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# Sympatric Diversification in the Upper Amazon

A Revision of the Eumaeine  
Genus *Paraspiculatus*  
(Lepidoptera: Lycaenidae)

*Robert C. Busby, Christophe Faynel,  
Alfred Moser, and Robert K. Robbins*

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WASHINGTON, D.C.  
2017

## ABSTRACT

Busby, Robert C., Christophe Faynel, Alfred Moser, and Robert K. Robbins. Sympatric Diversification in the Upper Amazon: A Revision of the Eumaeine Genus *Paraspiculatus* (Lepidoptera: Lycaenidae). *Smithsonian Contributions to Zoology*, number 649, viii + 65 pages, 130 figures, 4 tables, 2017.—The Neotropical lycaenid hairstreak genus *Paraspiculatus* is unusual because of a high frequency of sympatry in the upper Amazon Basin coupled with negligible interspecific variation of male genitalic structures and absence of male secondary sexual traits. Male sexual structures are postulated to promote species recognition by females and to contribute to reproductive isolation, for which reason a high incidence of sympatry in *Paraspiculatus* would not be expected.

A revision of *Paraspiculatus* was feasible because we increased the number of study specimens more than fivefold (by the extensive use of rotting fish as a bait for males) and sequenced the “barcode” part of the mitochondrial gene CO1 for almost all species. We recognize 19 *Paraspiculatus* species based on male wing patterns. We partition the 19 species into ten species complexes, which are monophyletic in all analyses of morphological characters, CO1 sequences, and a combined data set. Newly described are *Paraspiculatus apuya* Busby & Robbins, **new species**; *Paraspiculatus cosmo* Busby, Robbins & Faynel, **new species**; *Paraspiculatus transvesta* Robbins & Busby, **new species**; *Paraspiculatus grande* Busby, Robbins & Moser, **new species**; *Paraspiculatus honor* Busby, Robbins & Hall, **new species**; *Paraspiculatus emma* Busby & Robbins, **new species**; *Paraspiculatus sine* Busby & Robbins, **new species**; *Paraspiculatus azul* Busby, Robbins & Faynel, **new species**; *Paraspiculatus lilyana* Busby & Robbins, **new species**; and *Paraspiculatus noemi* Busby & Robbins, **new species**. All are described from Ecuador except for *P. transvesta* from Guatemala.

Male *Paraspiculatus* are attracted to traps baited with rotting fish in eastern Ecuador, but elsewhere this attraction is less frequent or absent. Using the behavior of other eumaeines as context, we briefly discuss these observations with respect to *Paraspiculatus* biology.

Ten of 19 *Paraspiculatus* species are sympatric in the upper Amazon Basin below 1,250 m. Five of these sympatric species are from a single species complex. This instance of apparent in situ diversification is responsible for much of the sympatric diversity in *Paraspiculatus* in the upper Amazon Basin.

**KEYWORDS:** Adult nutrition, CO1 barcoding, *Eumaeus* section, in situ diversification, male secondary sexual structures.

Cover images (from left): *Paraspiculatus orobia*; *P. sine*; *P. elis* (courtesy Rob Westerduijn); and *Mithras nautes* (courtesy Will and Gill Carter).

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Published by SMITHSONIAN INSTITUTION SCHOLARLY PRESS

P.O. Box 37012, MRC 957, Washington, D.C. 20013-7012

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### Library of Congress Cataloging-in-Publication Data

Names: Busby, Robert C. (Robert Carroll), 1948– author. | Smithsonian Institution Scholarly Press, publisher.

Title: Sympatric diversification in the Upper Amazon : a revision of the Eumaeine Genus *Paraspiculatus* (Lepidoptera: Lycaenidae) / Robert C. Busby [and three others].

Other titles: Smithsonian contributions to zoology ; no. 649. 0081-0282

Description: Washington, D.C. : Smithsonian Institution Scholarly Press, 2017. | Series: Smithsonian contributions to zoology, ISSN 0081-0282 ; number 649 | Includes bibliographical references.

Identifiers: LCCN 2017017880

Subjects: LCSH: *Paraspiculatus*—Amazon River Watershed. | Coexistence of species—Amazon River Watershed.

Classification: LCC QL561.L8 B87 2017 | DDC 333.95/5709811—dc23 | SUDOC SI 1.27:649

LC record available at <https://lcn.loc.gov/2017017880>

ISSN: 1943-6696 (online); 0081-0282 (print)

ZooBank registration: 3 August 2017 (LSID urn:lsid:zoobank.org:pub:D8F7819E-8121-4D07-AE95-8936A9DA0106)

Publication date (online): 15 August 2017

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# Sympatric Diversification in the Upper Amazon: A Revision of the Eumaeine Genus *Paraspiculatus* (Lepidoptera: Lycaenidae)

Robert C. Busby,<sup>1</sup> Christophe Faynel,<sup>2</sup> Alfred Moser,<sup>3</sup>  
and Robert K. Robbins<sup>4\*</sup>

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## INTRODUCTION

Perhaps the most unusual characteristic of the neotropical genus *Paraspiculatus* Johnson and Constantino, 1997 (Lycaenidae, Theclinae, Eumaeini, Figures 1–3) is that many of the species are sympatric in the upper Amazon Basin with little interspecific variation in traditional taxonomic characters, such as genitalic structures and male secondary sexual traits. Wing patterns also show a high degree of similarity. This situation contrasts sharply with most eumaeine genera. For example, in genera such as *Oenomaus* Hübner, diversification is accompanied by marked evolution of genitalic morphology among sympatric species (Faynel et al., 2012). In others, such as *Arcas* Swainson and *Lathecla* Robbins, sympatric species have conspicuously different male secondary structures (Robbins et al., 2012; Robbins and Busby, 2015). And in others, such as *Panthiades* Hübner and *Thepytus* Robbins, most species can be readily distinguished by elements of their wing patterns (Nicolay, 1976; Robbins, 2005; Robbins et al., 2010b).

The apparent lack of conspicuous male secondary structures in *Paraspiculatus* is distinctive because these structures occur in more than 95% of eumaeine species (Robbins, 2004a). Calycopidina Duarte and Robbins, *Contrafacia* Johnson, *Symbiopsis* Nicolay, *Dicya* Johnson, and *Paraspiculatus* are the major eumaeine taxa in which androconia are lacking on male wings. However, the vast majority of species belonging to the first three taxa have internal abdominal male secondary sexual structures called brush organs (Eliot, 1973; SEMs in Robbins, 1991; Duarte and Robbins, 2010), which are lacking without exception in *Paraspiculatus*. To the extent that male secondary structures are postulated to promote species recognition and to contribute to reproductive isolation among sympatric species (e.g., Löfstedt et al., 1991; Symonds and Elgar, 2008), the apparent high frequency of sympatry in *Paraspiculatus* is unexpected.

Little interspecific variation in genitalic structures, such as in *Paraspiculatus*, is not as unusual in the Eumaeini as the lack of male secondary structures. For example, *Arcas* species cannot be distinguished by their genitalia (Nicolay, 1976), but no two species share identical male secondary structures (Robbins et al., 2012). Interspecific genitalic differences among animals are hypothesized to result from sexual selection, which then facilitates sympatry between sister species following secondary contact (e.g., Lande, 1981; Hosken and Stockley, 2004; Eberhard, 2010; Simmons, 2014). Again, a low

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Received 4 May 2016; accepted 8 February 2017.



**FIGURES 1–4.** Adults in nature. 1. ♂ *Paraspiculatus orobia* feeding on a leaf coated with drops of liquid containing rotting fish, Apuya, Napo, Ecuador. 2. ♂ *P. sine* feeding on rotting fish, San Isidro, Morona Santiago, Ecuador. 3. ♂ *P. elis* feeding on dilute cow blood, Puerto Almendra, Loreto, Peru (image courtesy of Rob Westerduijn). 4. ♂ *Mithras nautes* on a leaf, Alta Floresta, Mato Grosso, Brazil (image courtesy of Gill and Will Carter). The latter two species have a similar, conspicuous transverse orange-yellow band on the hindwing. The ground color of *P. orobia* appears darker than that of *P. sine* because of the angle at which the image was taken, the lighting, and the worn condition of the latter individual.

incidence of sympatry in *Paraspiculatus* would be predicted. For example, in a four-species lineage of *Electrostrymon* Clench with uniform genitalia and without male secondary sexual traits on the wings—a situation similar to that in *Paraspiculatus*—sympatry was absent except for minor elevational overlap (Thompson and Robbins, 2016).

The lack of variation in traditional taxonomic characters in *Paraspiculatus* and paucity of specimens in museum collections have been limiting factors in documenting diversity within the genus. With the exception of a few species with distinctive ventral wing patterns, such as *P. elis* (Cramer, 1779) and *P. catrea* (Hewitson, 1874), the identification and taxonomic treatment of described species has been chronically incorrect, as noted in the species accounts below. Also, wing pattern similarity in females has precluded accurate association with males.

A revision of *Paraspiculatus* is feasible for the first time because of two factors. First, we increased the study material fivefold. At the beginning of this study, there were fewer than 150 specimens, including types, in major North American and European museums (listed below). Using traps baited with rotting fish, we added more than 450 specimens to the study series. Additional material was found in public museum collections in Latin America and in private collections. The sample size increase to 742 individuals allowed a markedly improved analysis of wing pattern variation. Second, we successfully sequenced the DNA “barcode region” of the mitochondrial gene CO1 for all but two *Paraspiculatus* species. These sequences were used primarily to associate the sexes—a nearly intractable problem for many species previously—and secondarily as another character set for distinguishing species.

The first purpose of this paper is to propose a species-level classification for *Paraspiculatus*. Variation of wing pattern characters—albeit characters that are sometimes subtle and difficult to assess in worn individuals—and of CO1 DNA sequences is largely congruent, which provides the evidence for recognizing

19 species, of which 10 are new. We associate the sexes, when the female is known, and provide a key to identify males by their wing pattern. We also summarize information on distribution, habitat, and behavior.

The second purpose is to establish monophyletic species complexes within *Paraspiculatus*. Although phylogenetic analyses yielded a variety of trees, a number of clades were monophyletic in all results based on morphology, molecules, and both data sets. Recognition of these clades as species complexes provides a more fine-grained classification and allows us to characterize the composition of the set of sympatric species in the upper Amazon.

## MATERIALS AND METHODS

The species-level taxonomy of *Paraspiculatus* is based primarily on an analysis of morphological variation among 742 pinned specimens from the following collections (most abbreviations from Evenhuis, 2015). We also examined more than a hundred other specimens with redundant data.

### ABBREVIATIONS FOR COLLECTIONS

AMNH	American Museum of Natural History, New York, New York, USA
BMNH	The Natural History Museum [formerly British Museum (Natural History)], London, UKCF Private collection of Christophe Faynel, Montpellier, France
CMNH	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA
DZUP	Museu de Entomologia Pe. Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Paraná, Brazil
LACM	Los Angeles County Museum of Natural History, Los Angeles, California, USA

JFLC	Private collection of Jean-François Le Crom, Bogotá, Colombia
JHKW	Jason P. W. Hall and Keith R. Willmott collection, Washington, D.C., USA
MC	Private collection of Alfred Moser, São Leopoldo, Rio Grande do Sul, Brazil
MECN	Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador
MGCL	McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MUSA	Museo de Historia Natural de la Universidad Nacional San Agustín, Lima, Peru
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru
RCB	Private collection of Robert C. Busby, Andover, Massachusetts, USA
SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt-am-Main, Germany
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA
ZMBH	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany

#### OTHER ACRONYMS AND ABBREVIATIONS

BIN	barcode index number
BOLD	Barcode of Life Data System
DFW	dorsal forewing
DHW	dorsal hindwing
HW	hindwing
ICZN	International Commission on Zoological Nomenclature
SEM	scanning electron microscope
VFW	ventral forewing
VHW	ventral hindwing

To supplement and confirm the morphological taxonomy, we used DNA barcode sequences belonging to the CO1 gene. Legs from 138 adults of 19 *Paraspiculatus* species in our study material were prepared and sequenced according to the protocol in Wilson (2012). Sequences longer than 200 base pairs were successfully extracted from 111 samples representing 17 *Paraspiculatus* species. The samples are listed in Appendix A with their museum vouchers and BOLD process numbers (Ratnasingham and Hebert, 2007). We visualized DNA sequence differences phenetically using the neighbor-joining methods on the BOLD website (Ratnasingham and Hebert, 2007), along with the recently introduced barcode index numbers (Ratnasingham and Hebert, 2013).

On the basis of morphological variation and phenetic DNA sequence differences, we recognize nine *Paraspiculatus* species that were previously described plus 10 new taxa, which are described according to the rules of the ICZN (1999). We associated

the sexes in some species, such as *P. elis*, by similarity of ventral wing pattern and distribution, and in others, such as *P. orobia* (Hewitson, 1867), by similarity of mitochondrial CO1 DNA sequences.

Standard references for morphological terminology are Comstock (1918) for insect wing veins; Klots (1970) and Robbins (1991) for Lepidoptera genitalia as modified for the Eumaeini; Robbins et al. (2012) for male secondary sexual structures; and Snodgrass (1935) for all other structures. Genitalic dissections are listed in Appendix B. Adult size was measured from the base of the forewing to its apex. For new species, size is reported by the mean, standard deviation, and sample size. To test whether male *P. colombiensis* Johnson and Constantino, 1997 are smaller than male *P. noemi* Busby and Robbins, we did a t-test with unequal variances in commercially available Microsoft Excel software and checked the calculations online using VassarStats (<http://vassarstats.net/index.html>; accessed 10 February 2016).

Labels on holotypes are recorded verbatim, with square brackets used for information not explicitly noted on the labels and for descriptions of the labels. Lines on holotype labels are separated by a forward slash (/). Otherwise, months are abbreviated by their first three letters in English. Localities and other data, especially within the Material Examined and Type Material sections, were transcribed as presented on specimen labels, with the result of minor inconsistencies of wording and format within those sections.

Nomenclaturally relevant information for *Paraspiculatus* and for each species is summarized in a nomenclatural list. Citations for original descriptions can be found in Lamas (2015).

Besides taxonomic history and morphological variation, species accounts include information on distribution, elevation, biogeography, habitat, and behavior. Maps are used to visualize distributions but, for practical reasons, unrelated species are sometimes placed on the same map. Biogeographic zones follow Brown (1982), who partitioned the forested nonmontane continental neotropics into the Transandean region, Amazon region, and Atlantic region. These general biogeographic regions were derived, in part, from vertebrate distributions (e.g., Ab'Sáber, 1977) and have proven useful for documenting the biogeography of forest butterflies (e.g., Willmott, 2003; Robbins et al., 2010a). Although more fine-grained biogeographical regions have been proposed, such as those in Morrone (2014) and Chazot et al. (2016), they include nonforested regions, such as cerrado, where *Paraspiculatus* are not known to occur. Further, the geographic data for many *Paraspiculatus* species are insufficient to examine these more finely partitioned biogeographic regions. Elevation zones are slightly modified from Elias et al. (2009) into lowland species (0–1,250 m), lower montane species (500–1,700 m), and montane species (>1,200 m). If adults were attracted to rotting fish, we note whether they were attracted to traps, which were hung 7 to 20 m above the ground, or to leaves near the ground. Many male eumaeines perch in “territories” at certain times of day to wait for receptive females to fly through and “defend” these areas by flying at other males that enter the territory (e.g.,

Powell, 1968; Alcock and O'Neill, 1987; Cordero et al., 2000; Faynel, 2003, 2006a). Recorded times from our fieldwork for "territorial" behavior are standard time at that locality.

We analyzed morphological characters and CO1 barcode sequences to identify monophyletic lineages within *Paraspiculatus*. *Mithras nautes* (Cramer, 1779) and *Theorema eumenia* (Hewitson, 1865) were used as outgroups for reasons given below under "Taxonomic History."

We coded 26 morphological characters for each *Paraspiculatus* species, *Mithras nautes*, and *Theorema eumenia*, and refer to them in the species accounts by their character number (Table 1). Most characters refer to male wing pattern because, as noted, there is little variation in genitalic morphology, and

male secondary sexual structures are lacking. The resulting matrix (Table 2) was 26 characters by 21 species (which include two outgroups).

We used 118 CO1 DNA barcode sequences longer than 600 base pairs in length from our study series (downloaded from the BOLD database). Of these, 105 were specimens of *Paraspiculatus* belonging to 17 species (data were lacking for *P. transvesta* Robbins and Busby and *P. vossoroca* Bálint and Moser, 2001); about 6 specimens per species. The other downloaded sequences belonged to the two outgroup species. We had identified each of the 118 adults from which DNA was extracted. We used Mesquite software to delete empty positions and corrected three base pairs that had been shifted to empty positions in three specimens.

TABLE 1. Morphological characters for *Paraspiculatus*.

Character number	Character and states
1.	Forewing shape at vein $M_2$ (0) continuously rounded, (1) angled.
2.	Male DFW basal edge dark apex extends to the distal side of discal cell (0) no, (1) yes.
3.	Male DFW inner edge of black border between $M_3$ and 2A (0) concave, (1) straight except for black scales in the middle of cell $Cu_2$ -2A extending basally, (2) straight without black scales in the middle of cell $Cu_2$ -2A extending basally, (3) border is a marginal dark line.
4.	Male DFW blue scales between the end of discal cell and the apex (0) present, (1) absent.
5.	Male DFW anterior half of discal cell entirely brown-black (0) absent, (1) present.
6.	Male VFW scales along costal margin (0) same as ventral wing color, (1) light brown/tan (some separation from base color), (2) white.
7.	Male VFW scales posterior of cubital vein (0) shining blue, (1) iridescent in flat plane (silvery blue), (2) iridescent only at an acute angle (brownish).
8.	Male VFW iridescent scales, anterior of cubital vein (0) iridescent silver-blue, (1) brown, (2) iridescent shining blue.
9.	Male VFW scales in limbal area just posterior of vein $Cu_2$ (0) a shade of brown, (1) bluish gray, (2) shining blue.
10.	Male VFW with scattered white scales next to the distal parts of vein 2A (0) absent, (1) present.
11.	Male HW shape (angle measured from end of vein $Cu_1$ to the anal lobe to the midpoint of inner margin) (0) angle greater than 90°, (1) angle 90°, (2) angle less than 90°.
12.	Male HW shape (0) rounded apex, (1) less rounded, more angular at vein $M_1$ .
13.	Male DHW basal side of cell $Sc+R_1$ -Rs (0) blue (same size/shape as other blue wing scales), (1) black/purple (same size/shape as blue wing scales), (2) gray/brown (slightly rounded tips, evenly spaced), (3) dark gray, iridescent edges (clustered in center of cell).
14.	Male DHW blue scales in cell $Rs-M_1$ (0) restricted, usually limited to basal and posterior sides, (1) extensive, fills most (75%) of cell.
15.	Male DHW anal lobe shape (0) small, with rounded inner margin, (1) large, with rounded inner margin, (2) elongated like a teardrop, (3) with a long, "straight" inner margin.
16.	Male DHW with distal greenish iridescent scales (0) absent, (1) present.
17.	Male VHW with scattered blue/white scales (0) absent, (1) present.
18.	Male VHW with postmedian line in cell $Sc+R_1$ -Rs displaced to the basal half of the cell (0) absent, (1) present.
19.	Male VHW with transverse orange ray through the disco-cellular veins (0) absent, (1) present.
20.	Male VHW postmedian line intersects vein 2A (0) closer to wing base than anal lobe, (1) much closer to anal lobe than to wing base.
21.	Male VHW band of blue/green scales between the posterior part of the postmedian line and the anal angle (0) absent, (1) present.
22.	Male VHW anal angle with white marginal scales at the end of 2A and at the inner margin at the edge of the anal lobe area (0) absent, (1) present.
23.	Male genitalia with longitudinal spiculate pad (0) absent, (1) present.
24.	Male genitalia with semi-hemispherical brush organs (0) present, (1) absent.
25.	Density of spines on the inner surface of the corpus bursae (0) not greater in the vicinity of the origin of the ductus seminalis, (1) greater in the vicinity of the origin of the ductus seminalis.
26.	Female ductus bursae with a narrow, lightly sclerotized medial "neck" (0) absent, (1) present.



TABLE 2. Morphological character matrix for *Paraspiculatus* with *Theorema* and *Mithras* as outgroups.

Taxon	Character number																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
<i>T. eumenia</i>	0	0	0	0	0	0	1	2	2	0	0	1	1	1	?	1	0	0	0	0	1	0	0	0	0	0
<i>M. nautes</i>	0	0	3	0	0	0	0	2	2	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0
<i>P. elis</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	1	1	0	0
<i>P. catrea</i>	1	0	2	0	0	2	2	1	0	1	2	1	0	1	2	0	1	1	0	0	0	1	0/1	1	1	1
<i>P. vossoroca</i>	1	0	2	0	0	2	?	1	0	1	2	0	0	0	2	0	0	1	0	0	0	?	1	1	1	1
<i>P. oroanna</i>	1	0	2	0	0	2	1	1	0	1	1	0	0	0	1	0	0	1	0	0	0	1	1	1	?	?
<i>P. apuya</i>	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	?	?
<i>P. hamelore</i>	0	0	0	0	0	2	1	0	0	0	1	1	0	0	0	0	0	1	0	1	0	1	1	1	1	1
<i>P. cosmo</i>	0	0	0	0	0	2	1	0	0	0	1	0	2	0	0	0	0	1	0	1	0	1	1	1	1	1
<i>P. orobia</i>	0	0	0	0	0	2	1	2	0	0	1	0	2	0	0	0	0	1	0	1	0	1	1	1	1	1
<i>P. orobiana</i>	0	1	1	1	0	1	2	1	0	0	1	0	0	0	0	0	0	1	0	1	0	1	1	1	1	1
<i>P. transvesta</i>	0	?	?	?	?	2	2	1	0	0	0	0	?	?	0	0	?	1	0	1	0	1	1	1	1	1
<i>P. grande</i>	0	1	1	1	0	2	1	0	0	0	1	0	3	0	3	0	0	1	0	1	0	0	1	1	1	1
<i>P. honor</i>	0	1	1	1	0	2	1	0	0	0	1	0	3	0	3	0	0	1	0	1	0	0	1	1	1	1
<i>P. orocana</i>	0	1	1	0	0	2	1	0	0	0	1	0	3	0	3	0	0	1	0	1	0	0	1	1	?	?
<i>P. emma</i>	0	0	0	0	0	2	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	?	?
<i>P. sine</i>	0	0	0	0	0	2	1	0	1	1	0	0	0	1	0	0	0	1	0	1	0	1	1	1	?	?
<i>P. colombiensis</i>	0	0	0	0	0	2	1	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	1	1	1	1
<i>P. azul</i>	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	1	1	1	1
<i>P. lilyana</i>	0	0	0	0	0	1	1	2	1	0	0	0	0	1	0	0	0	1	0	1	0	1	1	1	?	?
<i>P. noemi</i>	0	0	0	0	0	2	1	0	1	0	0	0	1	1	0	0	0	1	0	1	0	1	1	1	1	1

The resulting molecular matrix was made up of 654 base pairs for 118 specimens belonging to 17 *Paraspiculatus* and two outgroup species.

A third matrix combined the morphological and molecular data. We modified the molecular nexus file by adding *P. transvesta* and *P. vossoroca*, which were coded with question marks (?) for each molecular position. We then added the morphological data from the morphology matrix for each specimen. The resulting combined matrix had 680 characters (the first 654 were molecular sequences) for 120 specimens belonging to 19 *Paraspiculatus* and two outgroup species.

The morphological matrix was analyzed with equal-weight maximum parsimony using traditional search (5 random seeds, 100 replications, 1,000 trees saved per replication, collapse trees after search) in TNT software (Goloboff et al., 2008). To assess the assumption of equally weighted characters, implied weighting was performed over a range of values for the parameter K (3, 10, 100, 1,000). Standard bootstrap support values were also calculated in TNT. Strict consensus trees and mapping of character changes using unambiguous changes were done in WinClada software (Nixon, 2002).

The molecular matrix was analyzed with both Garli (Zwickl, 2006) and TNT. We ran PartitionFinder (Lanfear et al., 2012) and determined that TrN+I, F81, and TrN+G were the

best models for first, second, and third codon positions, respectively. The best maximum likelihood tree was derived in Garli using 100 search repetitions. We then analyzed the molecular matrix with equal-weight and implied-weight (K = 3, 10, 100, 1,000) maximum parsimony using traditional search in TNT.

The combined morphology and molecular matrix was analyzed with equal-weight and implied-weight (K = 3, 10, 100, 1,000) maximum parsimony using traditional search in TNT. Standard bootstrap support values were also calculated in TNT.

## NOMENCLATURE LIST

This list summarizes relevant nomenclatural information for *Paraspiculatus*.

### *Paraspiculatus* Johnson and Constantino, 1997

Type species: *Paraspiculatus colombiensis* Johnson and Constantino.

#### *Paraspiculatus elis* species complex

*Paraspiculatus elis* (Cramer, 1779) (*Papilio*), type locality: Suriname. [There is a possible syntype in the museum in Leiden.]

***Paraspiculatus catrea* species complex**

*Paraspiculatus catrea* (Hewitson, 1874) (*Thecla*), type locality: Brazil. [Syntypes in BMNH. D'Abrera (1995) called one of the syntype males a holotype, but under ICZN Article 74.5, this action cannot be construed as a lectotype designation.]

*Paraspiculatus vossoroca* Bálint and Moser, 2001, type locality: Brazil, Santa Catarina, Joinville. [Holotype in DZUP.]

***Paraspiculatus oroanna* species complex**

*Paraspiculatus oroanna* Bálint, 2002, type locality: Peru, Huánuco, Cushi. [Holotype in BMNH.]

***Paraspiculatus apuya* species complex**

*Paraspiculatus apuya* Busby and Robbins, new species, type locality: Ecuador, Napo, 14 km Tena–Puyo Road, 1°06.7'S, 77°46.9'W. [Holotype in USNM.]

***Paraspiculatus hannelore* species complex**

*Paraspiculatus hannelore* Bálint and Moser, 2001, type locality: Brazil, Rio Grande do Sul, Dois Irmãos, Picada Veraão. [Holotype in DZUP.]

***Paraspiculatus orobia* species complex**

*Paraspiculatus cosmo* Busby, Robbins, and Faynel, new species, type locality: Ecuador, Morona Santiago, Bosque de Domono, 2°11.0'S, 78°06.2'W. [Holotype in USNM.]

= *cosmophila* (Tessman, 1928) (*Thecla*), type locality: Peru, unavail., ICZN Art. 45.5.1.

= *cosmophila* (Bridges, 1988) (*Thecla*), type locality: Peru, unavail., ICZN Art. 45.5.1.

*Paraspiculatus orobia* (Hewitson, 1867) (*Thecla*), type locality: Brazil, Amazon. [Lectotype male unintentionally designated by Johnson and Constantino (1997) in BMNH.]

= *villaanna* Bálint, 2004, type locality: Colombia, Villavicencio (misspelled in original description). [Holotype in MNHN.]

***Paraspiculatus orobiana* species complex**

*Paraspiculatus orobiana* (Hewitson, 1867) (*Thecla*), type locality: Brazil, Amazon, Ega (AM). [Lectotype male unintentionally designated by Johnson and Constantino (1997) in BMNH.]

***Paraspiculatus transvesta* species complex**

*Paraspiculatus transvesta* Robbins and Busby, new species, type locality: Guatemala, Cayuga. [Holotype in USNM.]

***Paraspiculatus orocana* species complex**

*Paraspiculatus grande* Busby, Robbins, and Moser, new species, type locality: Ecuador, Esmeraldas, 12 km Lita–San Lorenzo Road, 0°53.1'N, 78°30.9'W. [Holotype in USNM.]

*Paraspiculatus honor* Busby, Robbins, and Hall, new species, type locality: Ecuador, Pichincha, Mindo, Río Napombillo. [Holotype in USNM.]

*Paraspiculatus orocana* (H. H. Druce, 1912) (*Thecla*), type locality: Peru, El Povenir. [Lectotype male unintentionally designated by Johnson and Constantino (1997) in BMNH.]

***Paraspiculatus colombiensis* species complex**

*Paraspiculatus emma* Busby and Robbins, new species, type locality: Ecuador, Napo, 14 km Tena–Puyo Road, 1°06.7'S, 77°46.9'W. [Holotype in USNM.]

*Paraspiculatus sine* Busby and Robbins, new species, type locality: Ecuador, Morona Santiago, 15 km S of Gualaquiza, 3°27.6'S, 78°33.1'W. [Holotype in USNM.]

*Paraspiculatus colombiensis* Johnson and Constantino, 1997, type locality: Colombia, Rio Ortequaza. [Holotype in AMNH.]

*Paraspiculatus azul* Busby, Robbins, and Faynel, new species, type locality: Ecuador, Napo, 14 km Tena–Puyo Road, 1°06.7'S, 77°46.9'W. [Holotype in USNM.]

*Paraspiculatus lilyana* Busby and Robbins, new species, type locality: Ecuador, Napo, 14 km Tena–Puyo Road, 1°06.7'S, 77°46.9'W. [Holotype in USNM.]

*Paraspiculatus noemi* Busby and Robbins, new species, type locality: Ecuador, Pichincha, 20 km Pacto–Guayabillas Road, 0°11.6'N, 78°51.5'W. [Holotype in USNM.]

**OVERVIEW OF PARASPICULATUS**

**TAXONOMIC HISTORY.** Johnson and Constantino (1997) characterized *Paraspiculatus*—and derived the name—from a “spiculate pad” on the posterior lateral edge of the fused vinculum/tegumen of the male genitalia. They applied the name to species that had been previously placed in the *Thecla orobia* species group (Draudt, 1919–1920). Bálint and Moser (2001) reported that the spiculate pad was lacking in *Paraspiculatus catrea* and suggested as an alternative that “the degree of sclerotization and the shape of the dorsal posterior pouch beneath the ductus seminalis” of the female genitalia was a synapomorphy.

