crom *et al*., 2004; Llorente *et al.*, 2016) seems warranted on the basis of its typically greater size and narrower wings, and different elevational range in comparison with lowland taxa, even though subspecies differentiation across the east Andean elevational gradient is observed, for example, in other dismorphiines, such as *Dismorphia theucharila* (Doubleday, 1848). Our analysis of COI barcode sequences is also consistent with this hypothesis, placing *M. ela* as sister to all remaining *Moschoneura*, although this result, based on a sequence from a single, rather old individual, requires confirmation. Furthermore, although our study contributes in no way to resolving the status of *M. methymna*, we follow Llorente *et al.* (2016) in treating it as a distinct species rather than a subspecies, in contrast to Freitas *et al*. (2018), since the former paper addressed the taxonomy of the genus more comprehensively than did the latter.

On the other hand, the COI barcode data for *M. pinthous* and *M. ithomia* (as defined by Llorente *et al.,* 2016) support their conspecificity, as treated by Lamas (2004a). Multiple samples of both taxa failed to show reciprocal monophyly or strong sequence divergence (Fig. 4). Also consistent with the hypothesis that these taxa are conspecific are reports of apparent hybridization (e.g., Le Crom *et al*., 2004), and the recurrence of analogous mimetic polymorphism within their primary ithomiine co-mimics, *Ithomia salapia* Hewitson, [1853] and *Scada reckia* (Hübner, [1808]), which show similarly low divergence in COI (see Elias *et al*., 2007; Dasmahapatra *et al*., 2010). We therefore restore the subspecies status of *M. pinthous ithomia* **stat. rev.**

The distributions and delimitation of other upper Amazonian *M. pinthous* subspecies could also benefit from further study. Lamas (2004b) described *M. p. patricia* (TL: Peru, Amazonas, 2 km S Puente Almendro), by comparing it to *M. p. ithomia*, stating that it differed in lacking white dorsal submarginal spots, and the same diagnosis was provided for *M. p. monica* Lamas, 2004 (in Le Crom *et al*., 2004; TL: Peru, Loreto, Castaña). The range of the former taxon was given as Amazonas to Huánuco in eastern Peru (Lamas, 2004b), and for the latter, from Colombia to Bolivia and west Brazil (Le Crom *et al*., 2004). Neither description mentioned the presumably neighboring taxon *M. p. proxima* (described from Tefé, further to the east in western Brazil), and its junior synonym *Dismorphia pinthaeus* [*sic*] *gracilis* Avinoff, 1926 (described from [Lago] Arimã, Rio Purus, some 300 km to the south-east). What seems to us to be the most distinctive feature of the type of *M. p. proxima* figured by Warren *et al.* (2017) is the pale orange VHW submarginal band, and several specimens matching this phenotype are known to us from the west and center of Venezuelan Amazonas state (in the collections of Mauro Costa and the first author). Thus, *M. p. proxima* may have a relatively extensive range in the middle Amazon basin at least. However, Llorente *et al*. (2016: 1149, 1151) stated "Puede advertirse que los especímenes machos de la cuenca del Napo conservan el fenotipo de *proxima*" ("It can be noted that male specimens from the Napo basin [eastern Ecuador, presumably *M. p. monica*] display the *proxima* phenotype"); although we have not seen any Ecuadorian specimens with a notably pale orange VHW submarginal band, this comment suggests that *proxima* might refer merely to a form rather than a subspecies. Our examination of the museum specimens available to us suggests that the phenotypes referable to currently recognized upper Amazonian subspecies belong to only weakly differentiated populations, with both local and geographic variation, as well as some geographic overlap. Furthermore, the status of the eastern and southern Amazonian specimens that we have examined also remains to be determined, and we designate these in Fig. 1A as the nominate subspecies. We suggest that a comprehensive review is needed to decide on the most appropriate taxonomy for the majority of these Amazonian populations.

The striking wing pattern differences separating *M. p. carmenae* **ssp. nov.** from remaining Amazonian *M. pinthous* taxa might, therefore, indicate that this taxon is potentially a distinct species. At least, such differences are no less significant than those separating *M. ela*, Amazonian *M. pinthous* and southeast Brazilian *M. methymna*. Nevertheless, we found no consistent differences in the male genitalia between *M. p. carmenae* and ten other examined specimens of *Moschoneura*, and analysis of COI barcodes suggests that the taxon is most closely related to the neighboring Guianan *M. p. pinthous*. For the present, therefore, it seems most reasonable to treat *M. p. carmenae* as a subspecies, pending a more thorough study of the genus with more extensive genetic data from numerous samples throughout the generic range.

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