Robbins (2004a,b) synonymized *Paraspiculatus* with the monotypic *Mithras* Hübner for two reasons. First, both genera have nonsocketed teeth on the posterior lateral edge of the vinculum. Second, *Paraspiculatus elis* possesses a ventral wing pattern that is very similar to that of *Mithras nautes* (Figures 3, 4), as noted by Draudt (1919–1920), but has the male genitalic structures of the *Thecla orobia* species group. However, this synonymy was provisional because structure of the spiculate pad is different in *Mithras* and *Paraspiculatus* (Figure 5). Further, whereas *Mithras nautes* possesses semi-hemispherical brush organs that surround the male genitalia—a conspicuous trait shared with *Eumaeus* Hübner and *Theorema* Hewitson (Robbins, 2004a)—*Paraspiculatus* lacks brush organs.

The molecular phylogenetic analysis of Quental (2008) included two species of the *Thecla orobia* species group, but not the type species of *Mithras*. However, the *Thecla orobia* species group did not group with *Eumaeus* and *Theorema*, although



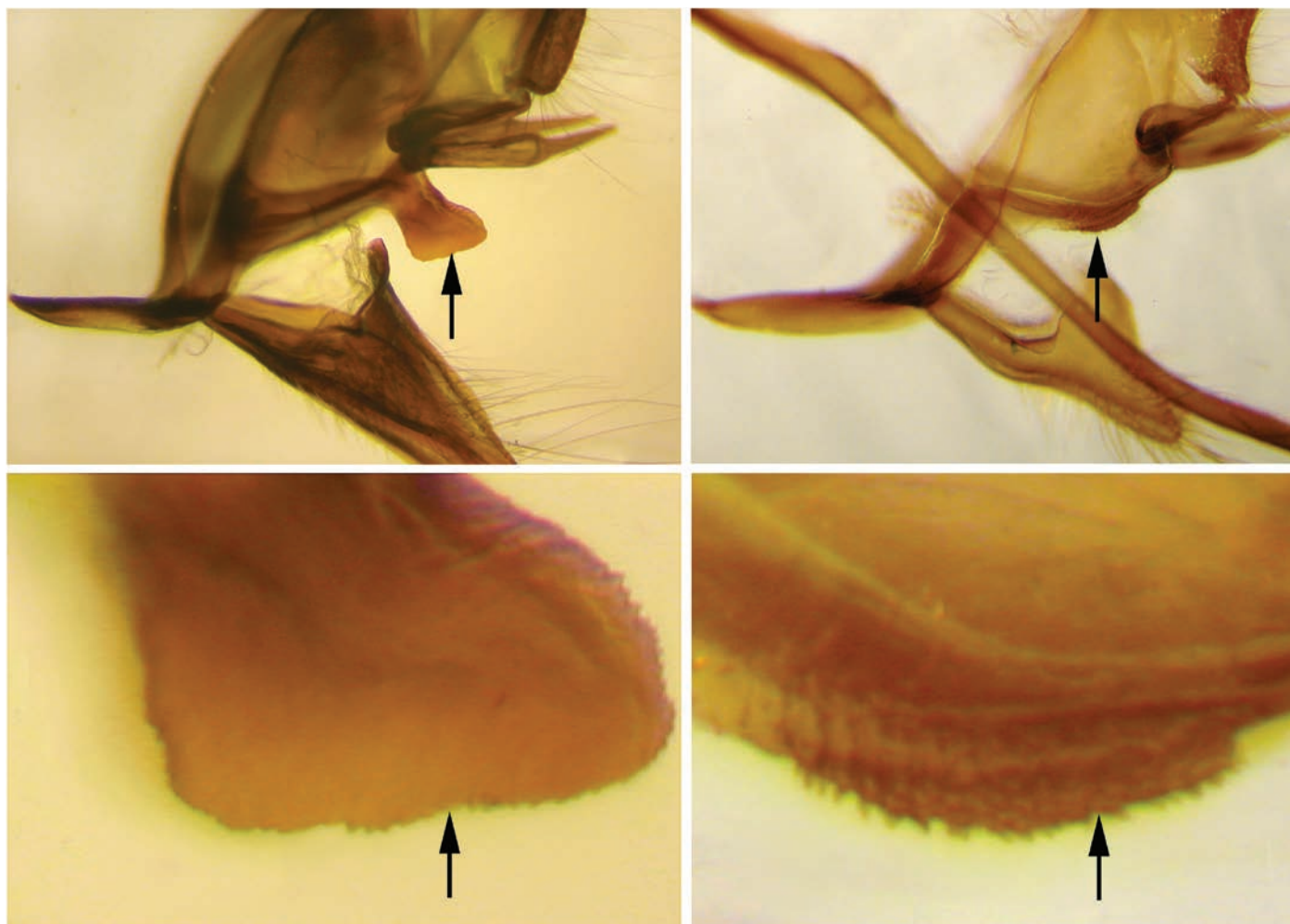


FIGURE 5. Male genitalia “spiculate pad” in lateral aspect (arrows) and enlarged (bottom) for *Mithras nautes* (left) and *Paraspiculatus colombiensis* (right).

they were closely related in some analyses. Rather, *Chalybs lineata* (Hewitson) was the weakly supported sister to the *Thecla orobia* species group. However, because *Chalybs lineata* shares no morphological similarity with *Paraspiculatus*, the molecular data need to be confirmed.

**RECOGNITION OF *PARASPICULATUS*.** Given the uncertainty in the phylogenetic relations of *Paraspiculatus* and relatives, we treat *Paraspiculatus* as a distinct genus characterized by the spiculate pad, as first proposed by Johnson and Constantino (1997). It is unique within the Eumaeini, so far as we are aware, and is a synapomorphy in the phylogenetic analyses in this paper. Bálint and Moser (2001) proposed a synapomorphy in the female genitalia, but we could discern no substantive basis for this proposal. We did code two characters of the female genitalia, but neither provides a synapomorphy for *Paraspiculatus* in phylogenetic analyses.

**WING PATTERN AND SHAPE.** Wing pattern in *Paraspiculatus* is characteristically homogeneous with a few exceptions (Figures 6–40). Apart from *P. transvesta* Robbins and Busby, the dorsal wings of most males have bright blue scaling with a black border whereas those of most females have less blue scaling, oftentimes none. The ventral wings of both sexes are dark brown with a postmedian line composed of shining blue dots and dashes. On the forewing, these spots form a disjointed line from the costa to vein  $Cu_2$ . On the hindwing the spots are usually arranged in a semicircle. The anteriormost hindwing spot (cell  $Sc+R_1-Rs$ ) is displaced basally. The blue spots are surrounded by a variable number of black scales, which enhance the contrast of the bright blue with the dark wing ground color. Distal of the hindwing postmedian line, there are scattered green or gold scales near the anal angle. A submarginal band on the hindwing is barely visible to absent because of the dark ground color.



FIGURES 6–13. Adults of *Paraspiculatus*, dorsal on left. 6. ♂ *P. elis* (Ecuador). 7. ♀ *P. elis* (Peru). 8. ♂ *P. catrea* (Brazil). 9. ♀ *P. catrea* (Brazil). 10. ♂ *P. vossoroca* (Brazil). 11. ♀ *P. vossoroca* (Brazil). 12. ♂ *P. oroanna* (Ecuador). 13. ♂ *P. apuya* (Ecuador). Scale 1 cm (lower left).

However, it is present in *P. hannelore* Bálint and Moser, 2001 and sometimes in other species such as *P. orobiana* (Hewitson, 1867) and *P. azul* Busby, Robbins, and Faynel. Most individuals of *Paraspiculatus* can be recognized by these characteristic wing pattern traits, but individuals belonging to other genera sometimes possess some or all of these traits.

*Paraspiculatus* wing shape is variable. Forewings are more elongate in some species, such as *P. elis*, than in others, such as *P. catrea*. Hindwing shape varies from round (*P. apuya* Busby and Robbins) to angular (*P. vossoroca*). Hindwing tails may be present in both sexes (*P. elis*), in females only (*P. catrea*), or absent in both sexes (*P. vossoroca*). In *P. orobia* and *P. noemi*, presence and length of hindwing tails vary geographically. Examples

of other eumaeines in which tail length and number vary geographically are *Arawacus jada* (Hewitson) and *Atlides halesus* (Cramer) (Godman and Salvin, 1887–1901; Clench, 1942).

**VARIATION IN MALE WING PATTERN.** Scaling on the wings of male *Paraspiculatus* is the primary source of morphological variation, which is used for both identification and inference of relationships. Here we summarize important aspects of this variation and provide figures to illustrate these characters (Figures 41–77). As a matter of terminology, we differentiate bright shining blue (Figure 65 left side—scales anterior of the cubital vein) from iridescent blue or silver-blue (Figure 65 right side—scales posterior of the cubital vein). Bright shining blue is bright blue regardless of the angle at which it is viewed.





FIGURES 14–21. Adults of *Paraspiculatus*, dorsal on left. 14. ♂ *P. hannelore* (Brazil). 15. ♀ *P. hannelore* (Brazil). 16. ♂ *P. cosmo* (Ecuador). 17. ♀ *P. cosmo* (Ecuador). 18. ♂ *P. orobia* (Brazil). 19. ♀ *P. orobia* (French Guiana). 20. ♂ *P. orobia* (Ecuador). 21. ♂ *P. orobia* (Peru). Scale 1 cm (lower left).

The two wing characters we found to be most useful for distinguishing species groups are as follows:

- (1) Scales on the basal half of the dorsal hindwing anterior of vein Rs are (a) blue (black in one species) and are similar to surrounding scales in size and shape (Figures 71–73), (b) dark gray with iridescent edges, concentrated in the center of the cell giving that area a sheen (Figure 74), or (c) brown/gray with slightly rounded tips, evenly spaced throughout the cell (Figures 75, 76).

- (2) The limbal area of the ventral forewing on the posterior side of vein  $Cu_2$  is either dull bluish gray (Figures 60–64) or a shade of brown (Figures 53–59).

Other wing characters that are important for species identification include:

- (1) Scales posterior of the ventral forewing cubital vein have an iridescent sheen when viewed at an angle. Scales anterior of the ventral forewing cubital vein may be bright shining blue



FIGURES 22–30. Adults of *Paraspiculatus*, dorsal on left. 22. ♂ *P. orobiana* (Brazil). 23. ♀ *P. orobiana* (Peru). 24. ♂ *P. transvesta* (Guatemala). 25. ♀ *P. transvesta* (Mexico). 26. ♂ *P. grande* (Ecuador). 27. ♀ *P. grande* (Panama). 28. ♂ *P. honor* (Ecuador). 29. ♀ *P. honor* (Ecuador). 30. ♂ *P. orocana* (Ecuador). Scale 1 cm (lower left).





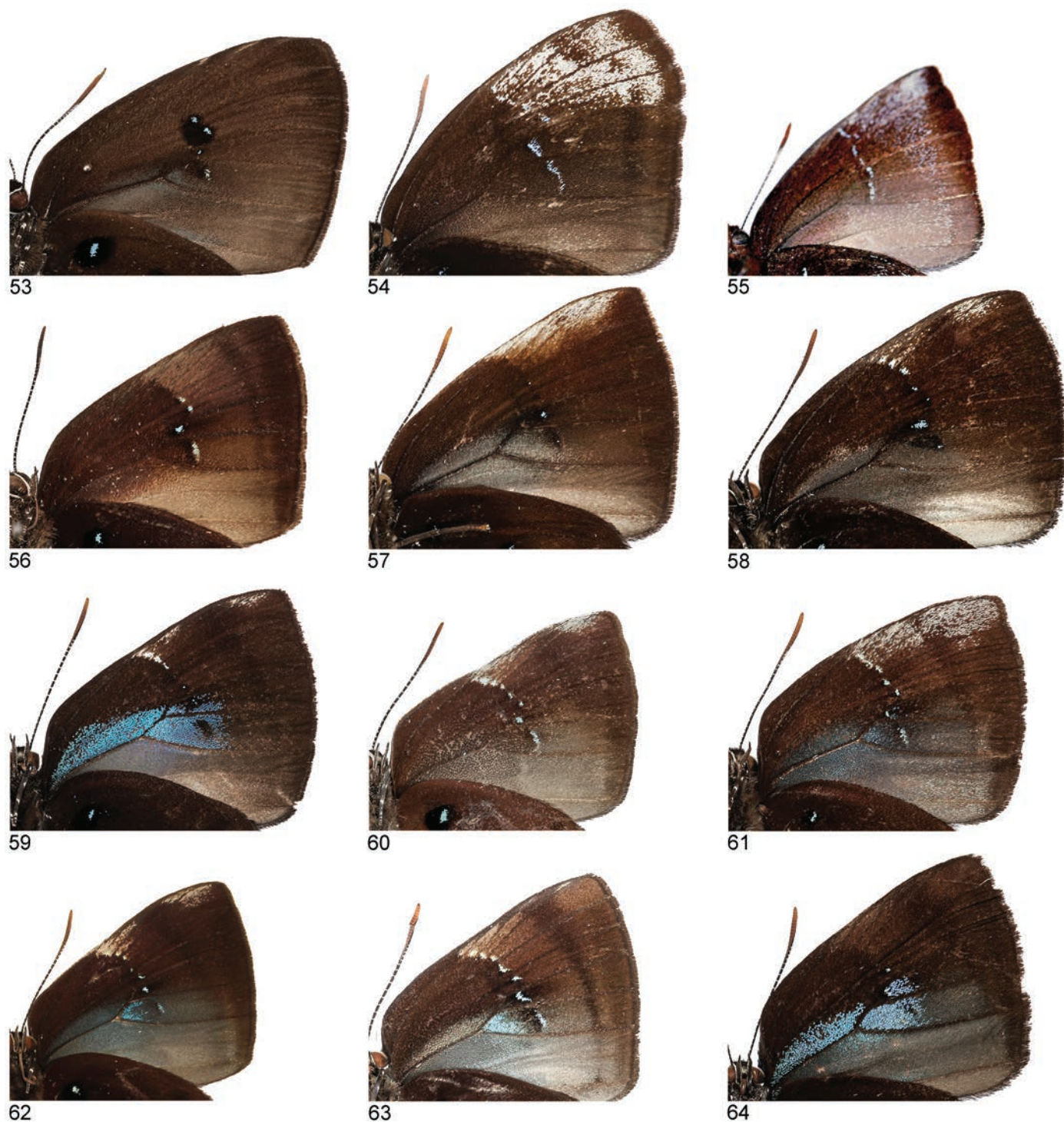
FIGURES 31–40. Adults of *Paraspiculatus*, dorsal on left. 31. ♂ *P. emma* (Ecuador). 32. ♂ *P. sine* (Ecuador). 33. ♂ *P. colombiensis* (Ecuador). 34. ♀ *P. colombiensis* (Ecuador). 35. ♂ *P. azul* (Ecuador). 36. ♀ *P. azul* (Peru). 37. ♂ *P. lilyana* (Ecuador). 38. ♂ *P. noemi* (Ecuador). 39. ♂ *P. noemi* (Mexico). 40. ♂ *P. noemi* (Costa Rica). Scale 1 cm (lower left).





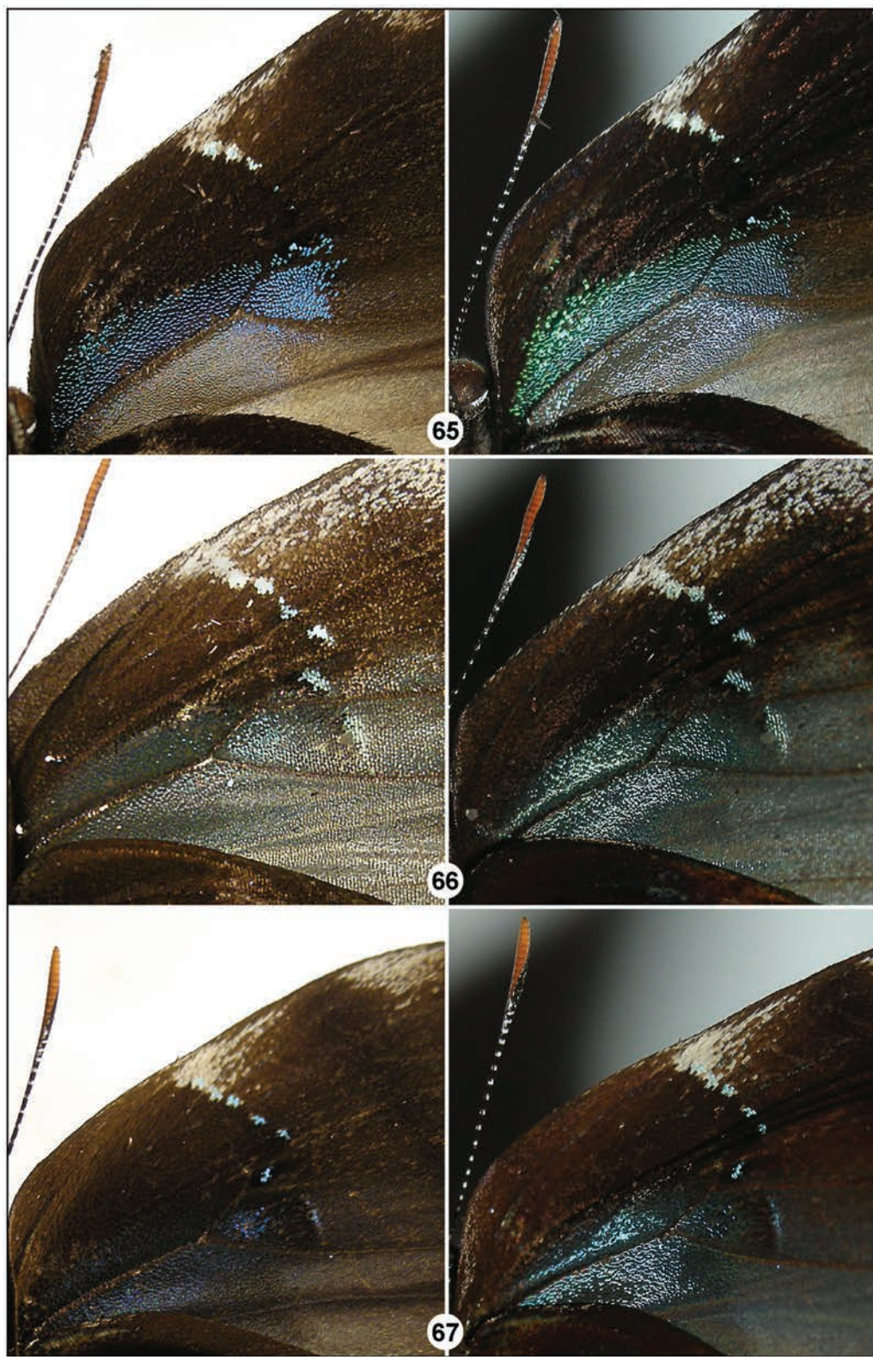
FIGURES 41–52. Male dorsal forewing variation in *Paraspiculatus*. See text for character states. 41. *P. elis*. 42. *P. oroanna*. 43. *P. catrea*. 44. *P. orobiana*. 45. *P. orocana*. 46. *P. grande*. 47. *P. orobia*. 48. *P. emma*. 49. *P. sine*. 50. *P. colombiensis*. 51. *P. azul*. 52. *P. lilyana*.





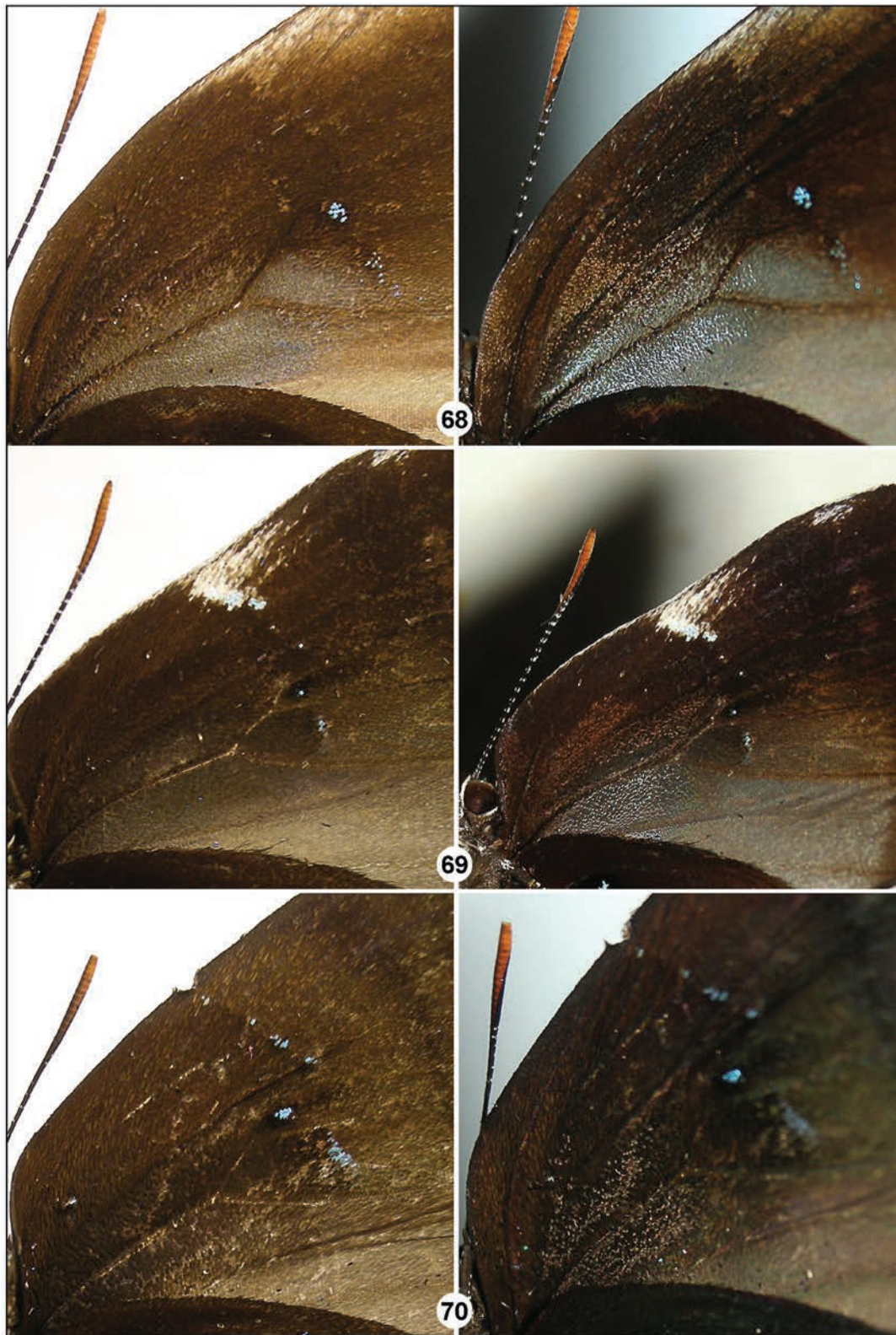
FIGURES 53–64. Male ventral forewing variation in *Paraspiculatus*. See text for character states. 53. *P. elis*. 54. *P. oroanna*. 55. *P. catrea*. 56. *P. orobiana*. 57. *P. orocana*. 58. *P. grande*. 59. *P. orobia*. 60. *P. emma*. 61. *P. sine*. 62. *P. colombiensis*. 63. *P. azul*. 64. *P. lilyana*.





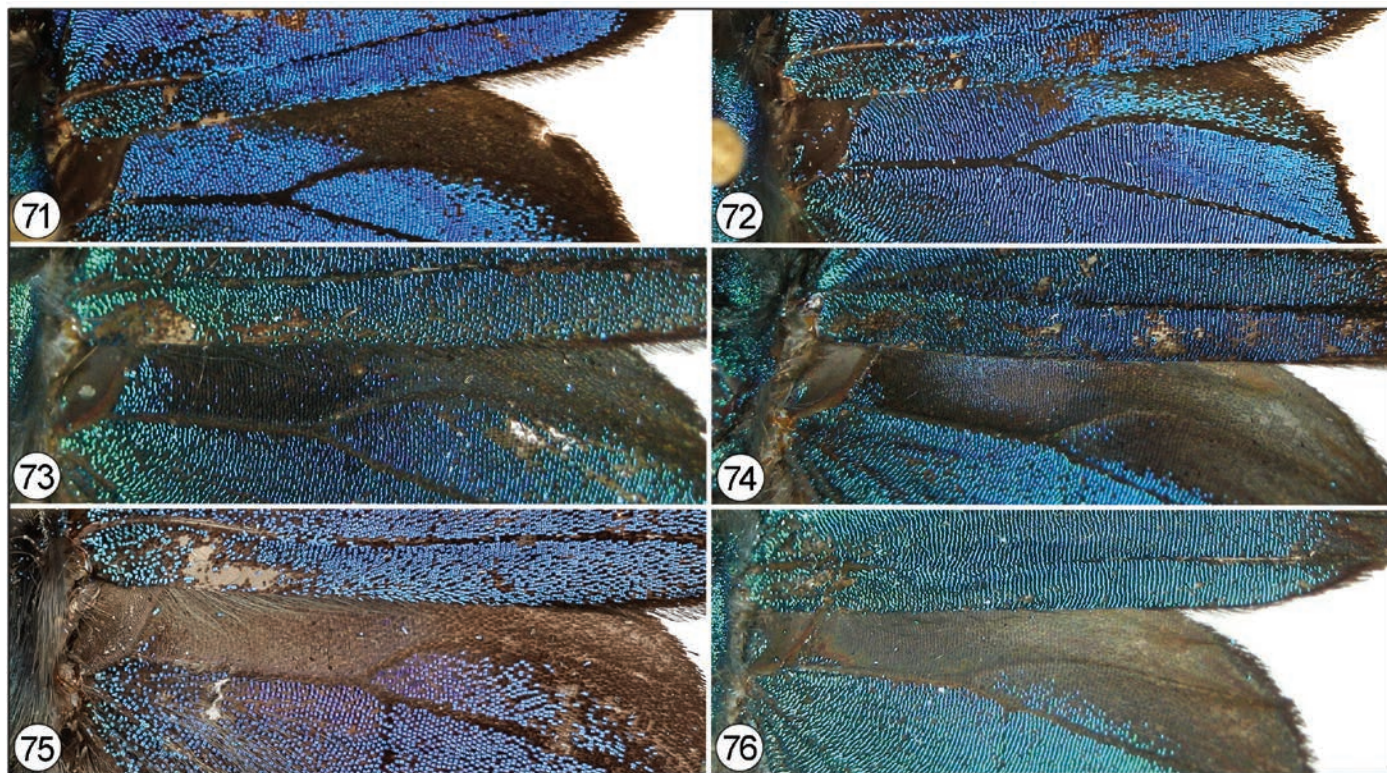
FIGURES 65–67. Male ventral forewing iridescence as a function of light from different angles. Light source perpendicular to the wings (left) and at an acute angle (same specimen on right). 65. *P. orobia*. 66. *P. sine*. 67. *P. colombiensis*.





FIGURES 68–70. Male ventral forewing iridescence as a function of light from different angles. Light source perpendicular to the wings (left) and at an acute angle (same specimen on right). 68. *P. orocana*. 69. *P. emma*. 70. *P. orobiana*.





FIGURES 71–76. Male dorsal hindwing variation at the costa. 71. *P. lilyana*. 72. *P. azul*. 73. *P. noemi*. 74. *P. grande*. 75. *P. orobia*. 76. *P. cosmo*. See text for explanation.



FIGURE 77. Male hindwing anal lobes (arrows). *P. orocana* (left), *P. colombiensis* (right).

(Figure 65) or iridescent (Figures 66–70). The iridescence varies from blue or silver-blue (Figures 66–69) to brownish bronze (Figure 70). The latter is somewhat difficult to see and generally requires the wing to be viewed at a very acute angle (45°) under bright light.

- (2) The postmedian line on the ventral forewing is composed of three blue/white dots near the costa with four more blue spots extending to cell  $Cu_1$ - $Cu_2$  in the majority of species (Figures 54, 55, 58–63). In others, the anterior dots are absent (Figures 53, 56, 57, 64). In some instances, the postmedian line is reduced to one or two posterior blue dots (Figure 57).
- (3) Apical white scales on the ventral forewing may be present (Figures 54, 55, 57–62) or absent (Figures 53, 56, 63, 64). When present (despite intraspecific variation in the number of white scales), the white scales may form a wide (Figures 54, 55) or narrow band (Figure 61), may be crescent shaped (Figure 57), or may be divided in two, with the distal patch at the apex (Figures 58–60, 62).
- (4) Color of blue scales on the dorsal surface is variable (Figures 41–52). Further, the blue color in the limbal area of the dorsal forewing in “fresh” individuals varies from a “smooth” appearance with few interspersed black scales (Figures 42–46, 51, 52) to a “grainy” appearance with equivalent numbers of black scales and blue scales (Figures 48–50). In a long series of specimens, differences among species are conspicuous. However, these differences “overlap” and may be difficult to discern in worn specimens, so color and texture tend to be less reliable traits for identification of a single individual.

Some conspicuous wing markings were not useful in distinguishing species in the large study samples that we accumulated. For example, black scales at the end of the forewing discal cell (Figures 45, 48, 52) do not provide useful information because of intraspecific variability.

Finally, the brown scales that make up most of the ventral surface often reflect different colors when rotated in sunlight. For example, at about 45 degrees, the matte brown areas in the distal forewing of *Paraspiculatus emma* Busby and Robbins are bright bronze; at a more acute angle, they are greenish. We have not quantified this aspect of the ventral surface, but mention this trait because it could contribute to species recognition among females of sympatric species.

**MALE GENITALIC MORPHOLOGY.** Ventrolateral processes of the fused vinculum and tegumen, which are typical of many Eumaeini, were first mentioned by McDunnough (1942: 1), who called them “finger-like projection(s) at the base of the tegumen.” Nonsocketed “teeth” are found on these projections in a variety of presumably unrelated eumaeines in addition to *Paraspiculatus* and *Mithras* (McDunnough, 1942; Duarte and Robbins, 2010). However, the slightly projecting lateral edge of the fused vinculum/tegumen with nonsocketed teeth in *Paraspiculatus* is unique within the Eumaeini. The projection with lateral teeth in *Mithras* is considerably longer than in *Paraspiculatus* and is immediately distinguishable (Figure 5).

Other than the nonsocketed teeth on the ventrolateral edge of the fused vinculum/tegumen, the male genitalia of *Paraspiculatus* are not especially distinctive. Compared to other eumaeines, the gnathos are relatively stout with a conspicuous apiculus, but not markedly so. The vinculum strut is horizontal where the spiculate pad occurs, but does not distinguish *Paraspiculatus* from other eumaeines. We found no structures in the male genitalia that provide evidence on the relationship of *Paraspiculatus* with other genera.

Interspecific variation of the male genitalia of *Paraspiculatus* is slight (Figures 78–95) and does not unambiguously distinguish any species other than *P. oroanna* Bálint, 2002. Shape of the valvae and saccus in ventral aspect is intraspecifically variable (Figure 96). The valvae of some species have the ventral surface at the base without setae and displaced ventrally, but the expression of this structure is highly variable intraspecifically. The penis has a terminal slender cornutus in all species. There is also a second minute terminal cornutus in all species except *Paraspiculatus oroanna*, *P. hannelore*, and *P. cosmo* Busby, Robbins, and Faynel.

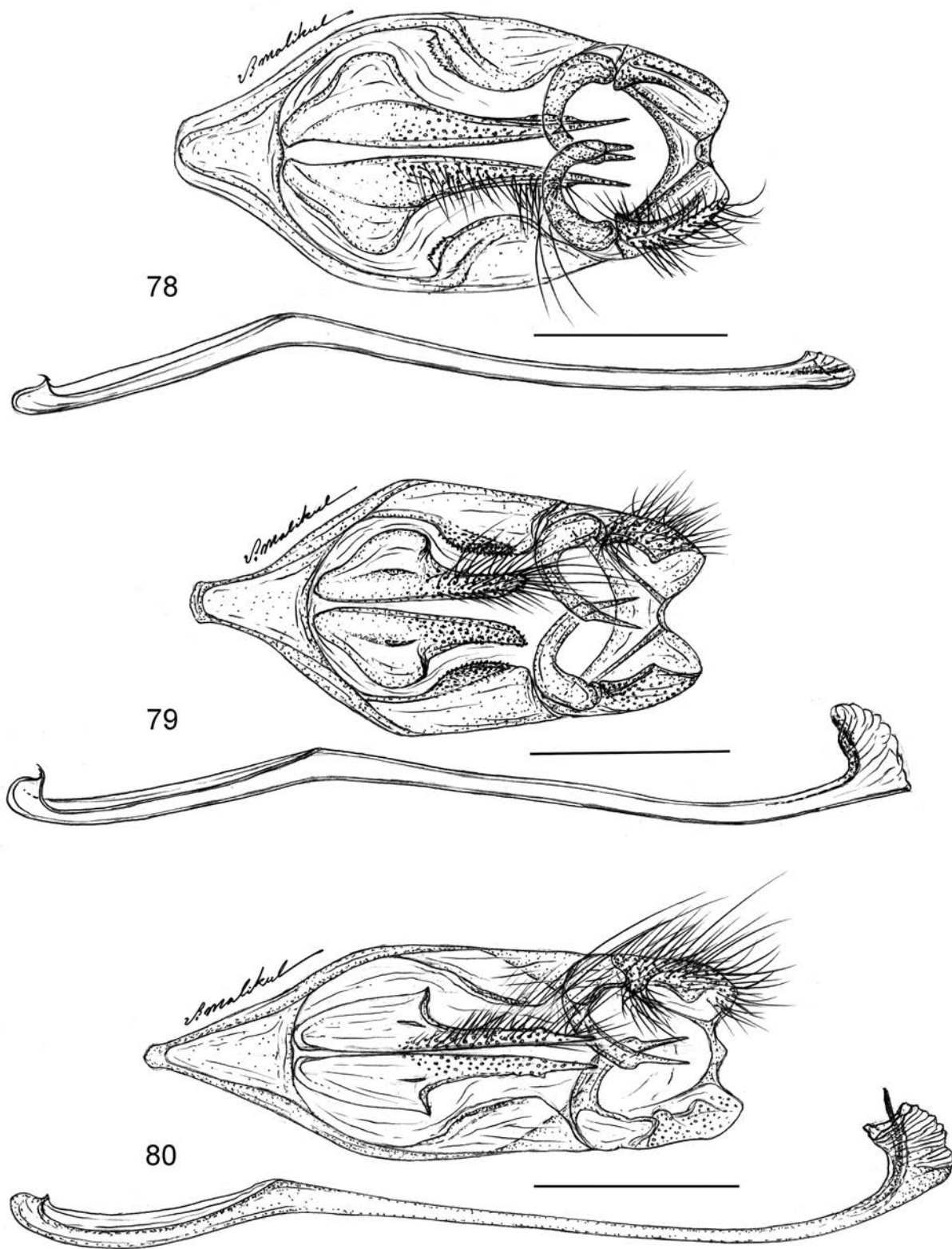
Expression of the distinctive nonsocketed teeth on the ventrolateral edge of the fused vinculum/tegumen also varies intraspecifically. For example, in one dissection of *P. catrea* the teeth are well expressed (Figure 79), but in two other dissections, they are absent (also noted in Bálint and Moser, 2001). As another example, in one dissection of *P. noemi* the teeth are well expressed (Figure 97), but in another dissection, the number of teeth is greatly reduced: they are almost entirely absent posteriorly. Otherwise these genitalia are indistinguishable. Other examples in which the location and size of the spiculate pad vary in *P. sine* Busby and Robbins and *P. apuya* are illustrated (Figures 98, 99).

**FEMALE GENITALIC MORPHOLOGY.** Females of six *Paraspiculatus* species are unknown (*P. oroanna*, *P. apuya*, *P. orocana* (Druce, 1912), *P. emma*, *P. sine*, and *P. lilyana*). The remaining species (Figures 100–112) share the following traits: (1) the signa on the corpus bursae are vestigial or absent; (2) the ductus seminalis attaches to the posterior corpus bursae considerably dorsal of the point where the ductus bursae attaches; and (3) in lateral aspect, the posterior ductus bursae is wider than the anterior ductus bursae.

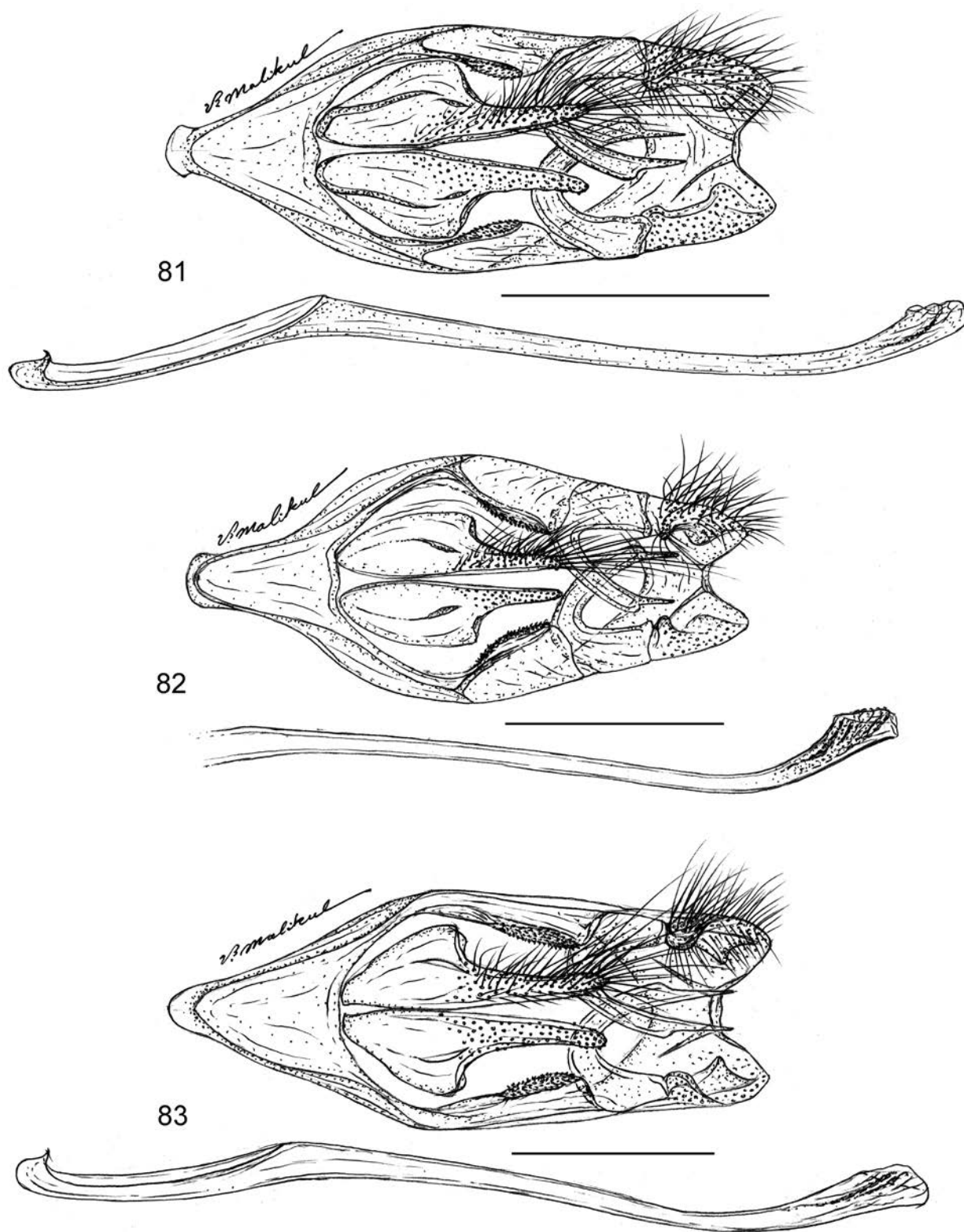
The most distinctive female genitalia belong to *Paraspiculatus elis* (Figure 100). It lacks the narrow, lightly sclerotized “neck” that occurs in the middle of the ductus bursae of the other species. It lacks a pouch on the posterior corpus bursae from which the ductus seminalis arises. With respect to these two traits, the female genitalia of *P. elis* are similar to those of *Mithras nautes*, as are aspects of its wing pattern, as already noted.

Interspecific variation of the female genitalia of *Paraspiculatus*, other than those of *P. elis*, is minimal (Figures 101–112). Length of the anterior and posterior parts of the ductus bursae varies quantitatively, but because of overlapping lengths, does not usually distinguish species. The posterior part of the



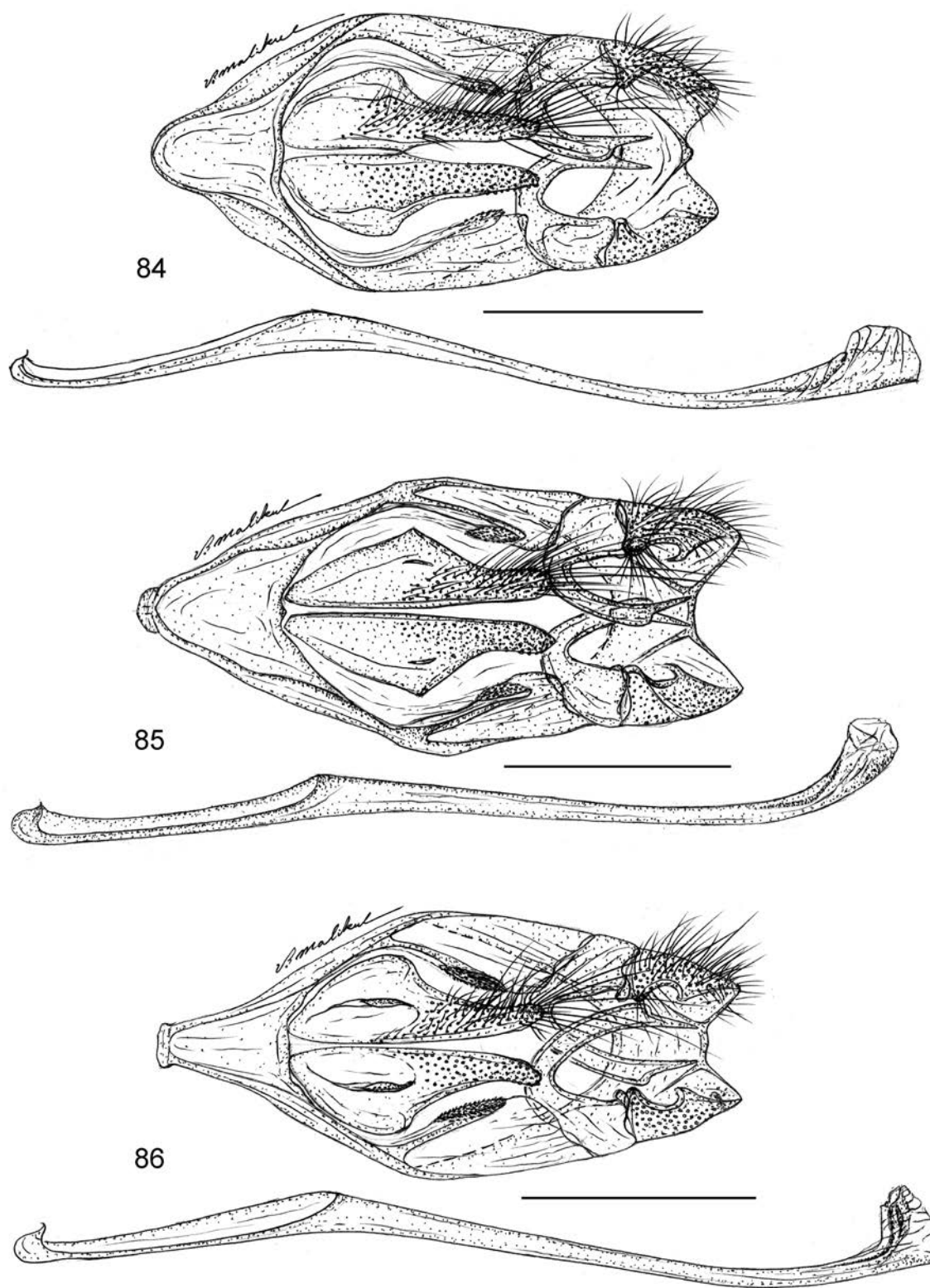


FIGURES 78–80. Male genitalia of *Paraspiculatus*, genital capsule in ventral aspect (top) and penis in lateral aspect. Posterior of butterfly to the right. Scale 1 mm. 78. *P. elis*. 79. *P. catrea*. 80. *P. oroanna*.

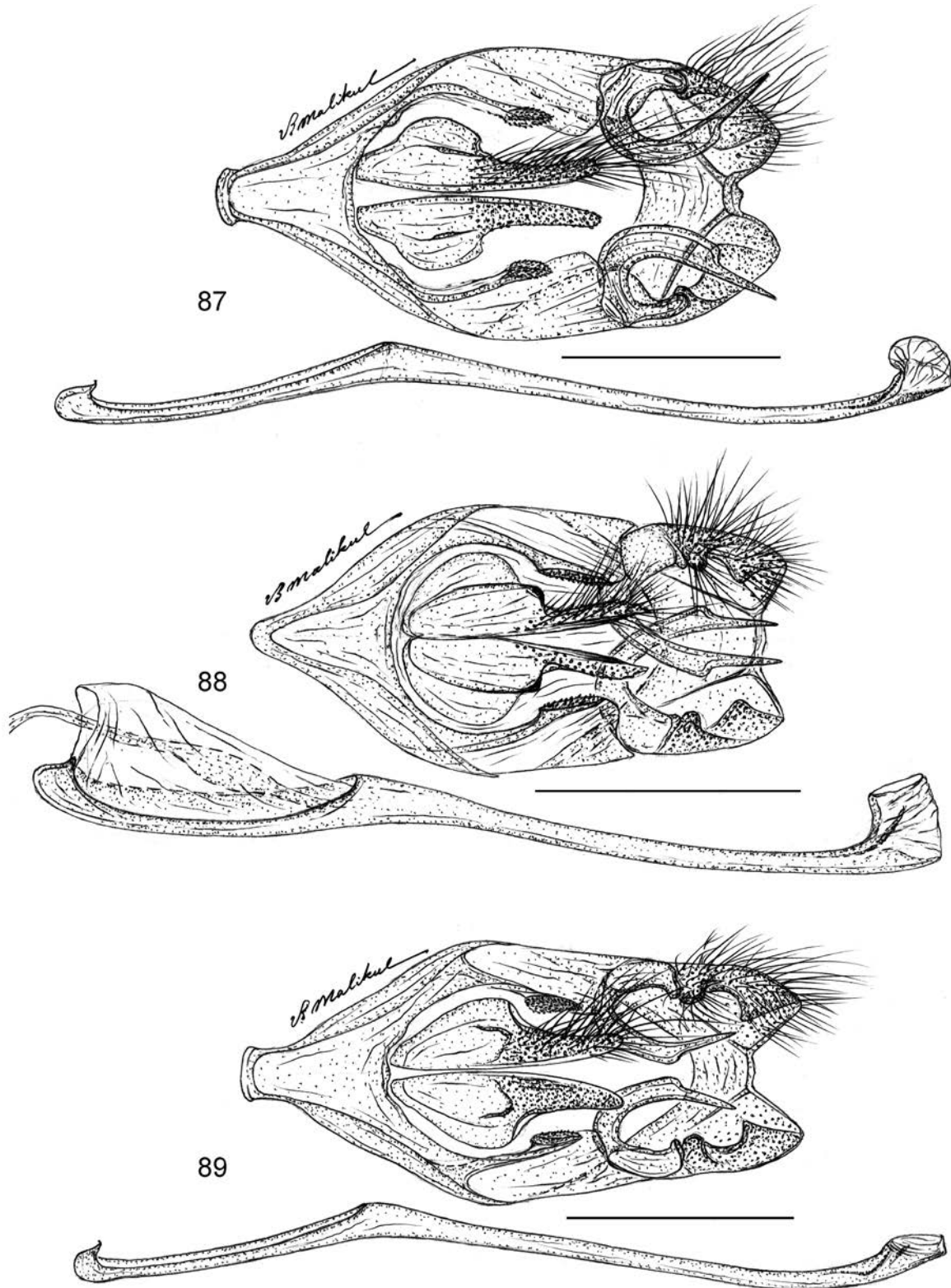


FIGURES 81–83. Male genitalia of *Paraspiculatus*, genital capsule in ventral aspect (top) and penis in lateral aspect. Posterior of butterfly to the right. Scale 1 mm. 81. *P. apuya*. 82. *P. orobiana*. 83. *P. transvesta*.



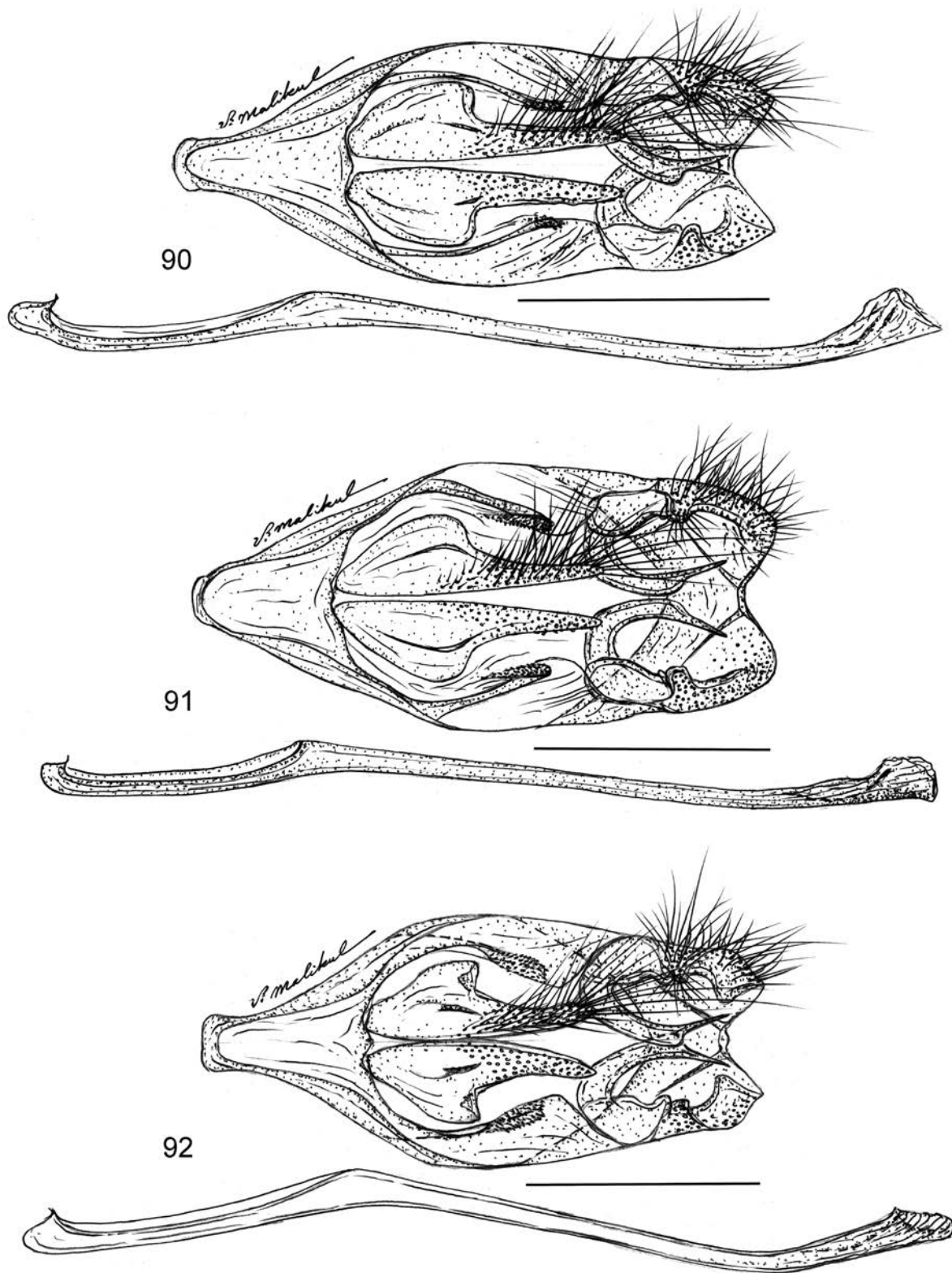


FIGURES 84–86. Male genitalia of *Paraspiculatus*, genital capsule in ventral aspect (top) and penis in lateral aspect. Posterior of butterfly to the right. Scale 1 mm. 84. *P. hannelore*. 85. *P. cosmo*. 86. *P. orobia*.



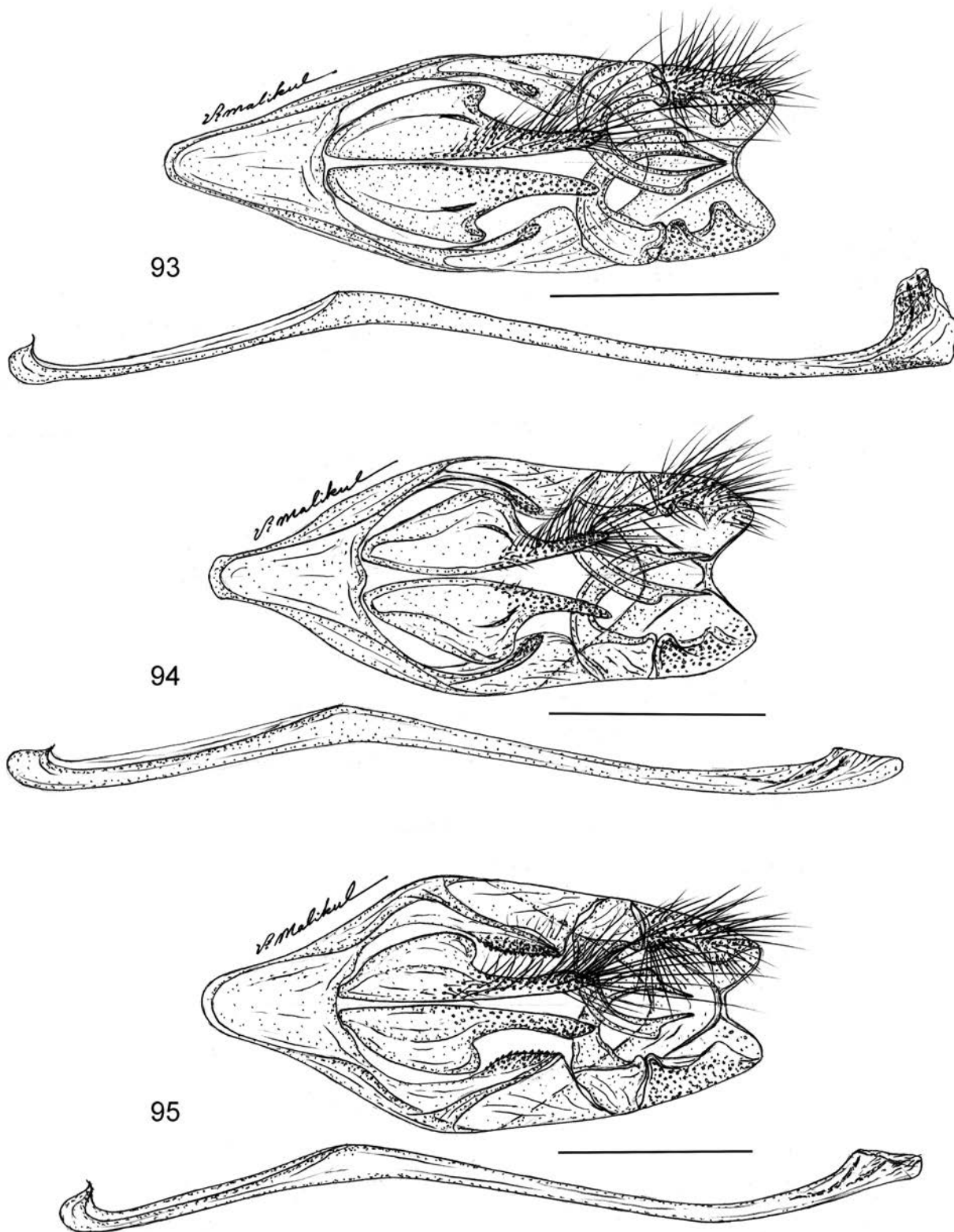
FIGURES 87–89. Male genitalia of *Paraspiculatus*, genital capsule in ventral aspect (top) and penis in lateral aspect. Posterior of butterfly to the right. Scale 1 mm. 87. *P. grande*. 88. *P. honor*. 89. *P. orocana*.





FIGURES 90–92. Male genitalia of *Paraspiculatus*, genital capsule in ventral aspect (top) and penis in lateral aspect. Posterior of butterfly to the right. Scale 1 mm. 90. *P. emma*. 91. *P. sine*. 92. *P. colombiensis*.





FIGURES 93–95. Male genitalia of *Paraspiculatus*, genital capsule in ventral aspect (top) and penis in lateral aspect. Posterior of butterfly to the right. Scale 1 mm. 93. *P. azul*. 94. *P. lilyana*. 95. *P. noemi*.

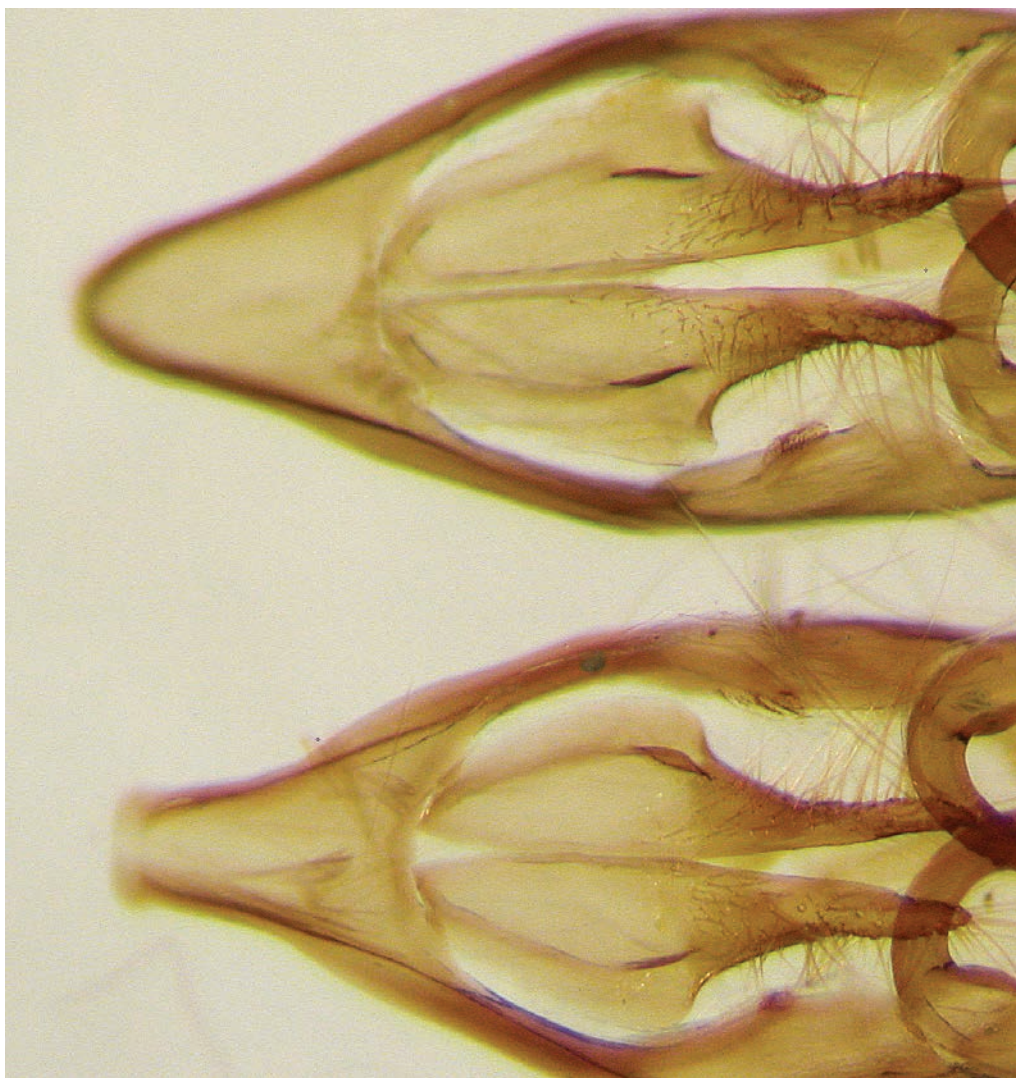


FIGURE 96. Variation of valvae and saccus in ventral aspect of *P. azul* from Ecuador.

corpus bursae varies from membranous to lightly sclerotized, but again, this trait does not distinguish species. The suggestion that morphology of the posterior corpus bursae represents a synapomorphy for *Paraspiculatus* (Bálint and Moser, 2001) has no substantive basis that we can discern.

**HABITAT.** Lowland and montane forest.

**CATERPILLAR FOOD PLANTS.** None recorded.

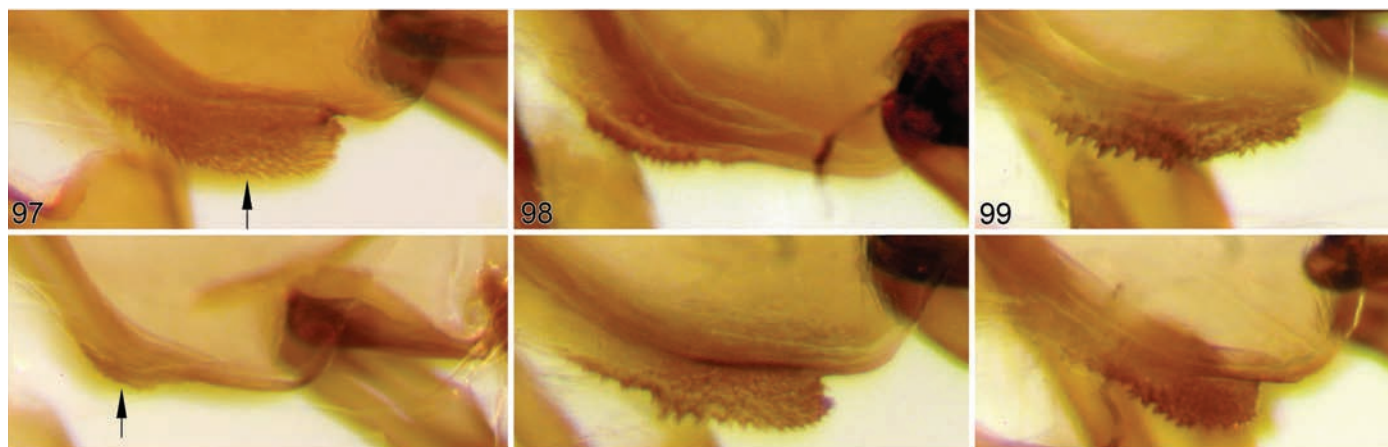
**BEHAVIOR.** Male *Paraspiculatus* in the upper Amazon Basin are attracted to traps baited with rotting fish and placed 7–20 m above the ground. Occasionally, male *Paraspiculatus* fly to liquefied fish poured on leaves near the ground. Female *Paraspiculatus* are almost never attracted to fish. In over 25 years of field work, there are only six records of females being attracted to traps, and all occurred at a single locality. In other geographic

regions, such as the western Andean slopes of Ecuador, collecting with rotting fish has been less successful. We elaborate on these observations in the Discussion.

Adults of *Paraspiculatus* are rarely encountered in the forest, so available information on adult behaviors is minimal. For example, male territoriality has been recorded for only *P. oranna* and *P. grande* Busby, Robbins, and Moser.

**IDENTIFICATION.** We recognize nine described and 10 undescribed *Paraspiculatus* species based on morphology. The following key allows males to be identified by wing pattern. Each of these species also clusters in a CO1 DNA sequence neighbor-joining phenogram (Figure 113), so DNA barcodes provide an alternate means of identification. However, the morphological species determinations for males agreed with BINs





FIGURES 97–99. Variation in the longitudinal spiculate pad in lateral aspect (arrows). 97. *P. noemi* (top Ecuador, bottom Mexico). 98. *P. sine* (both Ecuador). 99. *P. apuya* (top Ecuador, bottom Rondonia, Brazil).

in 92 of 95 males (96.8% concordance). The three extra BINs referred to geographic variants of *P. apuya*, *P. orobiana*, and *P. noemi* (blue-green highlight in Figure 113). Each of the 16 females with sequenced DNA barcodes clustered with one of the male species (yellow highlight in Figure 113).

**GEOGRAPHIC VARIATION.** We detail geographic variation in the morphology of *P. orobia* and *P. noemi* in the species accounts. As noted, there is geographic variation in CO1 sequences in *P. orobiana*, *P. noemi*, and *P. apuya* (Figure 113).

#### IDENTIFICATION KEY FOR MALES

1. With a transverse orange/yellow ray on VHW [Figure 3] ..... *P. elis*  
Without a transverse orange/yellow ray on VHW ..... 2
2. With an elongated anal lobe (teardrop shaped) on HW [Figures 8, 10] ..... 3  
Without an elongated anal lobe (rounded) on HW ..... 4
3. With a solid blue/white median line on VHW and scattered white markings ..... *P. catrea*  
With a series of blue dots in the median of the VHW and no white markings ..... *P. vossoroca*
4. With a predominately blue dorsal surface ..... 5  
With a predominately brown dorsal surface (some dull blue/green scales basally placed) ..... *P. transvesta*
5. With dark gray or gray/brown scales at the base of the DHW costa above vein  $R_s$  [Figures 74–76] ..... 6  
With regular blue (or black) scales at the base of the DHW costa [Figures 71–73] ..... 10
6. With tightly bunched dark gray scales in the center of cell  $Sc+R_1-R_s$  [Figure 74] ..... 7  
With evenly spaced gray/brown scales; not concentrated in the center of cell  $Sc+R_1-R_s$  [Figures 75,76] ..... 9
7. With three white/blue spots at median of VFW costal margin and four blue spots extending posteriorly to cell  $Cu_1-Cu_2$  ..... *P. grande*  
With a single blue spot (occasionally two) in the middle of the VFW and either no white spots or vestigial spots at the costal margin [Figure 57] ..... 8
8. With DFW black apex extending to the distal side of the discal cell ..... *P. honor*  
With DFW black apex not extending to the discal cell, blue scales fill approximately 1/3 of the space between the discal cell and apex ..... *P. orocana*
9. With a narrow black border on the DFW and a broad band of shiny blue scales [Figure 59] anterior of the cubital vein on the VFW ..... *P. orobia*  
With a black border of medium width on the DFW and no band of shiny blue scales on the VFW ..... *P. cosmo*
10. With blue/silver-blue iridescence posterior of the cubital vein on the VFW [Figures 65–69] ..... 11  
With brownish-bronze iridescence posterior of the cubital vein [Figure 70] and with broad black outer margin on DFW ..... *P. orobiana*

11. With dull bluish-gray scales in the limbal area of the VFW posterior to vein  $Cu_2$  [Figures 60–64] ..... 12  
 With brown or brownish-gray scales in the limbal area of the VFW posterior to vein  $Cu_2$  [Figures 53–59] ..... 17
12. With no white scales near VFW costa between median and apex [Figures 63, 64] ..... 13  
 With white scales near VFW costa between median and apex [Figure 60–62] ..... 14
13. With a band of shiny blue scales above the cubital vein on VFW and with a crisply delineated black border on the DFW ..... *P. lilyana*  
 Without a band of shiny blue scales on the VFW ..... *P. azul*
14. With white scales along the costa of the VFW, which are broken into two patches—one near the median and the second in the apex [Figures 60, 62] ..... 15  
 With a continuous, narrow band of white scales along the costa of the VFW between the median and apex [Figure 61] and no HW tails ..... *P. sine*
15. With mostly blue scales on the basal side of cell  $Sc+R_1-R_8$  on the DHW [Figures 71, 72] ..... 16  
 With mostly black (occasional purple) scales in cell  $Sc+R_1-R_8$  on the DHW [Figure 73] ..... *P. noemi*
16. With a narrow black outer border on the DFW and HW tails ..... *P. colombiensis*  
 With a black outer border of medium thickness and no HW tails ..... *P. emma*
17. With very broad black outer DFW border [Figures 12, 13] ..... 18  
 With a black outer DFW border which narrows below vein  $Cu_1$  [Figure 14] and with brown scales at the end of the discal cell on VHW ..... *P. hannelore*
18. With no white scales near the costa of the VFW between the median and apex and with black scales covering the anterior portion of the DFW discal cell ..... *P. apuya*  
 With a very broad band of white scales in the VFW apex between the costa and vein  $M_3$  ..... *P. oroanna*

## SPECIES-LEVEL TAXONOMY

### PARASPICULATUS ELIS SPECIES COMPLEX

#### *Paraspiculatus elis* (Cramer, 1779)

FIGURES 3, 6, 7, 41, 53, 78, 100, 113, 114, 126–130

**UPDATED DIAGNOSIS.** The lowland Amazonian *Paraspiculatus elis* and *Mithras nautes* have traditionally been treated as close relatives because of the similarity of their ventral wing patterns (Figures 3, 4), especially a single transverse orange-yellow band on the hindwing of both sexes (Draudt, 1919–1920). This similarity is one reason why *Paraspiculatus* was treated as a synonym of *Mithras* (Robbins, 2004b). The male genitalia of *P. elis* (Figure 78) and the lack of evident male secondary sexual traits, however, are the same as those of *Paraspiculatus*, which is the reason for its generic placement.

**FEMALE.** (Figure 7) The female is associated by similarities with the male in ventral wing pattern, geographic distribution, and CO1 sequence.

**GENITALIA.** (Figures 78, 100) The presence of a spiculate pad in a longitudinal plane in the male genitalia is the reason why this species is placed in *Paraspiculatus*. It is the only member of the genus that can be immediately distinguished by its female genitalia because it lacks a semimembranous “neck” in the ductus bursae.

**DISTRIBUTION.** (Figure 114) Widely distributed in the Amazon region of Brown (1982).

**HABITAT.** *Paraspiculatus elis* inhabits wet forest up to 900 m elevation.

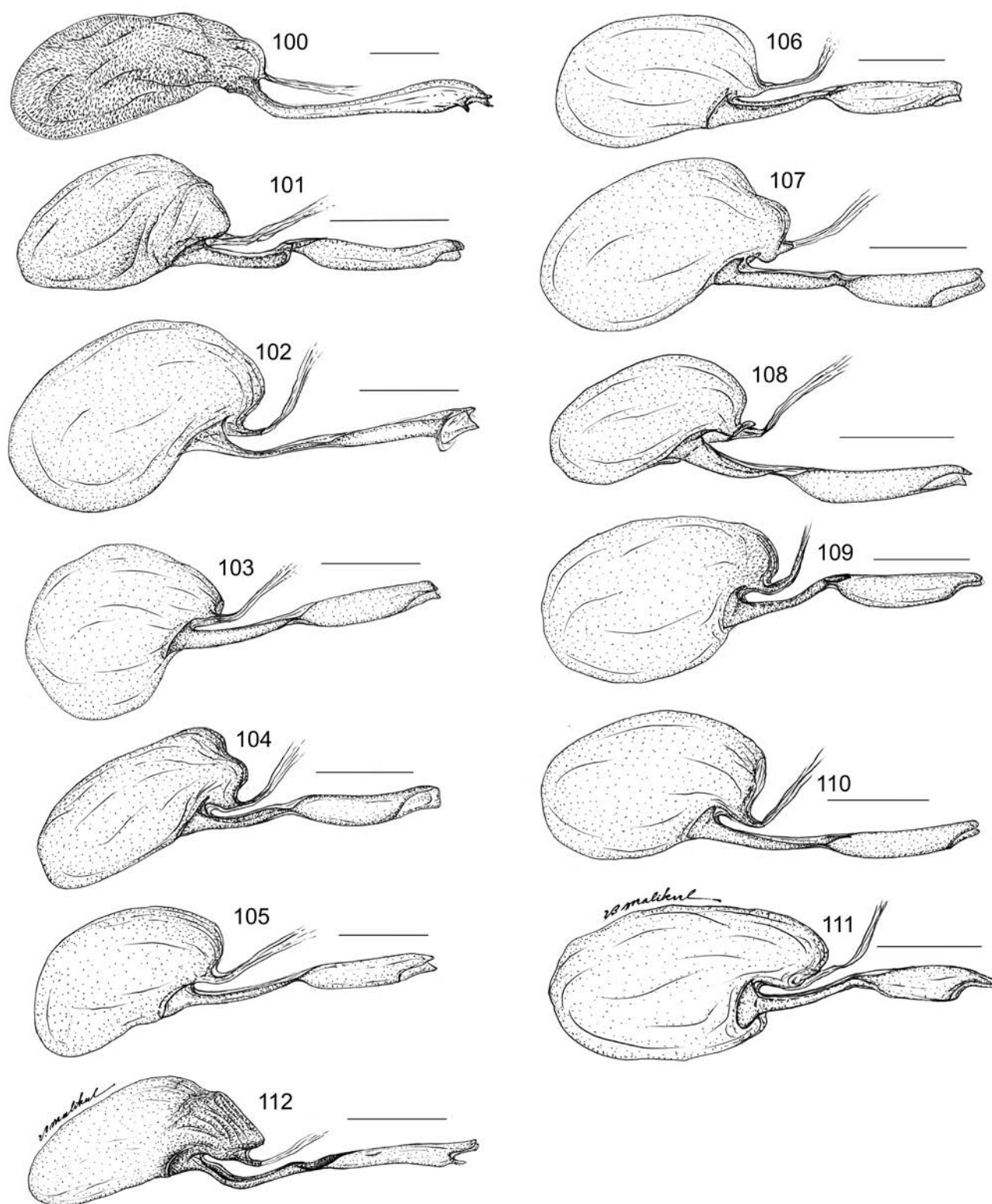
**BEHAVIOR.** Males of *P. elis* have been recorded on traps and plants baited with rotting fish or dilute cow blood (Figure 3).

**REMARKS.** This species is one of the largest *Paraspiculatus* and has a conspicuously recognizable ventral wing pattern, but is exceedingly rare. There are fewer than 20 specimens in major museum collections.

**MATERIAL EXAMINED** (15♂, 3♀). **ECUADOR**, *Morona Santiago*, 53.1 km Santiago–Puerto Morona Rd, 2°55.0'S, 77°42.7'W, 210 m, 17 Sep 2016, 1♂ (RCB); 3.2 km Mendez–Guarumales Rd, 2°41.9'S, 78°19.7'W, 550 m, 29 Sep 2004, 1♀ (RCB); *Napo*, 4 km S Tena–Pano Rd, 1°00.8'S, 77°50.1'W, 580 m, 5 Nov 1992, 1♂ (USNM); *Puerto Napo*, 650 m, 20 Sep 1987, 1♂ (USNM); *Río Pimpilala*, 1°04.6'S, 77°56.2'W, 600–900 m, Jun 2014, 1♂ (RCB); Sep 1996, 2♂ (JHKW), 1♀ (JHKW); 10 Sep 2006, 1♂ (RCB); *Orellana*, *Río Añangu*, middle *Río Napo*, 0°31.7'S, 76°23.7'W, 250 m, Oct–Dec 2005, 1♂ (JHKW); 22 km Loreto–San Jose de Payamino Rd, 0°34.9'S, 77°24.4'W, 825 m, 08 Nov 2010, 1♂ (RCB); *Pastaza*, 39.4 km Puyo–Villano Rd, 1°25.6'S, 77°43.8'W, 750 m, 01 Oct 2015, 2♂ (RCB). **PERU**, *San Martín*, Tarapoto, 1886, 1♂ (BMNH); 1♀ (BMNH); *Juanjui*, 1♂ (USNM); *Huánuco*, *Tingo Maria*, 800 m, 20 Jun 1982, 1♂ (USNM); *Loreto*, *San Pablo*, 4°01'S, 71°06'W, 100 m, Feb 2011, 1♂ (CF).

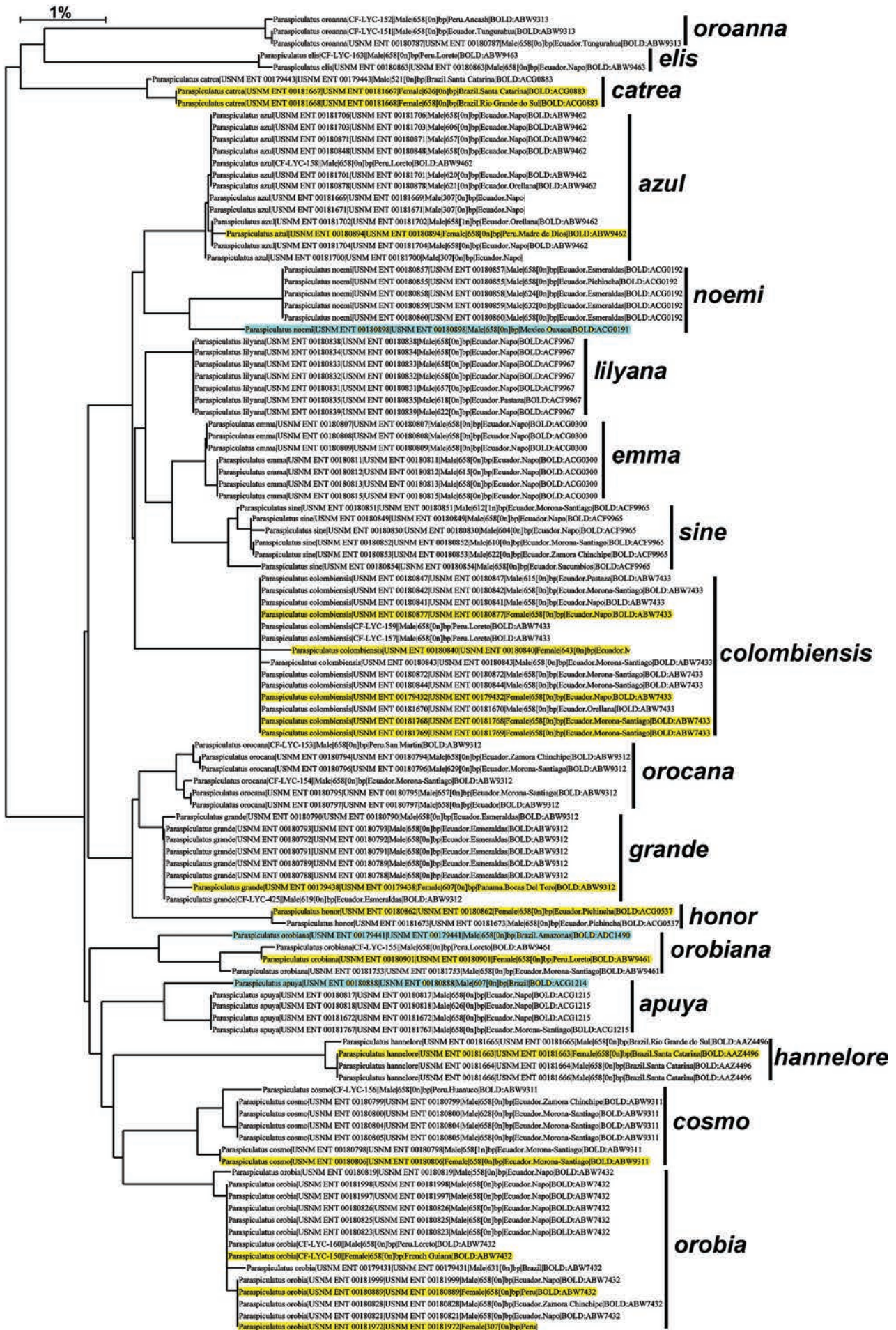
### PARASPICULATUS CATREA SPECIES COMPLEX

This lineage of two sympatric species is characterized by the shape of the hindwing anal angle (Table 1: Character 11) and



FIGURES 100–112. Female genitalia ductus copulatrix in lateral aspect, posterior of butterfly to the right. Scale 1 mm. 100. *P. elis*. 101. *P. catrea*. 102. *P. vossoroca*. 103. *P. hannelore*. 104. *P. cosmo*. 105. *P. orobia*. 106. *P. transvesta*. 107. *P. grande*. 108. *P. honor*. 109. *P. colombiensis*. 110. *P. azul*. 111. *P. noemi*. 112. *P. orobiana*. Scale 1 mm.





lobe (Character 15) as well as brownish iridescence below the cubital vein on the ventral forewing (Character 7).

### ***Paraspiculatus catrea* (Hewitson, 1874)**

FIGURES 8, 9, 43, 55, 79, 101, 113, 115, 126–130

**UPDATED DIAGNOSIS AND DESCRIPTION.** This species has been readily identifiable for more than a century by its distinctive ventral wing pattern and hindwing shape (Figure 8). The ventral characters noted by Hewitson include “a band of two or three linear white spots near the middle” of the forewing, “five or six lunular white spots” at the middle of the hindwing, and interspersed white scales on both wings. The white lines and spots are unique within *Paraspiculatus* (Figures 6–40).

Bálint and Moser (2001) transferred *Thecla catrea* to *Paraspiculatus* based on female genitalic structures. The presence of a spiculate pad in the male genitalia (Figure 79), the morphological similarity of the female genitalia to those of other *Paraspiculatus* species (Figures 100–112), and the similarity of CO1 DNA sequences (Figure 113) place this species in *Paraspiculatus*.

**FEMALE.** (Figure 9) The female is associated by similarities with the male in ventral wing pattern, geographic distribution, and CO1 DNA sequences.

**GENITALIA.** (Figures 79, 101) The spiculate pad of the male genitalia may be present or absent, as already noted.

**DISTRIBUTION.** (Figure 115) Southeastern Brazil from the state of Rio de Janeiro to Rio Grande do Sul.

**HABITAT.** *Paraspiculatus catrea* inhabits forest from 100 m elevation in the southern part of its range to 1,600 m elevation in the northern parts. It is the only lowland *Paraspiculatus* species that also occurs above 1,250 m elevation.

**REMARKS.** In all the phylogenetic analyses in this paper, *P. catrea* is placed within *Paraspiculatus*.

**MATERIAL EXAMINED** (8♂, 7♀). **BRAZIL**, *Santa Catarina*, São Bento do Sul, Rio Vermelho, 700 m, 23 Feb 1987, 1♂ (USNM); 24 Feb 1973, 1♀ (USNM); 23–25 Apr 2009, 1♀ (MC); 900 m, 16 Feb 1993, 1♀ (MC); Praia Grande, Serra do Faxinal, 700 m, 20 Nov 1994, 1♀ (MC); São Bento do Sul, Serra do Rio Natal, 700 m, 23 Apr 2009, 1♀ (MC); Nova Teutonia 300–500 m, 26 Jan 1954, 1♂ (USNM); 30 Dec 1949, 1♂ (USNM); *Paraná*, Ponta Grossa, Dec 1942, 1♀ (USNM); *Rio Grande do Sul*, Ivoti, 27 Dec 1998, 1♂ (MC); São Francisco de Paula, 900 m, 30 Mar 2002, 1♀ (MC); 3 Jun 1991, 1♂ (MC); Morro Reuter, Jammerhal, 300 m, 24 Sep 1994, 1♂ (MC); Morro Reuter, Faz. Padre Eterno, 500 m, 24 Dec 1996, 1♂ (MC); Guarani, 7 Jan 1973, 1♂ (USNM).

### ***Paraspiculatus vossoroca* (Bálint and Moser, 2001)**

FIGURES 10, 11, 102, 114, 126, 129, 130

**UPDATED DIAGNOSIS AND DESCRIPTION.** This species and *P. catrea* are immediately recognizable by their hindwing shape with an elongated anal angle (Figures 8–11). The ventral wing pattern of *P. vossoroca* differs markedly from that of *P. catrea* and is typical of the majority of *Paraspiculatus* species with a dark ventral surface with bright blue spots and line segments (Figures 10, 11). Male and female *P. vossoroca* lack tails whereas the female of *P. catrea* is tailed.

**FEMALE (FIGURE 11).** The female is associated with the male by similarity in hindwing shape, ventral wing pattern (especially the white scales near the costa of the forewing), and geographic distribution.

**GENITALIA** (Figure 102). Bálint and Moser (2001) published a photograph of the male genitalia that does not clearly show a spiculate pad. We examined the male holotype genitalia, which are almost indistinguishable from those of *P. catrea* (Figure 79), and they possess a spiculate pad. The female genitalia are morphologically similar to those of other *Paraspiculatus* species (Figures 100–112).

**DISTRIBUTION** (Figure 114). Southeastern Brazil in the states of Paraná and Santa Catarina.

**HABITAT.** *Paraspiculatus vossoroca* inhabits wet Atlantic coastal forest from 200 to 900 m elevation.

**REMARKS.** The type locality, Vossoroca, is approximately at the midpoint on the road between Curitiba (Paraná) and Joinville (Santa Catarina). Despite decades of collection (there are literally thousands of *Theclinae* in museum collections from Joinville, Curitiba, and the area in between), only three individuals of *P. vossoroca* have been found. A fourth, very old, specimen has uncertain provenance. This species has not been collected, so far as we are aware, in almost 40 years.

**MATERIAL EXAMINED** (1♂, 2♀). **BRAZIL**, *Santa Catarina*, Joinville, 200 m, Jan 1969, 1♂ holotype (DZUP); 10–200 m, 22 Feb 1977, 1♀ (USNM on loan from DZUP), *Paraná*, Tijucas do Sul, Vossoroca, 900 m, 4–13 Jan 1976, 1♀ (MC).

### **PARASPICULATUS OROANNA SPECIES COMPLEX**

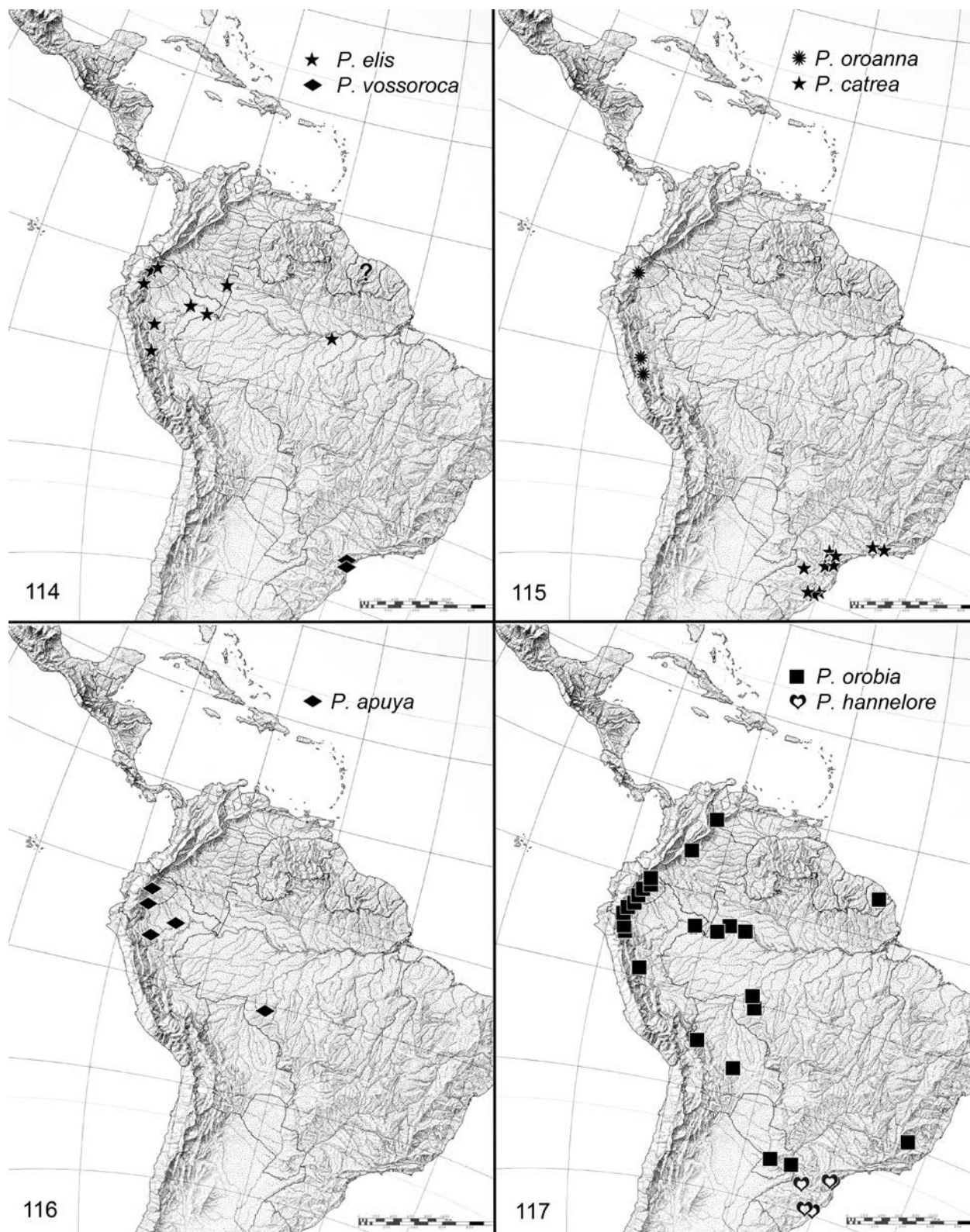
#### ***Paraspiculatus oroanna* (Bálint, 2002)**

FIGURES 12, 42, 54, 80, 113, 115, 126–130

**UPDATED DIAGNOSIS AND DESCRIPTION.** The male *Paraspiculatus oroanna* has a ventral wing pattern that is

**FIGURE 113.** (Opposite page) Neighbor-joining phenogram of 111 *Paraspiculatus* (17 species) based on CO1 barcode sequences. Yellow highlights the 16 females. Pale blue-green highlights the three specimens with divergent BINs (see text).





FIGURES 114–117. Geographic distributions. 114. *P. elis* (stars), *P. vossoroca* (diamonds). 115. *P. oroanna* (flowers), *P. catrea* (stars). 116. *P. apuya* (diamonds). 117. *P. orobia* (squares), *P. hannelore* (hearts).



typical of the genus, with dark brown ground color and bright blue spots and line segments (Figure 12). However, the extent of the white scales on the forewing apex is unique. These scales cover the distal half of the forewing from the costa to vein  $M_3$ . Some species, such as *P. sine*, have a smaller band of white scales extending from the costa to vein  $M_1$ . The forewing shape of *P. oroanna* is also more angular at vein  $M_2$  than in most other *Paraspiculatus* species. Finally, the hindwing anal lobes in *P. oroanna* are larger than those in the majority of species in the genus.

In the original diagnosis, Bálint differentiated *P. oroanna* from *P. orobiana* based on the “absence of the gleaming marking in the cell 3A+2A of the hind wing anal part on ventral side”. Iridescent (gleaming) scales in cell 2A-3A occur between the postmedian line and anal lobe in most *Paraspiculatus*, including *P. oroanna* and *P. orobiana*. The color of these markings varies from bright blue, in the case of *P. oroanna* and *P. grande*, to green-blue in *P. orobiana* and other *Paraspiculatus* species. Further, scale color can vary intraspecifically, and in worn specimens, scales are sometimes lost.

**FEMALE.** The female of *P. oroanna* is unknown.

**GENITALIA.** (Figure 80) We have examined the genitalia of only one male, but the long narrow male valvae appear to distinguish them from all other *Paraspiculatus*. The penis lacks a second cornutus.

**DISTRIBUTION.** (Figure 115) Eastern slope of the Andes in Ecuador and Peru.

**HABITAT.** *Paraspiculatus oroanna* inhabits montane forest from 1,600 to 2,000 m elevation. It might be sympatric with *P. orocana* at 1,600 m, but it otherwise occurs at higher elevations than any other *Paraspiculatus*.

**BEHAVIOR.** There are no records of this species being attracted to rotting fish. One male displayed territorial behavior at 11:30 hours, perching about 1 m above the ground (voucher in RCB).

**MATERIAL EXAMINED (11♂).** ECUADOR, *Tungurahua*, 1800–2200 m, Oct 2008, 2♂ (CF); Río Machay, 1°23.9'S, 78°17.0'W, 1600–1800 m, 15 Feb 2010, 1♂ (RCB); 28 Mar 2014, 1♂ (RCB). PERU, *Huánuco*, 1,500–2,000 m, Jul 2003, 1♂ (CF); Jul 2006, 1♂ (CF); Sep 2010, 2♂ (CF); Chinchao, Chaupiyunca, 1,800 m, Dec 2003, 1♂ (CF); Cushi, 1900 m, 1♂ holotype (BMNH); *Junín*, Satipo, Nov 2009, 1♂ (CF).

#### PARASPICULATUS APUYA SPECIES COMPLEX

##### *Paraspiculatus apuya* Busby and Robbins, new species

FIGURES 13, 81, 99, 116, 126–130

**DIAGNOSIS AND DESCRIPTION.** Males of *P. apuya* are distinguished from other *Paraspiculatus* by the dark dorsal forewing (Figure 13). This species has a broad black border on the dorsal forewing and is the only *Paraspiculatus* where the black scaling along the dorsal forewing costa covers the anterior portion of the discal cell (Character 5). The pattern on the

ventral forewing is unusual. The anterior portion of the postmedian line is made up of three white/light-blue spots, but there are no additional white scales along the costa (Character 6). The combination of white spots and no white scales is found in only one other *Paraspiculatus* species, *P. azul*, and this species is easily distinguished from *P. apuya* by its bright blue dorsal surface with relatively narrow black borders. Mean male forewing length is 16.6 mm (SD = 0.63,  $n = 8$ ). We illustrate the wing pattern (Figure 13) and genitalia (Figure 81).

**FEMALE.** Females of *P. apuya* are unknown.

**GENITALIA.** (Figures 81, 99) Variation in the male genitalia spiculate pad are illustrated.

#### TYPE MATERIAL.

**Holotype (♂):** (Figure 13) ECUADOR: Napo/ 14 km Tena–Puyo Road/ 1°06.7'S, 77°46.9'W 600 m/ 23 October 2010 (Apuya)/ I. Aldas, R. C. Busby, leg. [rectangular, white, printed], USNM ENT 00180817 [rectangular, white, printed barcode label], GENITALIA No./ 2013: 71 ♂/ C. FAYNEL [rectangular, green, printed], Holotype ♂/ *Paraspiculatus apuya* / Busby & Robbins [rectangular, red, printed]. Deposited in USNM.

**Paratypes (3♂):** ECUADOR, Napo, 14 km Tena–Puyo Road, 1°06.7'S, 77°46.9'W, 600 m, 06 Sep 2009, 1♂ (MECN); 20 km Tena–Puyo Road [=14 km], 27–30 Aug 1993, 1♂ (JHKW); Morona Santiago, 54.6 km Santiago–Puerto Morona Rd., 2°54.7'S, 77°42.4'W, 205 m, July 2014, 1♂ (RCB).

**Other Material Examined (4♂):** ECUADOR, Napo, Río Napo, 1♂ (BMNH). PERU, Loreto, Balsapuerto, Paranapura River, Feb 1933, 1♂ (AMNH); Loreto, Agua Blanca, 03°56'S, 73°28'W, 10 Jan 2004, 1♂ (MUSM). BRAZIL, Rôndônia, vic. Caucaulândia, 10°32'S, 62°48'W, 160–350 m, 16 Oct 1991, 1♂ (USNM).

**ETYMOLOGY.** This species is named for its type locality, Apuya (Napo, Ecuador). Six *Paraspiculatus* species have been found at Apuya, and a seventh (*P. elis*) is likely to occur there. The name is proposed as a nonlatinized noun in apposition.

**DISTRIBUTION** (Figure 116) Upper Amazon Basin in Ecuador, Peru, and Brazil.

**HABITAT.** *Paraspiculatus apuya* inhabits wet forest from 160 to 600 m elevation.

**BEHAVIOR.** Males are attracted to traps baited with rotting fish.

**REMARKS.** The CO1 sequence of the male *P. apuya* from Rondônia, Brazil (Appendix A) clusters with those from eastern Ecuador, but is slightly divergent (Figure 113). The Brazilian male is worn, but we found no evident differences in wing pattern.

#### PARASPICULATUS HANNELORE SPECIES COMPLEX

##### *Paraspiculatus hannelore* (Bálint and Moser, 2001)

FIGURES 14, 15, 84, 103, 113, 117, 126–130

**UPDATED DIAGNOSIS AND DESCRIPTION.** *Paraspiculatus hannelore* possesses a dark brown submarginal band

and a short dark line at the distal end of the discal cell on the ventral surface of the hindwing. Although these wing pattern elements occur occasionally in other *Paraspiculatus* species, they are considerably more conspicuous in *P. hannelore* because the postdiscal area of the hindwing is a lighter brown color. Also, the ventral forewing subapical and postdiscal areas are a somewhat lighter brown, as noted in the original description. One diagnostic character used by Bálint and Moser (2001) to separate *P. hannelore* from *P. orobiana* was a “subapical white spot” on the ventral hindwing of the latter, but there is no subapical “white spot” in our *P. orobiana* study series, which included the holotype.

**FEMALE.** (Figure 15). The female is associated by similarities with the male in ventral wing pattern (Figure 14), geographic distribution, and CO1 DNA sequences.

**GENITALIA.** (Figures 84, 103). The genitalic structures of *P. hannelore* are indistinguishable from those of *P. orobia* (see Remarks), except that the minute second terminal cornutus in the male genitalia appears to be absent in *P. hannelore*.

**DISTRIBUTION.** (Figure 117). Southeastern Brazil in the states of Rio Grande do Sul and Santa Catarina.

**HABITAT.** *Paraspiculatus hannelore* inhabits forest along the Atlantic coast from 200 to 900 m elevation and occurs as far inland as Nova Teutonia (SC).

**REMARKS.** *Paraspiculatus hannelore* was synonymized with *P. colombiensis* (Robbins, 2004b), but phylogenetic analyses suggest that this synonymy was incorrect.

**MATERIAL EXAMINED** (10♂, 4♀). **BRAZIL**, Rio Grande do Sul, Dois Irmãos, Picada Verão, 350 m, 22 Mar 1992, 1♂ holotype (DZUP); Ivoti, 200 m, 28 Dec 1994, 1♂ (MC); Nova Petropolis, 750 m, 16 Jan 2006, 2♂ (MC); São Francisco de Paula, 900 m, 1 May 1993, 1♂ (MC); Santa Catarina, Joinville, 200 m, 20 Jan 1992, 1♀ (MC); Joinville, Serrinha, 200 m, 20 Apr 2016, 1♂ (MC); São Bento do Sul, Serra Rio Natal, 600 m, 14 Jan 2001, 1♀ (MC); 20 Apr 2000, 1♂ (MC); 14 May 2001, 1♀ (MC); 04 Jul 2005, 1♂ (MC); Nova Teutonia, 27°11'S, 52°23'W, 300–500 m, 24 Feb 1954, 1♂ (USNM); Apr 1960, 1♀ (USNM); Seara, Nova Teutonia, 450–700 m, May 1977, 1♂ (USNM). One male in BMNH is labeled Mexico with no further data, but the known distribution of this species strongly suggests that the label is incorrect.

### PARASPICULATUS OROBIA SPECIES COMPLEX

*Paraspiculatus orobia* and *P. cosmo* have parapatric distributions and are sisters in our phylogenetic analyses. Morphologically, males in this lineage have regularly spaced gray/brown scales (Figures 75, 76) at the base of the male dorsal hindwing costa (Character 13).

### *Paraspiculatus cosmo* Busby, Robbins, and Faynel, new species

FIGURES 16, 17, 76, 85, 104, 113, 118, 126–130

**DIAGNOSIS AND DESCRIPTION.** Males of *Paraspiculatus cosmo* (Figure 16) and *P. orobia* (Figures 18, 20) differ

by (1) the lack of a band of blue scales above the cubital vein on the ventral forewing (Character 8, present in *P. orobia*), and (2) a moderately broad black border on the dorsal forewing (narrow in *P. orobia*). These differences are consistent in the study series.

Dark gray scales at the base of the male dorsal hindwing costa in *P. cosmo* also occur in *P. grande*, *P. orocana*, and *P. honor*. However, the scales in these other species are concentrated in the center of cell Sc+R<sub>1</sub>-Rs and often have an iridescent sheen (Figure 74) that is less apparent in *P. cosmo* (Figure 76). Further, male hindwing tails occur in *P. cosmo*, but are absent in the other three species.

Mean forewing length is 18.8 mm (SD = 1.35, *n* = 25) in males and 16.7 mm (SD = 0.57, *n* = 2) in females. We illustrate the wing pattern (Figures 16, 17) and genitalia (Figures 85, 104).

**GENITALIA.** (Figures 85, 104) As in *P. hannelore*, the second terminal cornutus appears to be absent.

**FEMALE.** (Figure 17) The female is associated by geographic distribution and CO1 DNA sequences. It has blue scaling dorsally.

The female type of the unavailable name *Thecla orobiana cosmophila* Tessmann also appears to be this species. This “type” is blue above, unlike the all-brown female of *P. orobiana*, and has conspicuous tails, unlike the females of *P. grande* and *P. honor*. The female of *P. orocana* is as yet unknown, but we expect it to be blue above and tailless.

### TYPE MATERIAL.

**Holotype** (♂): (Figure 16) ECUADOR: Morona-Santiago/ Bosque de Domono/ 2°11.0'S, 78°06.2'W 1325 m/ 03 September 2003/ Robert C. Busby, leg. [rectangular, white, printed], USNM ENT 00180800 [rectangular, white, printed barcode label], GENITALIA No./ 2013; 79 ♂/ C. FAYNEL [rectangular, green, printed], Holotype ♂/ *Paraspiculatus cosmo*/ Busby, Robbins & Faynel [rectangular, red, printed]. Deposited in USNM.

**Paratypes** (29♂, 2♀): **ECUADOR**, Morona Santiago, 14 km W of Macas, Río Abanico, [2°15.4'S, 78°11.7'W], 1,600 m, 08 Sep 1999, 1♂ (RCB); 09 Sep 1999, 1♂ (USNM); 15 Sep 2006, 1♂ (RCB); 19 Sep 1999, 3♂ (USNM); 21 Sep 1998, 1♂ (RCB); 23 Sep 1998, 1♂ (RCB); 25 Sep 1998, 1♂ (RCB); 27 Sep 1998, 1♂ (MECN); 28 Sep 1998, 1♀ (RCB); 30 Sep 1997, 1♂ (RCB); Oct 1995, 1♂ (JHKW); 1 km E of Río Abanico, [13 km W of Macas], 1,600 m, 11 Sep 2000, 1♂ (MECN), 1♂ (RCB); 13 Sep 2001, 2♂ (USNM); 15 km S San Juan Bosco, 1,600 m, 25 Sep 2001, 1♂ (RCB); 2 km N of San Isidro, 2°11.9'S, 78°09.4'W, 1,250–1,400 m, 17 Sep 2013, 1♂ (RCB); 30 Sep 2012, 2♂ (USNM); 29 Sep 2015, 2♂ (RCB); Nueve de Octubre, 2°13.0'S, 78°13.5'W, 1,600–1,800 m, 28 Jan 2014, 1♂ (MECN); Zamora Chinchipe, Zamora, 4°04.5'S, 78°58.1'W, 1,450 m, 06 Oct 2002, 1♂ (RCB), 2♂ (USNM); Napo, 49 km Tena–Loreto Road, 0°42.9'S, 77°44.4'W, 1,350 m, 29 Nov 2013, 1♂ (RCB); Sucumbíos, km 12 La Bonita–Rosa Florida old trail, 1,550 m, Mar 1995 (JHKW). **PERU**, Huánuco, Tingo Maria, 01 Oct 2003, 1♂ (CF); Chanchamayo, La Merced, Jun 1930, 1♀ (USNM).

**Other Material Examined** (3♂, 1♀): **PERU**, Amazonas, Mendoza, Yanohuaico [Llanohuaico], 1,500–2,000 m, Jan 2007,

1♂ (MC); Rodríguez de Mendoza, [6°25'S, 77°30'W], 1,500–2,000 m, Dec 1998, 1♂ (MC); Río Marañón, Numparque, 1,000 m, Oct 2006, 1♂ (MC); *Pasco*, between La Paz and La Salud, about 1,800 m, 1♀ (ZMHB). The last specimen is the type of the unavailable name, *Thecla cosmophila* Tessmann. The data label has an elevation of 2,000 m, but the original description was “in etwa 1800 m” [at approximately 1800 m].

**ETYMOLOGY.** This name is intended to be reminiscent of the old unavailable name for this species (see Nomenclature below). It is proposed as a nonlatinized noun in apposition.

**NOMENCLATURE.** The name *Thecla cosmophila* Tessman, which was proposed as a female form of *Thecla orobiana*, is unavailable because under ICZN Articles 45.5 and 45.6 a form relegated to one sex cannot be subspecific. Robbins and Lamas (2002) were incorrect in considering *Thecla cosmophila* Bridges, 1988 to be an available name because it was published after 1985.

**DISTRIBUTION.** (Figure 118) Eastern slope of the Andes in Ecuador and Peru.

**HABITAT.** Wet montane forest from 1,250 to 2,000 m.

**BEHAVIOR.** Males are attracted to rotting fish—most were collected on traps, but two were on leaves.

**REMARKS.** *Paraspiculatus cosmo* and *P. orobia* are sister species (see Phylogenetic Analyses) and appear to be elevationally parapatric. In our study material, the lowest elevation for *P. cosmo* is 1,250 m, which is the same as the highest recorded elevation for *P. orobia*.

### ***Paraspiculatus orobia* (Hewitson, 1867)**

FIGURES 1, 18–21, 47, 59, 65, 75, 86, 105, 113, 117, 126–130

**UPDATED DIAGNOSIS AND DESCRIPTION.** Males of *P. cosmo* and *P. orobia* are the only two *Paraspiculatus* species with regularly spaced gray/brown scales at the base of the male dorsal hindwing costa (Character 13, Figures 75, 76). The differences between these two taxa are noted in the account of *P. cosmo*.

The “black line at the end of the [dorsal forewing] cell” mentioned by Hewitson (1867:103) varies intraspecifically. The presence of tails in *P. orobia* varies geographically.

**FEMALE.** (Figures 19, 21) The female is associated by CO1 DNA sequences. The apparent differences in wing shape in the two illustrated females are primarily due to poor preparation of the latter specimen.

**GENITALIA.** (Figure 86, 105) Variation among nine male genitalic dissections provided no evidence to suggest more than one species is represented by this name. The base of each valve is displaced ventrally, and its ventral surface lacks setae.

**VARIATION.** *Paraspiculatus orobia* is the only species in the genus that occurs in two of Brown's (1982) major biogeographical zones. Perhaps because of its wide distribution, it is one of the most geographically variable species. Males and females from the lower Amazon Basin, as far west as Rondonia (Brazil), and the Atlantic region possess tails; those from the upper Amazon Basin, from Colombia to Bolivia, lack tails (Figures 18–21).

Those with and without tails do not differ in other morphological traits and do not differ in CO1 DNA sequences. No locality is known where both forms—and/or intermediate forms—occur. Males from the Amazon region have the characteristically well-developed shining blue scales anterior of the cubital vein on the ventral forewing (Figures 18, 59), but the expression of this blue patch is reduced in individuals from the Atlantic region.

**DISTRIBUTION.** (Figure 117) *Paraspiculatus orobia* is widely distributed in the lowland Amazon and Atlantic regions. There is one record (La Fria, Tachira, Venezuela) in the area of overlap between the Transandean and Amazon regions.

**HABITAT.** *Paraspiculatus orobia* inhabits wet forest from 100 to 1,250 m elevation.

**BEHAVIOR.** Males in the upper Amazon Basin are attracted to rotting fish. Of 79 specimens collected with bait, 62 were on traps and 17 were on leaves near the ground (Figure 1).

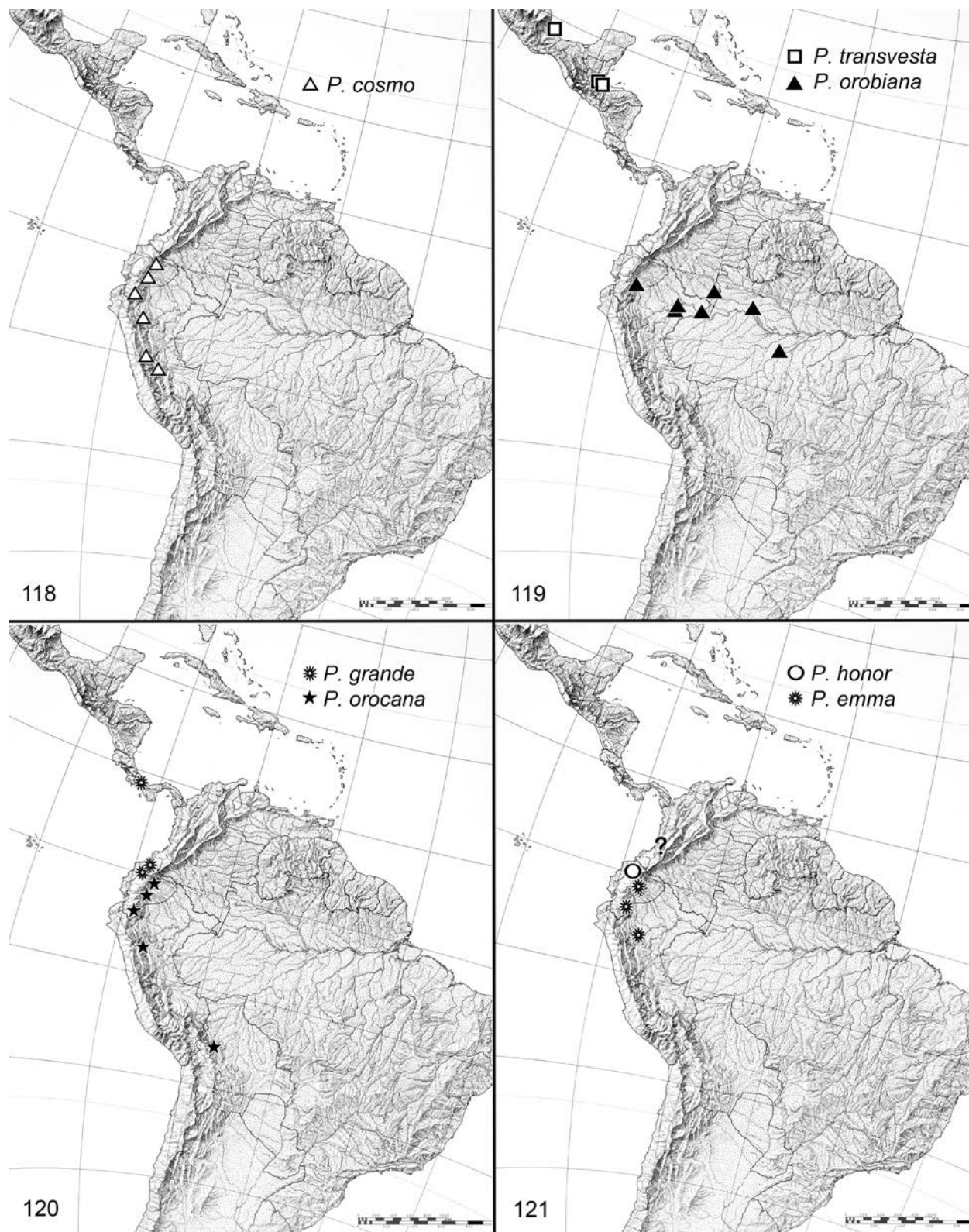
**REMARKS.** The closest relative of *P. orobia* is *P. cosmo* and they appear to be parapatric in elevation.

The identity of *P. orobia* has historically been confused. D'Abrera (1995:1194) illustrated six specimens as *Thecla orobia*, but they represent at least three species. Johnson and Constantino (1997) named *P. colombiensis* as the type of *Paraspiculatus*, but did not clearly differentiate it from *P. orobia*. Bálint and Moser (2001) figured a specimen of *P. colombiensis* as *P. orobia*, for which reason they incorrectly synonymized *P. colombiensis* with *P. orobia*. Bálint (2004) then named *P. villaanna* from a tailless specimen of *P. orobia*.

The “band of blue above the median nervure” on the ventral forewing, which was noted in Hewitson's original description, is a conspicuous characteristic of this species. However, it also occurs in *P. lilyana* and occasionally in *P. sine* (two individuals).

**MATERIAL EXAMINED** (207♂, 6♀). **FRENCH GUIANA**, Saül, 150 m, 7–10 Nov 2005, 1♀ (CF). **COLOMBIA**, Villavicencio, Ost, 400 m, 18 Dec 1924, 1♂ (MNHN). **ECUADOR**, *Morona Santiago*, 10 km E of Yanganza, 2°50.0'S, 78°15.0'W, 800 m, Sep 2003, 1♂ (RCB); 10 km Santiago–Patuca Rd, 3°00.8'S, 78°04.5'W, 460 m, 13 Sep 2003, 1♂ (RCB); 15 km S of Gualaquiza, 3°27.6'S, 78°33.1'W, 800 m, 15 Sep 2000, 2♂ (RCB); 2 km N of San Isidro, 2°11.9'S, 78°09.4'W, 1250–1450 m, 08 Jan 2012, 2♂ (CF); 29 Jan 2014, 1♂ (RCB); 12 Sep 2016, 2♂ (RCB); 13 Sep 2016, 2♂ (RCB); 14 Sep 2015, 2♂ (RCB); 16 Sep 2013, 1♂ (RCB); 17 Sep 2013, 1♂ (RCB); 28 Sep 2015, 1♂ (RCB); 29 Sep 2015, 6♂ (RCB); 30 Sep 2012, 1♂ (RCB); 30 Sep 2014, 1♂ (RCB); 30 Sep 2016, 6♂ (RCB); 01 Oct 2013, 1♂ (RCB); 01 Oct 2014, 2♂ (RCB); 16 Nov 2015, 1♂ (RCB); 17 Nov 2015, 1♂ (RCB); 28 Nov 2011, 3♂ (CF); Dec 2011, 4♂ (CF); 32.8 km Santiago–Puerto Morona Rd, 2°58.9'S, 77°48.1'W, 670–750 m, 17 Sep 2015, 1♂ (RCB); 27 Sep 2014, 1♂ (RCB); 28 Sep 2015, 1♂ (RCB); 38.2 km Santiago–Puerto Morona Rd, 2°57.8'S, 77°47.2'W, 265 m, 13 Sep 2011, 1♂ (RCB); 47.6 km Santiago–Puerto Morona Rd, 2°56.2'S, 77°44.8'W, 245 m, 25 Sep 2014, 1♂ (RCB); 53.1 km Santiago–Puerto Morona Rd, 2°55.0'S, 77°42.7'W, 210 m, 08 Jan 2016, 1♂ (RCB); 27 Sep 2016, 1♂ (RCB); 54.6 km Santiago–Puerto Morona Rd, 2°54.7'S, 77°42.4'W, 14 Sep 2014, 1♂ (RCB);





FIGURES 118–121. Geographic distributions. 118. *P. cosmo* (triangles). 119. *P. transvesta* (squares), *P. orobiana* (triangles). 120. *P. grande* (flowers), *P. orocana* (stars). 121. *P. honor* (circle, question mark), *P. emma* (flowers).

25 Sep 2014, 1♂ (RCB); 6 km Santiago–Patuca Rd, 3°01.0'S, 78°03.5'W, 350 m, 01 Oct 2003, 1♂ (RCB); 72 km Patuca–Santiago Rd, 3°02.1'S, 78°06.2'W, 380 m, 02 Oct 2002, 1♂ (RCB); Santiago (Hill North of Town), 3°02.3'S, 78°00.3'W, 350 m, 14 Sep 2014, 3♂ (RCB); 17 Sep 2015, 1♂ (RCB); 25 Sep 2013, 1♂ (RCB); 27 Sep 2014, 2♂ (RCB); 23 Oct 2013, 1♂ (RCB); 29 Oct 2013, 1♂ (RCB); Yakunk–Cutucú trail, 2°45.11'S 78°10.91'W, 1000 m, Dec 2003, 1♂ (JHKW); *Napo*, 12 km Tena–Puyo Rd (Finca San Carlo), 1°05.3'S, 77°47.4'W, 600 m, 15 Feb 2008, 1♂ (RCB); 21 Sep 2011, 1♂ (RCB); 23 Sep 2008, 1♂ (RCB); 26 Sep 2007, 1♂ (RCB); Sep 1996, 1♂ (JHKW); 14 km Tena–Puyo Rd (Apuya), 1°06.7'S, 77°46.9'W, 600 m, 10 Jan 2007, 1♂ (RCB); 10 Jan 2013, 1♂ (RCB); 17 Jan 2011, 1♂ (RCB); 18 Jan 2011, 1♂ (RCB); Feb 2010, 1♂ (RCB); 19 Feb 2008, 1♂ (RCB); 27 Feb 2005, 1♂ (RCB); 28 May 2010, 1♂ (RCB); Aug 1993, 1♂ (JHKW); 28 Aug 2009, 1♂ (RCB); 06 Sep 2009, 1♂ (RCB); 09 Sep 2006, 1♂ (RCB); 11 Sep 2005, 1♂ (RCB); 12 Sep 2015, 1♂ (RCB); 13 Sep 2005, 3♂ (RCB); 15 Sep 2013, 1♂ (RCB); 16 Sep 2012, 1♂ (RCB); 21 Sep 2011, 1♂ (RCB); 22 Sep 2005, 1♂ (RCB); 23 Sep 2008, 1♂ (RCB); 24 Sep 2010, 1♂ (RCB); 25 Sep 1997, 1♂ (RCB); 2–3 Oct 1997, 1♂ (RCB); 04 Oct 2013, 1♂ (RCB); 13 Oct 2011, 2♂ (RCB); 16 Oct 2010, 1♂ (RCB); 18 Oct 2010, 2♂ (RCB); 22 Oct 2010, 2♂ (RCB); 23 Oct 2010, 2♂ (RCB); 09 Nov 2010, 1♂ (RCB); 12 Nov 2011, 1♂ (RCB); 28 Nov 2012, 1♂ (RCB); 29 Nov 2013, 2♂ (RCB); Dec 1996, 1♂ (JHKW); Dec 2010, 1♂ (RCB); 28 km Tena–Puyo Rd (El Capricho), 1°11.3'S, 77°49.9'W, 800 m, 10 Jan 2013, 1♂ (RCB); 24 Oct 2010, 1♂ (RCB); 25 Oct 2010, 1♂ (RCB); Chichicorrumi, 450 m, 09 Sep 1996, 1♀ (USNM); lower hill N Misahualli, Jungle Lodge Hotel, 1°01.92'S, 77°39.69'W, 500 m, 22 Oct 2000, 1♂ (USNM); Río Pimpilala (SW of Talag), 1°04.6'S, 77°56.2'W, 600–900 m, April 2006, 1♂ (RCB); Oct 2005, 4♂ (RCB); Nov 2008, 2♂ (RCB); Satzayacu, Tena–Puyo Rd, 700 m, Sep 1996, 1♂ (JHKW); Yachana Reserve, 0°50.5'S, 77°13.8'W, 350 m, 17 Feb 2008, 1♂ (RCB); *Orellana*, 1.2 km Dayuma–Cononaco Rd, 0°40.7'S, 76°52.4'W, 325 m, 16 Jan 2012, 1♂ (RCB); 14 Nov 2010, 1♂ (RCB); 22 km Loreto–Payamino Rd, 0°34.9'S, 77°24.4'W, 825 m 20 Nov 2011, 1♂ (RCB); mouth of Río Añangu, middle Río Napo, 0°31.7'S 76°23.7'W, 250 m, Oct–Dec 2005, 1♂ (JHKW); upper Río Tipitini, Coca–Tiguino Rd, 0°40.7'S, 76°52.4'W, Mar 1995, 1♂ (JHKW); Jul 1994, 1♂ (JHKW); Sep 1995, 1♂ (JHKW); *Pastaza*, 25 km Puyo–Tena Rd, 1°20.0'S, 77°55.9'W, 1000 m, Dec 2009, 1♂ (RCB); 32 km S of Puyo, 1000 m, 01 Oct 1997, 1♂ (RCB); 39.4 km Puyo–Villano Rd, 1°25.6'S, 77°43.8'W, 750 m, 11 Sep 2016, 2♂ (RCB); 01 Oct 2016, 1♂ (RCB); 02 Oct 2015, 1♂ (RCB); 12 Oct 2015, 1♂ (RCB); Pitirishca, 1°57.8'S, 77°52.1'W, 800 m, 07 Sep 1999, 1♂ (RCB); 10 Sep 2000, 1♂ (RCB); 19 Sep 2000, 1♂ (RCB); 7.1 km E of Puyo–Macas Rd at km 32, 1°40.0'S, 77°47.7'W, 850 m, 05 Mar 2009, 1♂ (RCB); Hills W of Santa Clara, 1°14.5'S, 77°57.4'W, 900 m, 10 Sep 2000, 1♂ (RCB); *Sucumbíos*, 16 km Lumbacui–La Troncal Rd, 0°00.8'S, 77°15.0'W, 400–500 m, 06 Jan 2011, 2♂ (RCB); 03 Dec 2015, 1♂ (RCB); Cerro Lumbacui Norte, 0°01.7'N, 77°19.2'W, 900–1000 m, 30 Dec 2015,

1♂ (RCB); *Zamora Chinchipe*, 5 km W of Zamora (Qbda. de Chorillos), 1250 m, May 2000, 1♂ (JHKW); 21 May 2000, 1♂ (RCB); Namirez Bajo, 1200 m, 18 Sep 2001, 1♂ (RCB). **PERU**, *Amazonas*, Quebrada Chingaza, 5°22'S, 78°26'W, 500 m, 22 Sep 1999, 2♂ (USNM); *Huánuco*, Tingo Maria, Aug 2001, 1♂ (CF); Aug 2003, 1♂ (CF); Sept 2009, 1♂ (CF); Aug 2011, 1♂ (CF); Tingo Maria, 670 m, Sept 2001, 1♂ (MC); Sept 2003, 1♂ (MC); 650 m, Oct 2003, 1♂ (MC); Tingo Maria, Las Pavas, 08 Oct 1999, 1♂ (CF); Tingo Maria, Huallaga, Apr–Jun 1994, 1♂ (USNM); *Loreto*, Agua Blanca, 3°56'S, 73°28'W, 130 m, 06 Aug 2007, 1♀ (MUSM); Iquitos, 1♂ (MNHN); Iquitos, 100 m, Sep 1999, 1♂ (CF); 10 Sept 2003, 1♂ (MC); Oct 2003, 1♂ (CF); Oct 2005, 1♂ (CF); Nov 2012, 1♂ (CF); Nov 2002, 1♂ (MC); Dec 2006, 1♂ (MC); Iquitos, San Pablo, 04°01'S, 71°06'W, 100 m, Feb 2011, 2♂ (CF); Pantoja, Río Napo, Nov 2000, 1♂ (MC); Tamshiyacu, 100 m, Nov 2013, 1♂ (CF); Polis, Río Momon, 100 m, Jun 2010, 1♂ (CF); Picuroyacu, 03°37'S, 73°15'W, Jun 2010, 126 m, 1♂ (CF); May 2012, 1♂ (CF); Aug 2013, 1♂ (CF); Pévas, 03°19'S, 71°51'W, Jun 2010, 1♂ (CF); Aug 2010, 1♂ (CF); Río Sucusari, 22 Oct 2008, 1♀ (CF); *Madre de Dios*, 13 km SW Puerto Maldonado, 300 m, 22 Oct 1983, 1♂ (USNM); Boca Río La Torre, 300 m, 30 Oct 1983, 1♂ (USNM); Parque Manu, Pakitza, 11°55.8'S, 71°15.3'W, 340 m, 13 Oct 1991, 1♂ (USNM); 15 Oct 1991, 1♂ (USNM); Río La Torre, Tambopata Reserve, 300 m, 04 Oct 1986, 1♂ (USNM); *San Martín*, Moyobamba, Jan–Jun, 1887, 1♀ (BMNH); Pongo de Kainarakí, 350 m, Dec 2004, 1♂ (MC); *Cusco*, Río Araza, 500–700 m, Dec 1994, 1♂ (MC). **BOLIVIA**, [Santa Cruz], Buena Vista, 400 m, 01 Jul 1914, 1♂ (CMNH); 750 m, Aug–Apr 1906–1907, 1♂ (BMNH); [Buena Vista], 17°46.9'S, 63°05.6'W, 1♂ (USNM); [La Paz], Mapi, 1♂ (MNHN). **PARAGUAY**, [Sapucaí], 02 Nov 1904, 1♂ (BMNH). **BRAZIL**, *Amazonas*, Marã, Río Japura, Oct 1997, 1♂ (MC); Nov 1995, 1♂ (CF); Tonantins, 100 m, Nov 2013, 2♂ (CF); Fonte Boa, Oct 1994, 1♂ (MC); S. Paulo de Olivença, 11 Dec 1921, 1♂ (MNHN); Teffe, 08 Sep 1921, 1♂ (MNHN); Tocantins, 24 Sept 1992, 1♂ (MC); *Matto Grosso*, Parque F. Río Doce, 13 Nov 1977, 1♂ (USNM); Diamantino, Alto Río Arinos, 350 m, 21 Sep 1995, 1♂ (MC); Nobres, Serra do Tombador, 350 m, 21 Sep 1995, 1♀ (MC); *Paraná*, [Iguazu], Oct–Dec 1922, 1♂ (BMNH); *Rondônia*, Ariquemes, 12 Jul 1986, 1♂ (USNM); 62 km S Ariquemes, 10°53.0'S, 62°48.0'W, 165 m, 19–29 Sep 1996, 2♂ (USNM); vic. Caucaulândia, 10°32.0'S, 62°48.0'W, 160–350 m, 13 Oct 1991, 1♂ (USNM); Alto Paraíso, 9°44.0'S, 63°16.0'W, 120 m, 08 Aug 2005, 1♂ (MC).

#### PARASPICULATUS OROBIANA SPECIES COMPLEX

#### *Paraspiculatus orobiana* (Hewitson, 1867)

FIGURES 22, 23, 44, 56, 70, 82, 112, 113, 119, 126–130

**UPDATED DIAGNOSIS AND DESCRIPTION.** Males of *Paraspiculatus orobiana* (Figure 22) are most easily distinguished by (1) the absence of white scales along the distal portion of the ventral forewing costal margin (Character 6) and (2)



the absence of three white/light-blue spots at the anterior portion of the ventral forewing postmedian line (an uncoded character due to intraspecific variability, but three spots are present in most species). The area along the costa is often a lighter color distal of the postmedian line than basal of it, but this is due to lighter brown or tan scales, not white scales. We found slight variation in the second character noted above as one of eight male specimens had two of the three spots at the anterior portion of the postmedian line. The other seven had none.

According to Hewitson (1867:103), the dorsal surface of the forewing has “a black line at the end of the cell.” However, we could clearly distinguish this line in only two of the eight males in our study series because of variation in the width of the distal border.

Tessman (1928) described *Thecla orobiana* female form *cosmophila*, but, as already explained, this female belongs to the species that we name *P. cosmo*.

**FEMALE.** (Figure 23) The female of *P. orobiana* was associated by similarity with the male in CO1 DNA sequences. As with the male, the ventral forewing of the female lacks white scales on the distal side of the costa and lacks three white/light-blue spots at the anterior portion of the postmedian line.

Hewitson (1867:103) described the female of *P. orobiana* “like the male except for some white spots on the costal margin at the commencement of the band of blue on the underside of the anterior wing”. Hewitson associated the female because Bates collected it at the type locality of *P. orobiana* (Ega, Amazonas, Brazil), but the wing pattern description is inconsistent with the female wing pattern associated by DNA sequences. Both *P. orobiana* and *P. colombiensis* occur in the Brazilian state of Amazonas (Figures 117, 124) and possess white spots at the costa of the ventral forewing.

**GENITALIA.** (Figure 82, 112) The male and female genitalia are typical of *Paraspiculatus*, but have no distinctive traits.

**DISTRIBUTION.** (Figure 119) *Paraspiculatus orobiana* is widely distributed in the lowland Amazon region.

**HABITAT.** *Paraspiculatus orobiana* inhabits wet forest from 100 to 350 m elevation.

**BEHAVIOR.** Two males from Ecuador were attracted to traps baited with rotting fish.

**REMARKS.** The CO1 barcode sequence of the male *P. orobiana* from Amazonas, Brazil (Appendix A) is slightly divergent from the sequences of Ecuadorian and Peruvian specimens, but clusters with them (Figure 113). We found no evident wing pattern differences among these specimens.

**MATERIAL EXAMINED** (8♂, 1♀). **COLOMBIA**, Amazonas, Río Caquetá, La Pedrera, 1°18'S, 69°42'W, 120 m, 26 Apr 1992, 1♂ (MUSM). **ECUADOR**, Morona Santiago, Santiago (Hill North of Town), 3°02.3'S, 78°00.3'W, 350 m, 27 Sep 2014, 1♂ (RCB); 27 Sep 2015, 1♂ (RCB). **PERU**, Amazonas, Cavallo Cocho, May–Jul 1884, 1♂ (BMNH); Loreto, Iquitos, 4°16'S, 73°25'W, 100 m, Oct 2005, 1♂ (CF); Picuroyacu, 3°37'S, 73°15'W, 10 Nov 2008, 1♀ (USNM). **BRAZIL**, Amazonas, Ega,

1♂ holotype (BMNH); Marañ, Río Japurá, May 1995, 1♂ (MC); Manicore, 16 Aug 1976, 1♂ (USNM).

## PARASPICULATUS TRANSVESTA SPECIES COMPLEX

### *Paraspiculatus transvesta* Robbins and Busby, new species

FIGURES 24, 25, 83, 106, 119, 126, 129, 130

**DIAGNOSIS AND DESCRIPTION.** Males of *Paraspiculatus transvesta* are distinguished by the dull dorsal pattern, which lacks blue except for some greenish-blue scales near the base of the wings. The ventral forewing has brownish iridescent scaling posterior of the cubital vein that is visible when the wing is held at an acute angle under a bright light (Character 7), a trait that it shares with *P. orobiana*. The ventral wing pattern is typical for the genus and does not have unique characters. Mean forewing length is 17.4 mm (SD = 0.0,  $n = 1$ ) in the male and 17.3 mm (SD = 0.64,  $n = 2$ ) in the females. We illustrate the wing pattern of each sex (Figures 24, 25) and their genitalia (Figures 83, 106).

**FEMALE.** (Figure 25) The female is associated by similarities with the male in dorsal wing pattern and in geographic distribution. The pattern of basal green-blue scales on the dorsal wings of both the female and male is unique in the genus. The ventral pattern is the same as in the male. We were unable to obtain a CO1 sequence from either sex due to the age of the specimens.

#### TYPE MATERIAL.

**Holotype** (♂): (Figure 24) GUAT[EMALA]/ Cayuga [rectangular, white, printed], aug [rectangular, white, printed], Schaus and/ Barnes/ coll [rectangular, white, printed], USNM ENT 00179436 [rectangular, white, printed barcode label], GENITALIA No./ 1982: 210 ♂/ R. K. ROBBINS [rectangular, green, printed], Holotype ♂/ *Paraspiculatus transvesta* Robbins & Busby [rectangular, red, printed]. Deposited in USNM.

**Paratype** (1♀): **MEXICO**, [Veracruz], Sontecomapan, [18°30'N, 95°02'W], May 1955, 1♀ (MGCL).

**Other Material Examined** (1♀): **HONDURAS**, San Pedro Sula, 1895, 1♀ (BMNH).

**ETYMOLOGY.** We name this species *P. transvesta* because the male looks like a female. It is proposed as a nonLatinized noun in apposition.

**GENITALIA.** (Figures 83, 106) The male and female genitalia are typical of *Paraspiculatus*.

**DISTRIBUTION.** (Figure 119) Mexico to Honduras.

**HABITAT.** This species appears to be a denizen of lowland forest. Elevation within 10 km of the type locality is 50–500 m, within 10 km of Sontecomapan is 10–800 m, and within 10 km of San Pedro Sula is 50–1,100 m. The wide range of elevations in Figure 130 for *P. transvesta* is an artifact of imprecise labeling of specimens.

**REMARKS.** Many characters could not be scored for *P. transvesta* because we could not homologize the male's female-like wing pattern with males of other species.

### PARASPICULATUS OROCANA SPECIES COMPLEX

*Paraspiculatus orocana*, *P. grande*, and *P. honor* form a monophyletic lineage of allopatric/parapatric species. Males are distinguished by three characters. First, the dark gray scales on the dorsal hindwing cell Sc+R<sub>1</sub>-Rs are concentrated in the middle of the cell and have iridescent edges that give off a sheen under a bright light (Character 13, Figure 74). The gray/brown scales in male *P. orobia* and *P. cosmo* are less iridescent and more evenly spaced so that the center of the cell is not distinct (Figures 75, 76). Second, the *P. orocana* group males have a relatively straight inner margin of the anal lobe that contrasts in shape with the smaller, more rounded lobes of other *Paraspiculatus* species (Character 15, Figure 77). Finally, the ventral anal lobes in the *P. orocana* group have long, dark fringe scales that lack white scales at the end of vein 2A or anteriorly on the inner margin (Character 22) as in most other *Paraspiculatus* species. Other identifying male characters shared by the *P. orocana* group as well as other species in the genus are: (1) A broad black border and apex on the dorsal surface of the forewing (Figures 45, 46), with the border having a straight inner edge (Character 3), (2) a less rounded, more angular hindwing (Character 11), (3) an area of iridescent, silver-blue scales located both anterior and posterior of the cubital vein on the ventral forewing (Characters 7, 8, Figure 68), and (4) the absence of hindwing tails. The *P. orocana* species group is monophyletic in a phylogenetic analysis of CO1 sequences.

### *Paraspiculatus grande* Busby, Robbins, and Moser, new species

FIGURES 26, 27, 46, 58, 74, 87, 107, 113, 120, 126–130

**DIAGNOSIS AND DESCRIPTION.** Males of *Paraspiculatus grande* differ from other species in this complex by a postmedian line consisting of three light blue spots at the costal margin with four posterior blue spots (Figure 58). In *P. orocana* and *P. honor*, the anterior spots are absent or vestigial, and the number of posterior blue markings is limited to one or two spots (Figure 57). The white scales near the costa of the ventral forewing in *P. grande* form two separate patches, one on the distal side of the three median spots and the other at the apex. In contrast, the white scales in both *P. orocana* and *P. honor* form more of a single crescent-shaped cluster between the median and apex. Mean forewing length is 21.3 mm (SD = 0.64,  $n = 21$ ) in males and 20.4 mm (SD = 0.0,  $n = 1$ ) in the female. We illustrate the wing pattern of each sex (Figures 26, 27) and their genitalia (Figures 87, 107).

**FEMALE.** (Figure 27) The female is associated by CO1 DNA sequences. The only known female is from Panama whereas all males are from western Ecuador. Panama and western Ecuador are part of the Transandean biogeographic zone and have a high incidence of faunal overlap (Brown, 1982).

#### TYPE MATERIAL.

**Holotype** (♂): (Figure 26) ECUADOR: Esmeraldas/ 12 km Lita–San Lorenzo Road/ 0°53.1'N, 78°30.9'W 850 m/ 26

March 2011 Río Chuchuví/ I. Aldas, R. C. Busby, leg. [rectangular, white, printed], USNM ENT 00180789 [rectangular, white, printed barcode label], GENITALIA No./ 2013: 86 ♂/ C. FAYNEL [rectangular, green, printed], Holotype ♂ / *Paraspiculatus grande* / Busby, Robbins, and Moser [rectangular, red, printed]. Deposited in USNM.

**Paratypes** (22♂, 1♀): PANAMA, Bocas del Toro, nr. Chiriquí Grande, 1100 m, 19 Jun 1982, 1♀ (USNM). ECUADOR, Esmeraldas, 12 km Lita–San Lorenzo Road, 0°53.1'N, 78°30.9'W, 850 m, March 2001, Río Chuchuví, 1♂ (USNM); May 2011, 1♂ (USNM), 1♂ (RCB); 15 May 2014, 1♂ (RCB); 19 Jun 2011, 1♂ (RCB); 22 Jun 2011, 1♂ (RCB); Jul 1999 1♂ (JHKW); Jul 2005, 1♂ (RCB); Jul 2006, 1♂ (USNM); 14 Jul 2011, 2♂ (USNM); Aug 2006, 1♂ (MECN); Aug 2008, 1♂ (USNM); Oct 2008, 1♂ (MECN); 25 Oct 2014, 1♂ (RCB); 28 Oct 2014, 1♂ (USNM); El Encanto, km 17 Lita–San Lorenzo Road, 850 m, Jul 2003, 1♂ (JHKW); Alto Tambo, [0°54.7'N, 78°32.8'W], [725 m], Aug 2000, 2♂ (RCB); Lita, [0°52.5'N, 78°28.0'W], 600–1000 m, Apr 2002, 1♂ (MC); Carchi, El Baboso [Carmelo], 0°53.1'N, 78°26.5'W, 950 m, 17 Jun 2011, 1♂ (RCB).

**Other Material Examined** (2♂): ECUADOR, Pichincha, Pacto–Guayabillas Road, 01 May 2003, 1♂ (MC); Pacto, 1100 m, 20 Mar 2001, 1♂ (CF). These specimens (the southernmost data points) were excluded from the type series because of uncertainty regarding the exact locations.

**ETYMOLOGY.** *Paraspiculatus grande* is among the largest species in the genus. The name is proposed as a nonlatinized noun in apposition.

**GENITALIA.** (Figures 87, 107) The male and female genitalia are typical of *Paraspiculatus*. The ventral base of the valvae is similar to that of *P. orobia*, but this may be a superficial resemblance.

**DISTRIBUTION.** (Figure 120) Panama to the western slope of the Andes in Ecuador.

**HABITAT.** Wet lower montane forest from 725 to 1,100 m elevation.

**BEHAVIOR.** The vast majority of specimens in our study group were collected with a net. Several males exhibited territorial behavior, perching 3 to 4 m above the ground along a ridgetop in the early afternoon. Specific records for Río Chuchuví (Ecuador, Esmeraldas Province) are 12:30, 13:10, and 13:35 hours (vouchers in RCB and USNM). Only one male of *P. grande* was collected on a trap baited with fish.

**REMARKS.** *Paraspiculatus grande* occurs at localities below 1,100 m; *P. honor* occurs at elevations above 1,200 m. Also, *P. grande* is allopatric with *P. orocana* (Figure 120).

### *Paraspiculatus honor* Busby, Robbins, and Hall, new species

FIGURES 28, 29, 88, 108, 113, 121, 126–130

**DIAGNOSIS AND DESCRIPTION.** Although males of *P. grande* have four blue spots at the posterior end of the ventral forewing postmedian line, *P. honor* and *P. orocana* typically



possess only one or two of these blue spots. The postmedian-line white spots at the ventral forewing costa in *P. honor* are indistinct because they blend in with the median crescent-shaped patch of white scales that extends distally toward the apex. This pattern contrasts with the sharply defined spots in *P. grande* and the lack of spots in *P. orocana* (Figure 57). The black dorsal forewing apex of *P. honor* extends basally to the distal end of the discal cell (Character 2), in which it is similar to *P. grande*, but differs from *P. orocana*. In the latter, blue scales separate the discal cell from the black apex (Figure 45). CO1 DNA sequences of *P. honor* also distinguish this taxon from *P. grande* and *P. orocana*. Mean forewing length is 18.4 mm (SD = 1.55,  $n = 3$ ) in males and 18.8 mm (SD = 0.0,  $n = 1$ ) in the female. We illustrate the wing pattern of each sex (Figures 28, 29) and the genitalia (Figures 88, 108).

#### TYPE MATERIAL.

**Holotype** (♂): (Figure 28) ECUADOR: Pichincha/ Mindo, Río Napombillo/ 1200 m, 26 Aug 1999/ K. R. Willmott [rectangular, white, printed], USNM ENT 00171673 [rectangular, white, printed barcode label], Holotype ♂/ *Paraspiculatus honor*/ Busby, Robbins & Hall [rectangular, red, printed]. Deposited in USNM.

**Paratypes** (2♂, 1♀): ECUADOR, Pichincha, 5 km Nanegal-García Moreno Rd, 0°09.4'N, 78°39.4'W, 02 Jun 2015, (1,375–1,700 m), 1♂ (RCB); 16 Jun 2012, 1♀ (RCB); Charchi, Chical, 0°57.7'N, 78°12.2'W, 1391 m, 19 Aug 2016, 1♂ (RCB).

**Other Material Examined** (2♂): COLOMBIA, [no further locality data], 2♂ (AMNH).

**FEMALE.** (Figure 29) The female of *P. honor* was recognized by its CO1 DNA sequence. It was found in the same location as the male paratype, a montane habitat 30 km distant from where the male holotype was collected.

**ETYMOLOGY.** This beautiful, rare butterfly is named for Honor Leslie-Melville, at the request of Keith Willmott and Julia Robinson Willmott, in celebration of the friendship and support of the Leslie-Melville family over many years. Keith Willmott and Jason Hall were first to discover this species in Ecuador. The name is a noun in apposition.

**GENITALIA.** (Figures 88, 108) The male and female genitalia are typical of *Paraspiculatus*. The distal cornutus is minute.

**DISTRIBUTION.** (Figure 121) Northwestern Ecuador and Colombia. We assume the two specimens labeled “Colombia S.A., collected by Felipe Ovalle” are from western Colombia as most specimens collected by him occur in western Colombia.

**HABITAT.** *Paraspiculatus honor* inhabits wet montane forest from 1,200–1,700 m elevation.

**BEHAVIOR.** The holotype was attracted to a trap baited with rotting fish (JHKW, personal communication). Another male was attracted to a leaf baited with rotting fish.

### *Paraspiculatus orocana* (H. H. Druce, 1912)

FIGURES 30, 45, 57, 68, 77, 89, 113, 120, 126–130

**UPDATED DIAGNOSIS AND DESCRIPTION.** Males of *P. orocana* (Figure 30) are separated from *P. honor* and *P. grande* by the presence of blue scales on the dorsal forewing

between the distal end of the discal cell and broad black border (Character 2). Two characters on the ventral forewing that distinguish *P. orocana* from the other species in *Paraspiculatus* (except for *P. honor*) are (1) a crescent-shaped patch of white scales along the distal side of the costa and (2) a single postmedian blue spot (occasionally two) instead of a line composed of between four and seven spots and line segments.

The original description by Druce (1912) distinguishes *P. orocana* from *P. orobia* based on “black [dorsal] veins and tail” in the latter. Our study material shows that the dorsal black veins occur in many *Paraspiculatus* species including *P. orocana* and that the amount of black varies intraspecifically and with age of the specimen. Druce also mentions the scarcity of “metallic green scales towards the anal angle” in *P. orocana*. As in the case of black dorsal veins, this character is highly variable and of little diagnostic value.

**FEMALE.** Unknown. Females of *P. honor* and *P. grande* share the same dorsal wing pattern (dark gray with basal blue), suggesting that females of *P. orocana* will be similar.

**GENITALIA.** (Figure 89) The male genitalia are typical of *Paraspiculatus*.

**DISTRIBUTION.** (Figure 120). *Paraspiculatus orocana* is widely distributed in the eastern Andes.

**HABITAT.** *Paraspiculatus orocana* inhabits forest from 1,250 to 1,600 m elevation in Ecuador, but the holotype from Peru was collected at 900 m. For this reason, we tentatively classify it as a lower montane species.

**BEHAVIOR.** In Ecuador, the males in our study material were attracted to rotting fish in traps (12 individuals) and on leaves (one individual).

**MATERIAL EXAMINED** (31♂). ECUADOR, *Morona Santiago*, 14 km W of Macas (Río Abanico), [2°15.4'S, 78°11.7'W], 1600 m, 12 Sep 1999, 1♂ (RCB); 2 km N of San Isidro, 2°11.9'S, 78°09.4'W, 1250–1450 m, 07 Jan 2013, 1♂ (RCB); 14 Aug 2011, 1♂ (CF), 12 Sep 2016, 1♂ (RCB); 13 Sep 2016, 2♂ (RCB); 14 Sep 2015, 1♂ (RCB); 19 Sep 2012, 1♂ (RCB); 29 Sep 2015, 1♂ (RCB); 29 Sep 2016 1999, 1♂ (RCB); 30 Sep 2016, 1♂ (RCB); 28 Nov 2011 1999, 2♂ (CF); Bosque de Domono, 2°11.0'S, 78°06.2'W, 1325 m, 16 Sep 2003, 1♂ (RCB); *Napo*, 49 km Tena-Loreto Rd., 0°42.9'S, 77°44.4'W, 1350 m, Nov 2012, 1♂ (RCB); *Pastaza*, N of Mera, 1350 m, Jul 2015, 1♂ (JHKW); *Tungurahua*, El Tigre, Topo, 14 Aug 1998, 1♂ (CF); *Zamora Chinchipe*, 5 km W of Zamora (Qbda. de Chorillos), 1250 m, Apr 1995, 1♂ (JHKW); May 2000, 3♂ (JHKW); 17 May 2000, 3♂ (RCB); 19 Sep 2001, 1♂ (RCB); Zamora, 4°04.5'S, 78°58.1'W, 06 Oct 2002, 1♂ (RCB); 08 Oct 2002, 1♂ (RCB). PERU, *San Martin*, Afluente, 7°18'S, 77°12'W, 1,350 m, 01 Aug 2007, 1♂ (CF); El Porvenir, 900 m, Oct 1909, 1♂ holotype (BMNH); Jorge Chaves, 1400 m, Nov 2003, 1♂ (MC). BOLIVIA, [La Paz], Nor Yungas, Caranavi, 1000–1500 m, Jan 2003, 1♂ (MC).

### PARASPICULATUS COLOMBIENSIS SPECIES COMPLEX

*Paraspiculatus colombiensis*, *P. azul*, *P. sine*, *P. noemi*, *P. lilyana*, and *P. emma* form a monophyletic lineage we call the

*P. colombiensis* species complex. In males, the scales on the distal part of the ventral forewing posterior to vein  $Cu_2$  are dull bluish gray (Character 9, Figures 60–64), in contrast to other members of the genus, where these scales are brown or brownish gray (Figures 53–59). Other characteristic male traits (not necessarily unique within *Paraspiculatus*) are (1) blue and black wing scales (Figures 71–73) in the basal half of the dorsal hindwing anterior to vein Rs (Character 13) that do not differ from scales on other parts of the wing, (2) an area of iridescent, blue or silver-blue scales (Figures 66, 67) posterior to the cubital vein of the ventral hindwing (Character 7), (3) a rounded hindwing (Character 11), and (4) a black forewing border (Figures 48–52) with a concave inner edge (Character 3). Phylogenetic analysis of DNA sequences also shows this lineage to be monophyletic.

The females of *P. colombiensis* and *P. azul* are brown dorsally without blue scales as in *P. orobia* and *P. orobiana*. The other females in this complex are unknown.

### ***Paraspiculatus emma* Busby and Robbins, new species**

FIGURES 31, 48, 60, 69, 90, 113, 121, 126–130

**DIAGNOSIS AND DESCRIPTION.** Males of *Paraspiculatus emma* are distinguished from others in the *P. colombiensis* species group by (1) a wider black border on the dorsal forewing, and (2) less blue at the hindwing apex in cell  $Rs-M_1$  (Character 14). The silver-blue iridescent scales found on the posterior side of the cubital vein (Figure 69) are not as prominent on the anterior side as in the other species of this group. The white scales along the costa of the ventral forewing in *P. emma* are lumped into two patches, a trait shared with *P. colombiensis* and *P. noemi*. The hindwing in *P. emma* has no tails, a character also found in *P. sine* and *P. lilyana*. Mean forewing length is 16.3 mm (SD = 0.92,  $n = 38$ ) in males. We illustrate the wing pattern (Figure 31) and male genitalia (Figure 90).

**FEMALE.** Females of *P. emma* are unknown.

#### **TYPE MATERIAL.**

**Holotype** (♂): (Figure 31) ECUADOR: Napo/ 14 km Tena–Puyo Road/ 1°06.7'S, 77°46.9'W 600 m/ 21 September 2005 (Apuya/ Robert C. Busby, leg. [rectangular, white, printed], 11:00 hrs/ 5 m [rectangular, white, handwritten, blue ink], USNM ENT 00180812 [rectangular, white, printed barcode label], GENITALIA No./ 2013: 69 ♂/ C. FAYNEL [rectangular, green, printed], Holotype ♂/ *Paraspiculatus emma* Busby & Robbins [rectangular, red, printed]. Deposited in USNM.

**Paratypes** (51♂): ECUADOR, Napo, 14 km Tena–Puyo Road, 1°06.7'S, 77°46.9'W 600 m, Apuya, 05 Aug 2012, 1♂ (USNM); 28 Aug 2009, 2♂ (RCB); 06 Sep 2009, 1♂ (RCB); 9 Sep 2006, 1♂ (USNM); 9 Sep 2010, 1♂ (USNM); 10 Sep 2010, 1♂ (RCB); 11 Sep 2016, 1♂ (RCB); 13 Sep 2005, 1♂ (USNM); 20 Sep 2011, 1♂ (RCB); 21 Sep 2005, 1♂ (USNM); 21 Sep 2011, 2♂ (USNM), 1♂ (RCB); 23 Sep 2008, 5♂ (RCB), 2♂ (USNM); 23 Sep 2010, 1♂ (RCB); 24 Sep 2011, 1♂ (RCB); Oct 2005, 1♂ (USNM); 2–3 Oct 1997, 1♂ (RCB); 11 Oct 2011, 1♂ (USNM); 12 Oct 2011, 2♂ (RCB); 18 Oct 2010, 1♂ (RCB); 22

Oct 2010, 1♂ (USNM); Nov 2011, 1♂ (CF); 12 Nov 2011, 1♂ (MECN); 03 Jan 2012, 1♂ (RCB); 08 Jan 2011, 1♂ (MECN), 1♂ (RCB); 13 Jan 2010, 1♂ (MECN); 17 Jan 2011, 2♂ (RCB); 18 Jan 2011, 1♂ (USNM); 07 Mar 2009, 1♂ (USNM); 11 Mar 2005, 1♂ (RCB); 28 km Tena–Puyo Road, 1°11.3'S, 77°49.9'W, 800 m, El Capricho, 05 Aug 2012, 1♂ (RCB); 11 Sep 2006, 1♂ (USNM); 04 Jan 2007, 1♂ (USNM); Río Pimpilala (SW of Talag), 1°04.6'S, 77°56.2'W, 600–900 m, Jul 2004, 1♂ (USNM); 23 Sep 2010, 1♂ (MECN); Dec 2005, 1♂ (RCB); 07 Jan 2006, 1♂ (RCB); 12 km Tena–Puyo Road (Finca San Carlo), 1°05.3'S, 77°47.4'W, 600 m, 02 Oct 2013, 1♂ (RCB), 23 Sep 2008, 1♂ (USNM); Morona Santiago, Bomboiza nr. Gualaquiza, 850 m, Jul 1993, 1♂ (JHKW).

**Other Material Examined** (2♂): ECUADOR, Morona Santiago, Nueva Tarqui, 15 Sep 2000, 1♂ (RCB). PERU, [Loreto], Balsapuerto, [5°50'S, 76°36'W], 1♂ (MNHN). These specimens were not made paratypes because their elevations are uncertain. The elevation of Nueva Tarqui is 900 m with nearby ridges over 1,150 m. The elevation of Balsapuerto, Peru is 200 m (Lamas, 1976). However, at the time that the Peruvian male of *P. emma* was collected, there was a well-frequented trail between Moyobamba and Balsapuerto that went through the mountains southwest of Balsapuerto. It is unclear if this specimen was collected in Balsapuerto, which is at lower elevation than the paratypes listed above, or at higher elevation on this trail.

**ETYMOLOGY.** We name this beautiful species *P. emma* in honor of Emma Rose Hughes, granddaughter of Robert C. Busby. The name is a noun in apposition.

**GENITALIA.** (Figure 90) The genitalia are typical of *Paraspiculatus*, but lack evident distinctive traits.

**DISTRIBUTION.** (Figure 121) Eastern slope of the Andes in Ecuador and Peru.

**HABITAT.** Wet lower montane forest. The majority of specimens were sampled in a relatively small area in Napo Province at an elevation range of 600–900 m.

**BEHAVIOR.** Males are attracted to traps baited with rotting fish.

**REMARKS.** *Paraspiculatus emma* is sympatric with four of the other five species in the *P. colombiensis* species complex (excluding *P. noemi*) in eastern Ecuador at 800 m elevation.

### ***Paraspiculatus sine* Busby and Robbins, new species**

FIGURES 2, 32, 49, 61, 66, 91, 98, 113, 123, 126–130

**DIAGNOSIS AND DESCRIPTION.** Males of *Paraspiculatus sine* are distinguished from the other species in the *P. colombiensis* group by the unique pattern of white scales along the costa of the ventral forewing (Character 6). These scales form a narrow band that extends distally from the anterior part of the postmedian line to the apex (Figure 61). White scales almost always cover part of the dark submarginal band in the apex. In contrast, *P. colombiensis* (Figure 62), *P. noemi*, and *P. emma* (Figure 60) have two separate patches of white scales, one median and one at the apex, and *P. azul* (Figure 63) and *P. lilyana* (Figure 64) lack

white scales along the ventral forewing costa. Another trait of *P. sine* is the round hindwing with no tail (shared with *P. lilyana* and *P. emma*). The dorsal color in the limbal part of the forewing in *P. sine* has a “grainy” appearance caused by the intermixing of many black scales (Figure 49), which contrasts with the much smoother look of *P. azul* and *P. lilyana* (Figures 51, 52). Mean male forewing length is 16.9 mm (SD = 1.11,  $n = 18$ ). We illustrate the wing pattern (Figure 32) and male genitalia (Figure 91).

**FEMALE.** Females of *P. sine* are unknown.

**TYPE MATERIAL.**

**Holotype** (♂): (Figure 32) ECUADOR. Morona Santiago/ 15 km S of Gualaquiza/ 3°27.6'S, 78°33.1'W 850 m/ 16 September 2000/ Robert C. Busby, leg. [rectangular, white, printed], USNM ENT 00180851 [rectangular, white, printed barcode label], GENITALIA No./ 2013. 58 ♂/ C. FAYNEL [rectangular, green, printed], Holotype ♂/ *Paraspiculatus sine* / Busby and Robbins [rectangular, red, printed]. Deposited in USNM.

**Paratypes** (23♂): ECUADOR, Morona Santiago, 15 km S of Gualaquiza [Bomboiza], 3°27.6'S, 78°33.1'W, 850 m, Jul 1993, 1♂ (JHKW); 16 Sep 2000, 1♂ (USNM); 29 Sep 2000, 1♂ (USNM); 05 Oct 2002, 1♂ (RCB); 2 km N of San Isidro, 2°11.9'S, 78°09.4'W, 1,250–1,400 m, 29 Jan 2014, 1♂ (RCB); 13 Sep 2014, 1♂ (MECN), 1♂ (RCB); 16 Sep 2013, 1♂ (RCB); 17 Sep 2013, 1♂ (USNM); 30 Sep 2013, 1♂ (USNM), 1♂ (MECN); 30 Sep 2014, 1♂ (RCB); Napo, 25 km S of Tena [nr. Pimpilala], 1°04.3'S, 77°56.5'W, 875 m, 08 Oct 2003, 1♂ (RCB); Río Pimpilala, 1°04.6'S, 77°56.2'W, [900 m], Nov 2008, 1♂ (USNM); Aug 2016, 2♂ (RCB); 28 km Tena–Puyo Road (El Capricho), 1°11.3'S, 77°49.9'W, 800 m, 05 Jan 2007, 1♂ (USNM); Zamora Chinchipe, Zamora, 4°04.5'S, 78°58.1'W, 1,450 m, 08 Oct 2002, 1♂ (RCB); 10 km Los Encuentros–El Pangui Rd., 3°42.2'S, 78°36.0' , 1,000–1,200 m, 04 Oct 2007, 1♂ (RCB); Pastaza, 25 km N of Puyo, 1,000 m, 9–11 Oct 1988, 1♂ (RCB); 37 km Puyo–Arajuno Road, 1°22.6'S, 77°42.6'W, 1,100 m, 11 Jan 2012, 1♂ (USNM); Sucumbios, Cerro Lumbaquí Norte, 0°01.7'N, 77°19.2'W, 900–1,000 m, 01 Jan 2007, 1♂ (RCB). PERU, Cusco, Carretera a Manu km 87, Chontachaca, 13°01.8'S, 71°29.7'W, 972 m, 24–25 Oct 2014, 1♂ (CF).

**ETYMOLOGY.** The name *P. sine* is derived from a nickname that we gave this species when we first began to work on *Paraspiculatus*. The name is proposed as a nonlatinized noun in apposition.

**VARIATION.** Two of 24 males examined have a band of shining blue scales on the anterior side of the cubital vein on the ventral forewing, similar to those in *P. orobia* and *P. lilyana*.

**GENITALIA.** (Figures 91, 98) The genitalia are typical of *Paraspiculatus* and lack distinctive characters. Variation in the male genitalia spiculate pad is illustrated (Figure 98).

**DISTRIBUTION.** (Figure 123) Eastern slope of the Andes in Ecuador.

**HABITAT.** *Paraspiculatus sine* inhabits wet lower montane forest from 800 to 1,450 m elevation.

**BEHAVIOR.** Males are attracted both to traps and plants (Figure 2) baited with rotting fish.

**REMARKS.** *Paraspiculatus sine* appears to be the highest-elevation species in the *P. colombiensis* complex. However, its range overlaps that of *P. emma*, *P. lilyana*, *P. azul*, and *P. colombiensis* from 800 to 900 m elevation in eastern Ecuador.

## ***Paraspiculatus colombiensis* Johnson and Constantino, 1997**

FIGURES 5, 33, 34, 50, 62, 67, 77, 92, 109, 113, 124, 126–130

**UPDATED DIAGNOSIS AND DESCRIPTION.** Males of *Paraspiculatus colombiensis* are best diagnosed using the following combination of characters: (1) blue wing scales in the basal half of the dorsal hindwing anterior to vein Rs (Character 13, shared with five species in the *P. colombiensis* species group; the exception is *P. noemi* whose scales are mostly black), (2) white scales along the costa in the distal part of the ventral forewing (Character 6, excludes *P. azul* and *P. lilyana*), (3) the white scales on the ventral forewing divided into two parts—one median and one near the apex (character not coded, excludes *P. sine*), and (4) relatively narrow dorsal forewing black margin near the tornus (character not coded, excludes *P. emma* whose forewing margin is much broader). Also of note, *P. colombiensis* has tails (shared with *P. noemi* and *P. lilyana*) and a somewhat darker dorsal blue color than *P. azul*, *P. lilyana*, or *P. sine*. Unfortunately, characters such as the presence or absence of tails and color differences become less reliable in old specimens.

The original diagnosis by Johnson and Constantino is confusing because it mainly focuses on differences between *P. colombiensis* and the “traditional *orobia*-Group” (*P. orobia*, *P. orocana*, and *P. orobiana*). These species have different wing patterns, and the diagnostic comparisons do not apply in every case. The only specific comparison of *P. colombiensis* to *P. orobia* is based on ventral ground color, which is highly variable and of no diagnostic value.

**FEMALE.** (Figure 34) The female was associated with the male using CO1 DNA sequences.

**GENITALIA.** (Figures 92, 109) The genitalia of *P. colombiensis* are typical of *Paraspiculatus*, but lack evident distinctive traits.

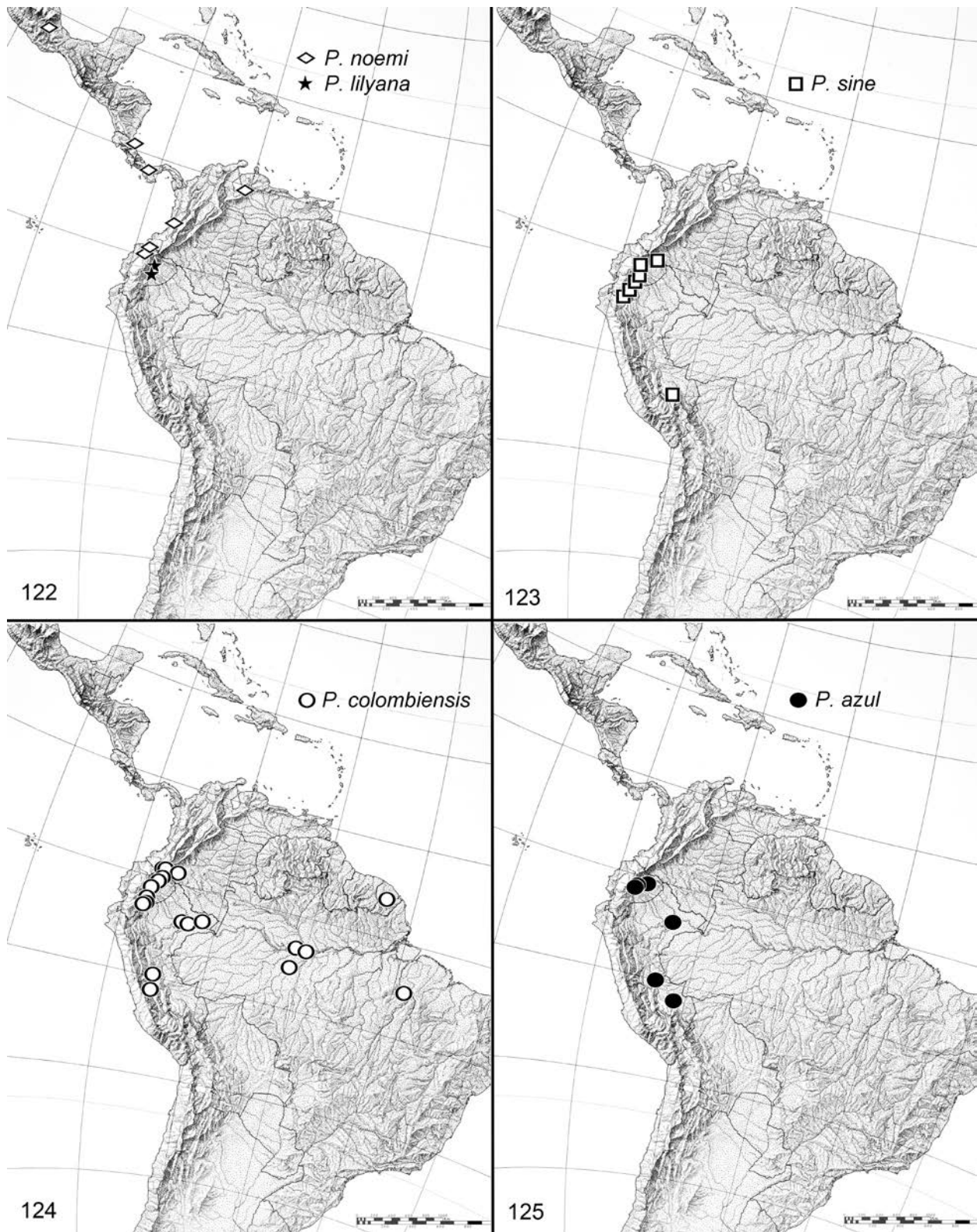
**DISTRIBUTION.** (Figure 124) *Paraspiculatus colombiensis* is widely distributed throughout the Amazon region.

**HABITAT.** *Paraspiculatus colombiensis* inhabits wet forest from approximately 100 to 1,300 m elevation.

**BEHAVIOR.** Males in the upper Amazon Basin are attracted to traps baited with rotting fish. Recently, six females of *P. colombiensis* were collected on traps at Santiago, Morona Santiago, Ecuador. These are the first records of female *Paraspiculatus* coming to bait and is especially interesting because Santiago has been sampled for years without encountering females.

**REMARKS.** Bálint and Moser (2001) synonymized *P. colombiensis* with *P. orobia* based on a misidentified individual of the latter. Robbins (2004b) corrected this error, listing both as distinct species.





FIGURES 122–125. Geographic distributions. 122. *P. noemi* (diamonds), *P. lilyana* (stars). 123. *P. sine* (squares). 124. *P. colombiensis* (circles). 125. *P. azul* (bullets).

**MATERIAL EXAMINED** (210♂, 10♀). **FRENCH GUIANA**, Saül, 12 Jun 2005, 1♂ (CF). **COLOMBIA**, [Putumayo], Umbría, 1♂ (MNHN); Mocoa, Oct 1927, 1♂ (MNHN); [Caqueta], Río Ortequaza, 400 m, 15 Sep 1947, 1♂ holotype (MNHN). **ECUADOR**, *Morona Santiago*, 1.8 km Santiago–Puerto Morona Rd, 3°02.4'S, 77°59.7'W, 350–500 m, 13 Jan 2011, 1♂ (RCB); 19 Sep 2006, 2♂ (RCB); Aug 2015, 1♂ (JHKW); 10 km E of Yanganza, 2°50.0'S, 78°15.0'W, 800 m, Sep 2003, 3♂ (RCB); 15 km S of Gualaquiza, 3°27.6'S, 78°33.1'W, 800 m, May 1994, 1♂ (JHKW); 15 Sep 2000, 2♂ (RCB), 1♀ (RCB); 16 Sep 2001, 2♂ (RCB), 27 Sep 2000, 1♂ (RCB); 29 Sep 2000, 3♂ (RCB); 05 Oct 2002, 1♂ (RCB); 24.5 km Santiago–Puerto Morona Rd, 2°58.1'S, 77°50.5'W, 600 m, 13 Sep 2011, 1♂ (RCB); 17 Sep 2010, 1♂ (RCB); 22 Sep 2012, 2♂ (RCB); 26 Sep 2013, 1♂ (RCB); 26 km Santiago–Puerto Morona Rd, 2°58.4'S, 77°49.9'W, 550 m, 17 Sep 2005, 2♂ (RCB); 32.8 km Santiago–Puerto Morona Rd, 2°58.9'S, 77°48.1'W, 670–750 m, 26 Sep 2014, 1♀ (RCB); 26 Sep 2016, 2♂ (RCB); 27 Sep 2014, 1♂ (RCB); 28 Sep 2014, 1♂ (RCB); 29 Sep 2014, 1♂ (RCB); 47.6 km Santiago–Puerto Morona Rd, 2°56.2'S, 77°44.8'W, 245 m, 24 Sep 2013, 4♂ (RCB); 24 Sep 2014, 1♂ (RCB); 25 Sep 2014, 1♂ (RCB); 53.1 km Santiago–Puerto Morona Rd, 2°55.0'S, 77°42.7'W, 210 m, 17 Sep 2016, 1♂ (RCB); 27 Sep 2016, 1♂ (RCB); 54.6 km Santiago–Puerto Morona Rd, 2°54.7'S, 77°42.4'W, 205 m, 14 Sep 2014, 1♂ (RCB); 25 Sep 2014, 1♂ (RCB); Santiago (Hill North of Town), 3°02.3'S, 78°00.3'W, 350 m, 06 Jan 13, 1♂ (RCB); 06 Jan 13, 1♂ (RCB); 07 Jan 16, 1♂ (RCB); 08 Jan 15, 2♂ (RCB); 11 Jul 14, 1♂ (RCB); 31 Aug 2009, 1♂ (RCB); 01 Sep 2009, 1♂ (RCB); 14 Sep 2014, 1♂ (RCB); 14 Sep 2015, 1♂ (RCB); 15 Sep 2011, 2♂ (RCB); 16 Sep 2011, 2♂ (RCB); 16 Sep 2014, 2♂ (RCB); 16 Sep 2016, 1♂ (RCB); 17 Sep 2011, 3♂ (RCB); 17 Sep 2015, 1♂ (RCB); 18 Sep 2011, 2♂ (RCB); 18 Sep 2015, 1♂ (RCB); 19 Sep 2015, 1♂ (RCB); 20 Sep 2010, 1♂ (RCB); 21 Sep 2012, 2♂ (RCB); 22 Sep 2016, 2♂ (RCB); 23 Sep 2012, 1♂ (RCB); 23 Sep 2014, 2♂ (RCB), 1♀ (RCB); 23 Sep 2015, 1♂ (RCB); 24 Sep 2015, 1♂ (RCB); 25 Sep 2012, 1♂ (RCB); 25 Sep 2013, 7♂ (RCB); 25 Sep 2015, 1♀ (RCB); 26 Sep 2014, 1♂ (RCB), 1♀ (RCB); 26 Sep 2016, 2♂ (RCB); 27 Sep 2013, 4♂ (RCB); 27 Sep 2014, 1♀ (RCB); 28 Sep 2012, 1♂ (RCB); 28 Sep 2014, 1♀ (RCB); 29 Sep 2012, 1♂ (RCB); 29 Sep 2014, 1♂ (RCB); 15 Oct 2011, 4♂ (RCB); 23 Oct 2013, 4♂ (RCB); 29 Oct 2013, 1♂ (RCB); 3 km Bella Union–Patuca Rd, 650 m, 20 Sep 2012, 2♂ (RCB); Nueva Tarqui, [1000 m], 15 Sep 2000, 1♂ (RCB); Yaupi, 300 m, Sep 2010, 1♂ (JHKW); *Napo*, 12 km Tena–Puyo Rd (Finca San Carlo), 1°05.3'S, 77°47.4'W, 600 m, 18 Jan 2011, 1♂ (RCB); Sep 1996, 1♂ (JHKW); 12 Sep 2010, 1♂ (RCB); 23 Sep 2008, 1♂ (RCB); 01 Oct 2012, 2♂ (RCB); 14 km Tena–Puyo Rd (Apuya), 1°06.7'S, 77°46.9'W, 600 m, 03 Jan 2006, 1♂ (RCB); 03 Jan 2012, 1♂ (RCB); 03 Jan 2016, 1♂ (RCB); 11 Jan 2013, 1♀ (RCB); 14 Jan 2012, 1♂ (RCB); 17 Jan 2011, 3♂ (RCB); Apr 2006, 1♂ (RCB); May 2009, 1♂ (RCB); 06 Sep 2009, 2♂ (RCB); 06 Sep 2011, 2♂ (RCB); 10 Sep 2016,

2♂ (RCB); 11 Sep 2005, 1♂ (RCB); 12 Sep 2005, 1♂ (RCB); 13 Sep 2005, 1♂ (RCB); 15 Sep 2013, 1♂ (RCB); 21 Sep 2005, 1♂ (RCB); 23 Sep 2008, 3♂ (RCB); 24 Sep 2011, 1♂ (RCB); Oct 2010, 2♂ (RCB); 02 Oct 2013, 1♂ (RCB); 03 Oct 2013, 2♂ (RCB); 04 Oct 2013, 2♂ (RCB); 12 Oct 2011, 1♂ (RCB); 12–14 Oct 1996, 1♂ (RCB); 13 Oct 2011, 1♂ (RCB); 17 Oct 2010, 1♂ (RCB); 18 Oct 2010, 1♂ (RCB); 12 Nov 2011, 1♂ (RCB); Dec 1996, 2♂ (JHKW); 28 km Tena–Puyo Rd (El Capricho), 1°11.3'S, 77°49.9'W, 800 m, 12 Sep 2006, 1♂ (RCB); 6.7 km SW of Puerto Napo (Yutzupino), 1°04.3'S, 77°49.8'W, 600 m, 22 Sep 2011, 2♂ (RCB); 02 Oct 2012, 1♂ (RCB); NW of Misahuallí, 1°01.5'S, 77°39.4'W, 610 m, 18 Oct 2000, 1♀ (USNM); Río Pimpilala (SW of Talag), 1°04.6'S, 77°56.2'W, 900 m, 04 Jan 2006, 1♂ (RCB); 600 m, Sep 1996, 1♂ (JHKW); 20 km Puerto Napo–La Punta Rd, 1°03.0'S, 77°40.8'W, 500 m, 23 Sep 2005, 1♂ (RCB); *Orellana*, 22 km Loreto–Payamino Rd, 0°34.9'S, 77°24.4'W, 825 m, 15 Jan 2012, 1♂ (RCB); nr. Coca (Río Napo), 0°28.0'S, 76°59.0'W, 300 m, 22 Oct 2005, 1♂ (JHKW); upper Río Tiputini (Coca–Tiguino Rd), 300 m, Sep 1996, 1♂ (JHKW); *Pastaza*, 39.4 km Puyo–Villano Rd, 1°25.6'S, 77°43.8'W, 750 m, 03 Jan 2016, 1♂ (RCB); 11 Sep 2016, 1♂ (RCB); 02 Oct 2015, 2♂ (RCB); 02 Oct 2016, 2♂ (RCB); Pitirishca, 1°57.8'S, 77°52.1'W, 800 m, 07 Sep 1999, 1♂ (RCB); 20 Sep 1998, 2♂ (RCB); 24 Sep 1999, 2♂ (RCB); *Sucumbios*, 16 km Lumbacui–La Troncal Rd, 0°00.8'S, 77°15.0'W, 400–500 m, 25 Aug 2009, 1♂ (RCB). **PERU**, *Huánuco*, Pangana, 230 m, Jun 2013, 1♂ (MC); *Junín*, Chanchamayo (Río Ulcumayo), 10°59.0'S, 75°27.0'W, 1250–1370 m, 3♂ (USNM); Pampa Hermosa, 11°02.0'S, 75°24.0'W, 1300 m, 09 Oct 2003, 1♂ (MUSM); 10°59.0'S, 75°25.4'W, 1230 m, 30 Sep 2008, 1♂ (MUSM); *Loreto*, Contaya, 16 Oct 2008, 1♂ (CF); 24 Oct 2008, 1♂ (CF); Iquitos, 100 m, Jul 2002, 1♂ (MC); Sept 2006, 1♂ (MC); El Milagro, 21 km Iquitos–Nuata Rd, Oct 2010, 1♂ (CF); km 28 Iquitos–Nauta Rd, 03°59.0'S, 73°26.0'W, 180 m, 30 Oct 2003, 1♂ (USNM); Nueva Esperanza, Feb 2012, 1♂ (CF); San Pablo, 04°01'S, 71°06'W, 100 m, Feb 2011, 1♂ (CF); Pévas, 03°59.0'S, 73°26.0'W, 180 m, 01 Feb 2011, 1♂ (CF); Picuroyacu, 03°37.0'S, 71°15.0'W, 126 m, 01 Feb 2011, 1♂ (CF); 10 Nov 2008, 1♂ (CF); *Madre de Dios*, 30 km SW Puerto Maldonado, 300 m, 27 Oct 1983, 1♂ (USNM); 50 km WSW Puerto Maldonado, 12°45.0'S, 69°35.0'W, 250 m, Sep–Nov 1992, 1♂ (USNM); Boca Río La Torre, 300 m, 26 Oct 1983, 1♀ (USNM); 29 Oct 1983, 1♂ (USNM); Parque Manu, Pakitza, 11°55.8'S, 71°15.3'W, 340 m, 05 Oct 1991, 1♂ (USNM); 10 Oct 1991, 1♂ (USNM); 13 Oct 1991, 1♂ (USNM); 14 Oct 1991, 1♂ (USNM); 400 m, 1♂ (USNM); *Pasco*, La Salud, [1200 m], 28 May 1942, 1♂ (LACM); *San Martín*, Rioja, Dec 2004, 1♂ (MC); *Ucayali*, Pucallpa, 150 m, Aug 2005, 1♂ (MC). **BOLIVIA**, [Santa Cruz], Buena Vista, 450 m, 22 Feb 1927, 1♂ (MNHN). **BRAZIL**, *Acre*, Bujari, Sena Madureira, 200 m, 12 Sept 2003, 1♂ (MC); *Amazonas*, Manicore, 18 Dec 1924, 1♂ (MNHN); Tonantins, Jul–Sep 1880, 1♂ (BMNH); Uypiranga, Jul–Sep 1880, 1♂ (BMNH); *Rondonia*, Alto Paraíso, Rio Candeias, 6 Aug 1998, 1♂ (MC).



***Paraspiculatus azul* Busby, Robbins,  
and Faynel, new species**

FIGURES 35, 36, 51, 63, 72, 93, 96, 110, 113, 125, 126–130

**DIAGNOSIS AND DESCRIPTION.** Males of *Paraspiculatus azul* are distinguished from other members of the *P. colombiensis* group by (1) the lack of white scales in the distal part of the ventral forewing (Character 6), shared with *P. lilyana* (Figures 63, 64), (2) the presence of blue scales (in most specimens) anterior of vein Rs in the apex of the dorsal hindwing ((Figure 72), character not coded, shared with some specimens of *P. noemi*), and (3) a lighter dorsal blue color with a very smooth, non-grainy appearance ((Figure 51), character not coded, shared with *P. lilyana*). The “smooth look” is a result of a uniform pattern of blue wing scales, with few intermixed black scales. This phenotype contrasts with *P. noemi* and *P. sine* (Figure 49) which have significant intermixing of black scales, especially in the distal area of the forewings. Another character that is almost always present in *P. azul* is a tiny patch of shining blue scales on the ventral forewing at the junction of veins Cu<sub>1</sub> and Cu<sub>2</sub> (Figure 63). However, the diagnostic value of this trait is less important because similar blue scales are occasionally found in *P. sine*, *P. colombiensis*, and *P. noemi*. *Paraspiculatus azul* is separated from its nearest relative, *P. lilyana*, by the lack of a broad band of shining blue scales anterior of the cubital vein on the ventral forewing and the presence of tails on the hindwing. *Paraspiculatus azul* is most easily confused with *P. colombiensis*, but is differentiated by its lighter blue dorsal color, lack of white scales along the ventral forewing costa, and more pronounced submarginal band on the ventral forewing. Mean forewing length is 16.9 mm (SD = 0.68, *n* = 15) in males and 15.7 mm (SD = 1.41, *n* = 2) in the females. We illustrate the wing pattern of each sex (Figures 35, 36) and their genitalia (Figures 93, 110).

**FEMALE.** (Figure 36) The brown female of *P. azul* was recognized by its CO1 DNA sequence. As in the male, the female ventral forewing lacks white scales along the costa.

**TYPE MATERIAL.**

**Holotype** (♂): (Figure 35) ECUADOR: Napo/ 14 km Tena–Puyo Road/ 1°06.7'S, 77°46.9'W 600 m/ 12 November 2011 (Apuya)/ I. Aldas, R. C. Busby, leg. [rectangular, white, printed], USNM ENT 00180848 [rectangular, white, printed barcode label], Trap [rectangular, white, handwritten, black ink], GENITALIA No./ 2013: 54 ♂/ C. FAYNEL [rectangular, green, printed], Holotype ♂/ *Paraspiculatus azul* / Busby, Robbins, and Faynel [rectangular, red, printed]. Deposited in USNM.

**Paratypes** (11♂, 1♀): ECUADOR, Napo, 14 km Tena–Puyo Road, 1°06.7'S, 77°46.9'W, 600 m, (Apuya), 07 Mar 2009, 1♂ (USNM); 13 Sep 2005, 1♂ (RCB); 24 Sep 2005, 1♂ (USNM); 22 Oct 2010, 1♂ (RCB); 1 km NE of Misahuallí, 1°01.5'S, 77°39.4'W, 575 m, 09 Oct 2003, 1♂ (USNM); 12 km Tena–Puyo Road (Finca San Carlo), 1°05.3'S, 77°47.4'W, 600 m, Aug 2005, 1♂ (RCB); Pimpilala, Río Jatunyacu, [1°05.3'S, 77°47.4'W], 600 m, 14–15 Sep 1996, 1♂ (JHKW); Tena–Puyo Rd. [28 km],

[1°05.3'S, 77°47.4'W], 800 m, 26 Oct 1996, 1♂ (JHKW); Orellana, 1.2 km Dayuma–Cononaco Rd., 0°40.7'S, 76°52.4'W, 325 m, 06 Nov 2011, 1♂ (MECN); 16 Nov 2011, 1♂ (RCB). PERU, M. de Dios, Parque Manu Pakitza, 11°55.5'S, 71°15.2'W, 340 m, 20 Oct 1991, 1♀ (USNM); Loreto, Picuroyacu, 3°37'S, 73°15'W, 126 m, 01 Feb 2011, 1♂ (CF).

**Other Material Examined** (8♂): ECUADOR, Napo, 14 km Tena–Puyo Road, 1°06.7'S, 77°46.9'W, [600 m], (Apuya), Nov 2011, 2♂ (CF); Morona Santiago, 53.1 km Santiago–Puerto Morona Rd., 2°55.0'S, 77°42.7'W, 210 m, 26 Sep 2015, 1♂ (RCB); 27 Sep 2016, 1♂ (RCB); Pastaza, 39.4 km Puyo–Villano Rd., 1°25.6'S, 77°43.8'W, 750 m, 02 Oct 2015, 1♂ (RCB); 02 Oct 2016, 2♂ (RCB). PERU, Loreto, Iquitos, 100 m, Nov 2012, 1♂ (CF).

**ETYMOLOGY.** *Paraspiculatus azul* was originally recognized by its bright blue dorsal coloration, which distinguished it from the darker blue hues found in other species, such as *P. colombiensis*. This name is proposed as a nonlatinized noun in apposition.

**GENITALIA.** (Figures 93, 96, 110) The genitalia of *P. azul* are typical of *Paraspiculatus*, but lack evident distinctive traits. Variation in shape of the valvae and saccus are illustrated.

**DISTRIBUTION.** (Figure 125) Eastern slope of the Andes in Ecuador and Peru.

**HABITAT.** Wet lowland and montane forest from 126 to 800 m elevation.

**BEHAVIOR.** Males are attracted to traps baited with rotting fish.

**REMARKS.** *Paraspiculatus azul* and *P. lilyana* are closely related (see Phylogenetic Analyses) and sympatric in eastern Ecuador between 600 and 800 m.

***Paraspiculatus lilyana*  
Busby and Robbins, new species**

FIGURES 37, 52, 64, 71, 94, 113, 122, 126–130

**DIAGNOSIS AND DESCRIPTION.** Males of *Paraspiculatus lilyana* are distinguished from others in the *P. colombiensis* group by (1) a broad band of shining blue scales on the ventral forewing anterior of the cubital vein (Character 8, Figure 64), (2) a light dorsal blue color with a crisp black border (Figure 52), which is shared with *P. azul* (this character was not coded because it was difficult to quantify in species with more diffuse borders), (3) a ventral forewing postmedian line that often lacks white spots near the costa (Figure 64), which is shared with no other species in the *P. colombiensis* group, and (4) light brown or tan scales (not white) in the distal part of the ventral forewing along the costa (Character 6), which is shared with *P. azul*. Mean male forewing length is 16.7 mm (SD = 0.50, *n* = 10). We illustrate the wing pattern (Figure 37) and male genitalia (Figure 94).

**FEMALE.** The female is unknown.

**TYPE MATERIAL.**

**Holotype** (♂): (Figure 37) ECUADOR: Napo/ 14 km Tena–Puyo Road/ 1°06.7'S, 77°46.9'W 600 m/ 20 September



2011 (Apuya)/Robert C. Busby, leg. [rectangular, white, printed], USNM ENT 00180831 [rectangular, white, printed barcode label], 1550 hrs/ Trap [rectangular, white, handwritten, black ink], GENITALIA No./ 2013: 66 ♂/ C. FAYNEL [rectangular, green, printed], Holotype ♂/ *Paraspiculatus lilyana* / Busby and Robbins [rectangular, red, printed]. Deposited in USNM.

**Paratypes** (10♂): **ECUADOR**, *Napo*, 14 km Tena–Puyo Road, 1°06.7'S, 77°46.9'W, 600 m, 28 Aug 2009, 1♂ (RCB); 10 Sep 2010 1♂ (MECN); 12 Sep 2005, 1♂ (USNM), 1♂ (RCB); 04 Oct 2013, 1♂ (RCB); 13 Oct 2011, 1♂ (RCB); 12 km Tena–Puyo Road, 1°05.3'S, 77°47.4'W, 600 m, (Finca San Carlo), 14 Sep 2004, 1♂ (USNM); Chichicorrumi nr. Jatun Sacha, 450 m, Sep 1993, 1♂ (JHKW); *Pastaza*, Pitirishca, 800 m, 1°57.8'S, 77°52.1'W, 10 Sep 2000, 1♂ (RCB); 19 Sep 2000, 1♂ (USNM).

**ETYMOLOGY.** We name this beautiful species *P. lilyana* in honor of Lily Elizabeth Hughes, granddaughter of Robert C. Busby. The name is a noun in apposition.

**GENITALIA.** (Figure 94) The genitalia of *P. lilyana* are typical of *Paraspiculatus*, but lack evident distinctive traits.

**DISTRIBUTION.** (Figure 122) The eastern slope of the Andes in Ecuador.

**HABITAT.** *Paraspiculatus lilyana* inhabits wet montane forest from 450–800 m elevation.

**BEHAVIOR.** Males are attracted to traps baited with rotting fish.

**REMARKS.** *Paraspiculatus lilyana* and *P. azul* are closely related and sympatric in eastern Ecuador at 450–600 m elevation. *Paraspiculatus lilyana* and *P. orobia* share a broad band of shining blue scales on the ventral forewing anterior to the cubital vein (Character 8), but this represents convergence according to the phylogenetic analyses.

### ***Paraspiculatus noemi* Busby and Robbins, new species**

FIGURES 38–40, 73, 95, 97, 111, 113, 122, 126–130

**DIAGNOSIS AND DESCRIPTION.** Males of *Paraspiculatus noemi* are distinguished from the other species in the *P. colombiensis* group by the predominance of dark wing scales at the base of the dorsal hindwing costa (Character 13, Figure 73). This pattern contrasts with the other species in the group in which a majority of the scales are normally bright blue (Figures 71, 72). The scales in *P. noemi* are the same size and shape as the “regular” blue wing scales, but are predominately black, occasionally purple. The overall appearance of this area is dark and is easily distinguished from the other species in the *P. colombiensis* group. These dark scales differ from both the dark gray, iridescent scales in the *P. orocana* species group and the gray/brown scales in *P. orobia* and *P. cosmo*. Another diagnostic factor which helps to separate *P. noemi* from the other species in the *P. colombiensis* species group is the bold white triangle which is formed by a large patch of white scales (Figure 38) at the median of the ventral forewing along with the three white/light-blue spots at the anterior of the postmedian line. This basic pattern is also

shared by *P. colombiensis* and *P. emma*, but tends to be more conspicuous and consistent in *P. noemi*, especially in specimens from western Ecuador and Colombia. There is more intraspecific variation in the amount of white scales in both *P. colombiensis* and *P. emma*, although occasional specimens have a well-formed white triangle similar to those in *P. noemi*. Finally, the tails in Ecuadorian *P. noemi* are short, a character that is unique within the *P. colombiensis* species group. Unfortunately, this trait is of limited practical value because tail length is geographically variable in *P. noemi* and because the tails of worn specimens (of other “tailed species”) may be broken or absent. Mean forewing length is 19.0 mm (SD = 0.74,  $n = 14$ ) in males and 18.1 mm (SD = 0.0,  $n = 1$ ) in the female from Costa Rica. We illustrate the wing pattern (Figures 38–40) and genitalia (Figures 95, 111) of *P. noemi*.

**FEMALE.** (Figure 40) The female is associated by geographic distribution.

#### **TYPE MATERIAL.**

**Holotype** (♂): (Figure 38) **ECUADOR**: *Pichincha* 20 km Pacto–Guayabillas Road/ 0°11.6'N, 78°51.5'W 900 m/ 14 July 2011/I. Aldas, R. C. Busby, leg. [rectangular, white, printed], USNM ENT 00180855 [rectangular, white, printed barcode label], GENITALIA No./ 2013: 60 ♂/ C. FAYNEL [rectangular, green, printed], Holotype ♂/ *Paraspiculatus noemi*/ Busby and Robbins [rectangular, red, printed]. Deposited in USNM.

**Paratypes** (13♂): **ECUADOR**, *Pichincha*, 21 km Pacto–Guayabillas Road, 0°11.2'N, 78°51.8'W, 875 m, 28 May 2008, 2♂ (RCB); *Esmeraldas*, 12 km Lita–San Lorenzo Road, 0°53.1'N, 78°30.9'W, 850 m, Río Chuchuví, Mar 2003, 2♂ (RCB); 25 Mar 2011, 1♂ (USNM); 27 Mar 2011, 1♂ (USNM); May 2003, 1♂ (MECN); Jun 2004, 1♂ (RCB); Jul 2002, 2♂ (JHKW); Aug 2008, 1♂ (MECN); Calderón, 01.06 N, 78.42 W, [100 m], 18 Nov 2014, 1♂ (CF); *Carchi*, Río Sabalera, [0°11.2'N, 78°51.8'W], 500 m, Aug 2014, 1♂ (RCB).

**Other Material Examined** (4♂, 1♀): **MEXICO**, *Oaxaca*, Sierra Juarez (Gulf Slope), 2500 ft, April 1992, 1♂ (USNM). **COSTA RICA**, *Heredia*, La Selva, 10°26'N, 84°01'W, 50–100 m, 11 Jul 1993, 1♀ (USNM). **PANAMA**, Veraguas, 1♂ (BMNH). **COLOMBIA**, *Cauca*, Juntas, [2°27'N, 76°36'W], fin [Aug or later] 1897–Jan 1898, 1♂ (BMNH). **VENEZUELA**, Merida, Briceno, 1♂ (BMNH).

**ETYMOLOGY.** We name *P. noemi* in honor of Noemi Patiño Artega, wife of Ismael Aldas Villafuerte, who made significant contributions to the study of *Paraspiculatus* through his field work at the type locality and elsewhere in Ecuador. The name is a noun in apposition.

**VARIATION.** In contrast to specimens from western Ecuador, the three *P. noemi* from Mexico and Central America have fewer white scales along the ventral costa of the forewing. Two of these three specimens have longer tails than those from Ecuador. The Mexican male has more blue at the apex of the dorsal hindwing anterior to vein Rs than the Ecuadorian males. Although CO1 DNA sequences from the Mexican male cluster with those from western Ecuador, they are also slightly divergent (Figure 113).

**GENITALIA.** (Figures 95, 97, 111) The genitalia of *P. noemi* are typical of *Paraspiculatus*, but lack evident distinctive traits. Variation in the spiculate pad is illustrated.

**DISTRIBUTION.** (Figure 122) Transandean. Mexico throughout Central America to the western slope of the Andes in northwestern Ecuador and to northern Venezuela.

**HABITAT.** Wet montane forest from 50–800 m elevation.

**BEHAVIOR.** Males are occasionally attracted to traps with rotting fish. Two individuals from Ecuador were attracted to leaves baited with fish (vouchers in RCB).

**REMARKS.** The Mexican and Central American part of the range of *P. noemi* is representative of the remarkable rarity of most *Paraspiculatus* in museum collections. In the approximately 135 years since Godman and Salvin (1887–1901) first reported it in Panama (originally identified as *Thecla orobia*), only one male and one female *P. noemi* have subsequently been collected in Mexico and Central America.

As documented, *P. noemi* varies geographically. That the Mexican and Central American specimens represent a species distinct from *P. noemi*—rather than a geographic variant—is a viable alternate hypothesis, but we lack sufficient supporting evidence.

*Paraspiculatus noemi* and *P. colombiensis* are not sister species on the consensus cladogram shown below in Phylogenetic Analyses. Male wing pattern differences between them are consistent, and male *P. colombiensis* (mean wing size 17.4 mm) are statistically smaller than male *P. noemi* ( $t$  test, unequal variances,  $t = 5.13$ ,  $df = 43$ ,  $p < 0.0001$ ). Despite these differences, phylogenetic resolution in the *P. colombiensis* group is not robust, and we would not be surprised if further molecular data showed that these two species are geographically allopatric phylogenetic sisters.

## PHYLOGENETIC ANALYSES

Equal-weight parsimony for the morphological matrix analysis yielded four trees of 57 steps. Implied-weight parsimony analysis ( $K = 1000, 100, 10, 3$ ) resulted in one tree, which is also one of the equal-weight trees (Figures 126, 127). Since it is the shortest tree in all analyses, we consider it to be the best estimate of phylogeny based on morphology. Bootstrap support values are given in Figure 126. *Paraspiculatus* monophyly was supported by five synapomorphies, but the only one unique to *Paraspiculatus* within the Eumaeini is the spiculate pad (Character 23). It is appropriate that the genus was named for this feature.

Analyses of the molecular data set yielded a variety of trees. We derived the best maximum likelihood tree in Garli (Figure 128). There were 20 trees of 271 steps in the equal-weight parsimony analysis, two trees (271 equal-weight steps) with the implicit-weight parameter  $K = 1000$  or 100, two trees with  $K = 10$  (both 272 steps), and one tree with  $K = 3$  (276 steps).

Analysis of the combined morphology and molecular matrix resulted in 40 trees of 334 steps in equal-weight parsimony,

one 334-step tree in implied-weight parsimony ( $K = 1000, 100$ , and 10), and one 335-step tree in implied-weight parsimony ( $K = 3$ ) (Figure 129).

Despite the number of trees resulting from the analyses of the molecular and morphology data sets, some results were consistent. Each of the 17 *Paraspiculatus* species for which we had molecular data (an average of six specimens per species) was monophyletic in the resulting trees. The six-species *P. colombiensis* complex (*P. emma*, *P. sine*, *P. colombiensis*, *P. azul*, *P. lilyana*, and *P. noemi*) was monophyletic in all analyses. The three-species *P. orocana* species complex (*P. grande*, *P. honor*, and *P. orocana*) was monophyletic in all analyses. The two-species *P. catrea* species complex (*P. catrea* and *P. vossoroca*) was monophyletic in all analyses of morphology (molecular data are lacking for *P. vossoroca*). Finally, the *P. orobia* species complex (*P. orobia* and *P. cosmo*) was monophyletic in all analyses. These multispecies lineages are reflected in the classification of species complexes.

## DISCUSSION

### MORPHOLOGY, MOLECULES, AND FEMALE CHOICE

Eumaeini systematics has historically been based on three major morphological character sets: (1) wing pattern and shape, (2) genitalic structures, and (3) male secondary sexual traits (e.g., Ziegler, 1960; Clench, 1961, 1964; Nicolay, 1971a,b; Johnson, 1989; Robbins, 1991). These structures were used because they are frequently variable interspecifically, relatively conspicuous, and easily scored. Other characters, such as those of the head and legs, infrequently provided useful taxonomic information (Eliot, 1973; Robbins, 1986, 1991; Robbins and Venables, 1991). Characters of the immatures were rarely used because of the paucity of preserved immatures and because scoring larval characters and assessing their variation was labor intensive (Ballmer and Pratt, 1988). This pattern of morphological character usage in the Eumaeini remains largely unaltered (e.g., Duarte and Robbins, 2009, 2010; Faynel et al., 2012; Robbins et al., 2012; Robbins and Busby, 2015).

The morphological, ecological, and behavioral traits that adult females use to recognize and reject courting non-conspecific males are the bases of reproductive isolation among sympatric species. Direct evidence that lycaenid females can use each of the three major morphological characters sets listed in the previous paragraph to choose between conspecific and non-conspecific males is limited. For wing pattern and shape, female lycaenids can distinguish conspecific males by wing pattern details (Fordyce et al., 2002). For genitalic structures, sexual selection is the primary explanation for evolving differences (e.g., West-Eberhard, 1983; Eberhard, 1985, 2010; Hosken and Stockley, 2004; Simmons, 2014), but direct evidence for sexual selection among lycaenids is lacking. For male secondary sexual structures, pheromones dispersed by lycaenid wing androconia are

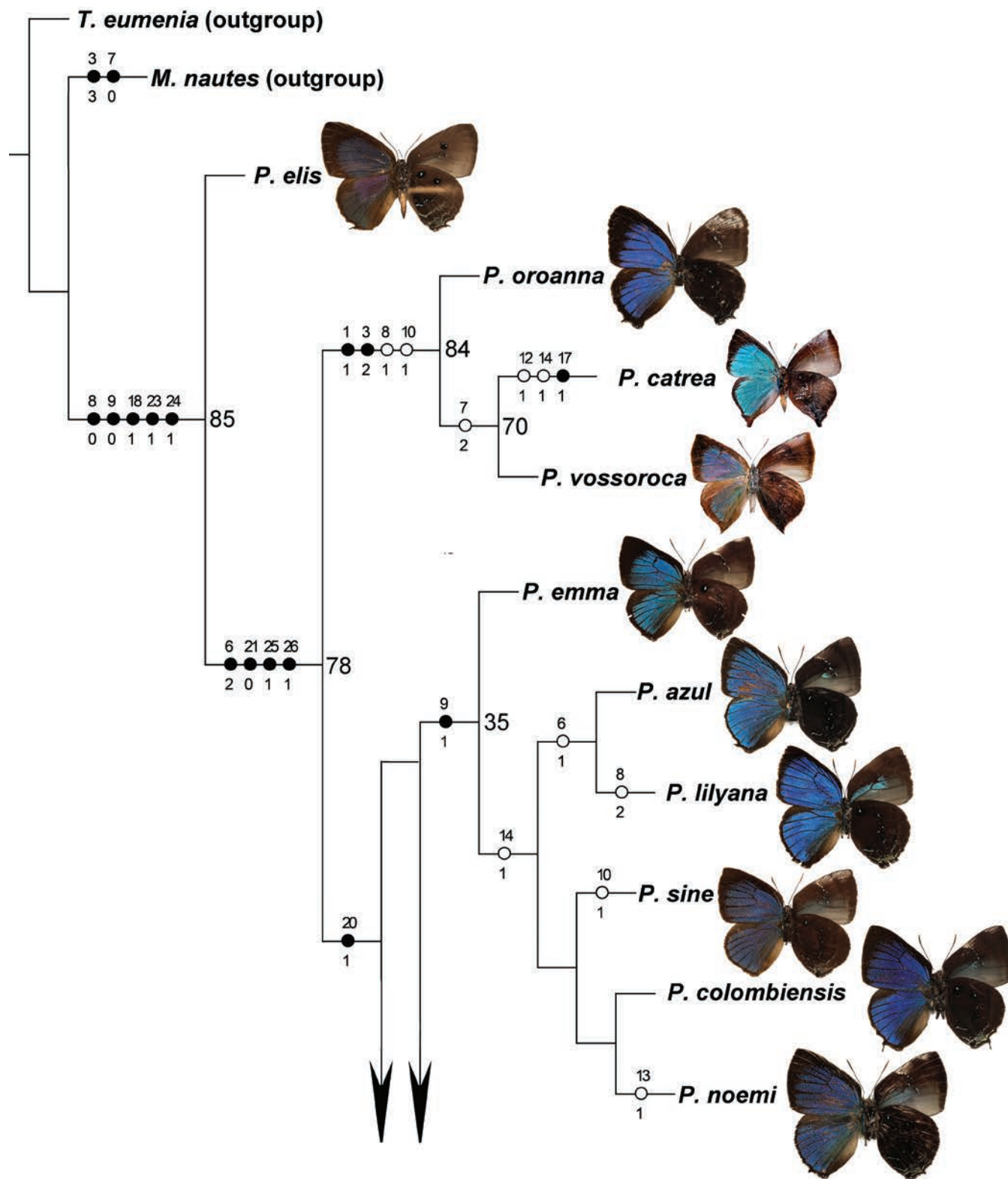


FIGURE 126. Top of a most parsimonious tree for *Paraspiculatus* based on morphological characters (Table 2), showing where characters evolved (open circles are homoplastic changes). This was the only most parsimonious equal-weight and implied-weight tree with a variety of values for the parameter K from 3 to 1,000. Bootstrap values noted.



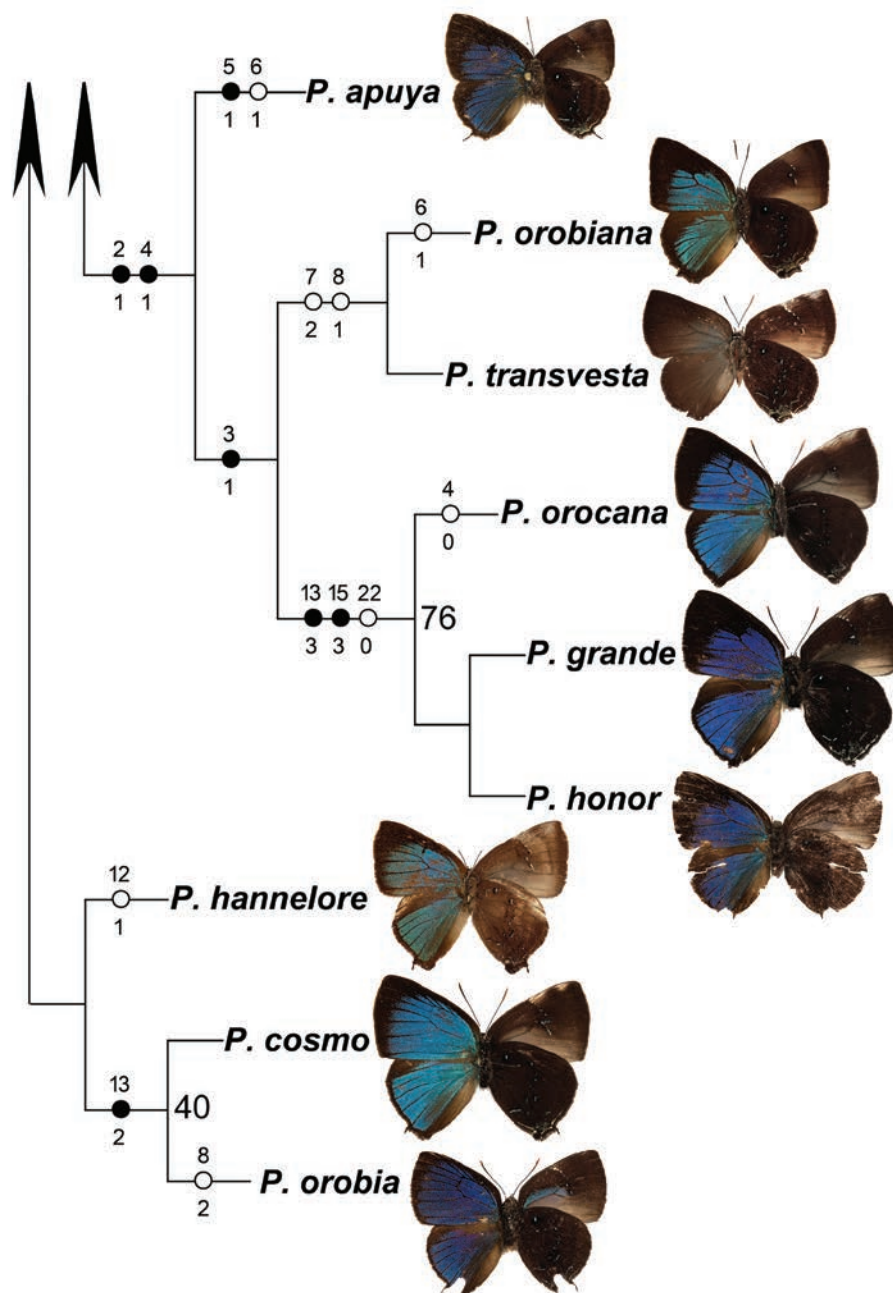


FIGURE 127. Bottom of a most parsimonious tree for *Paraspiculatus* based on morphological characters (Table 2), showing where characters evolved (open circles are homoplastic changes). This was the only most parsimonious equal-weight and implied-weight tree with a variety of values for the parameter K from 3 to 1,000. Bootstrap values noted.

used during courtship (Lundgren and Bergström, 1975; Ômura et al., 2013).

The indirect evidence that female Eumaeini routinely use at least one of the three major morphological character sets to determine male conspecificity is accumulating. When wing patterns

are interspecifically uniform, such as within most of the genus *Oenomaus*, each species has conspicuously different male genitalia (Faynel et al., 2012). Further, in those few cases within *Oenomaus* where wing pattern has changed markedly, change in the male genitalia is slight (C. Faynel et al., unpublished data). When

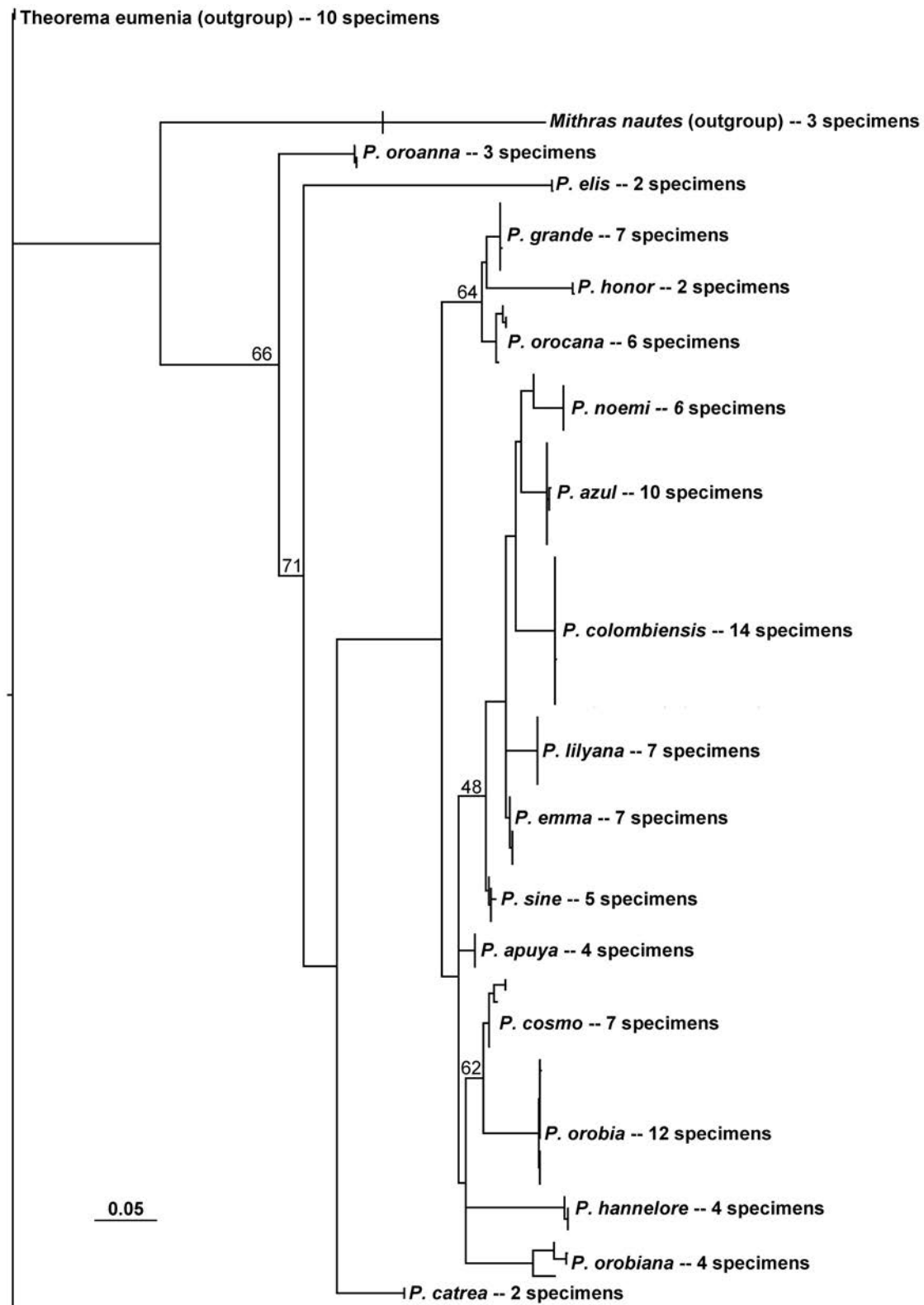


FIGURE 128. Maximum likelihood tree using the molecular data set. Numbers following the taxa are the number of specimens of that species. All species were monophyletic. Bootstrap values noted.

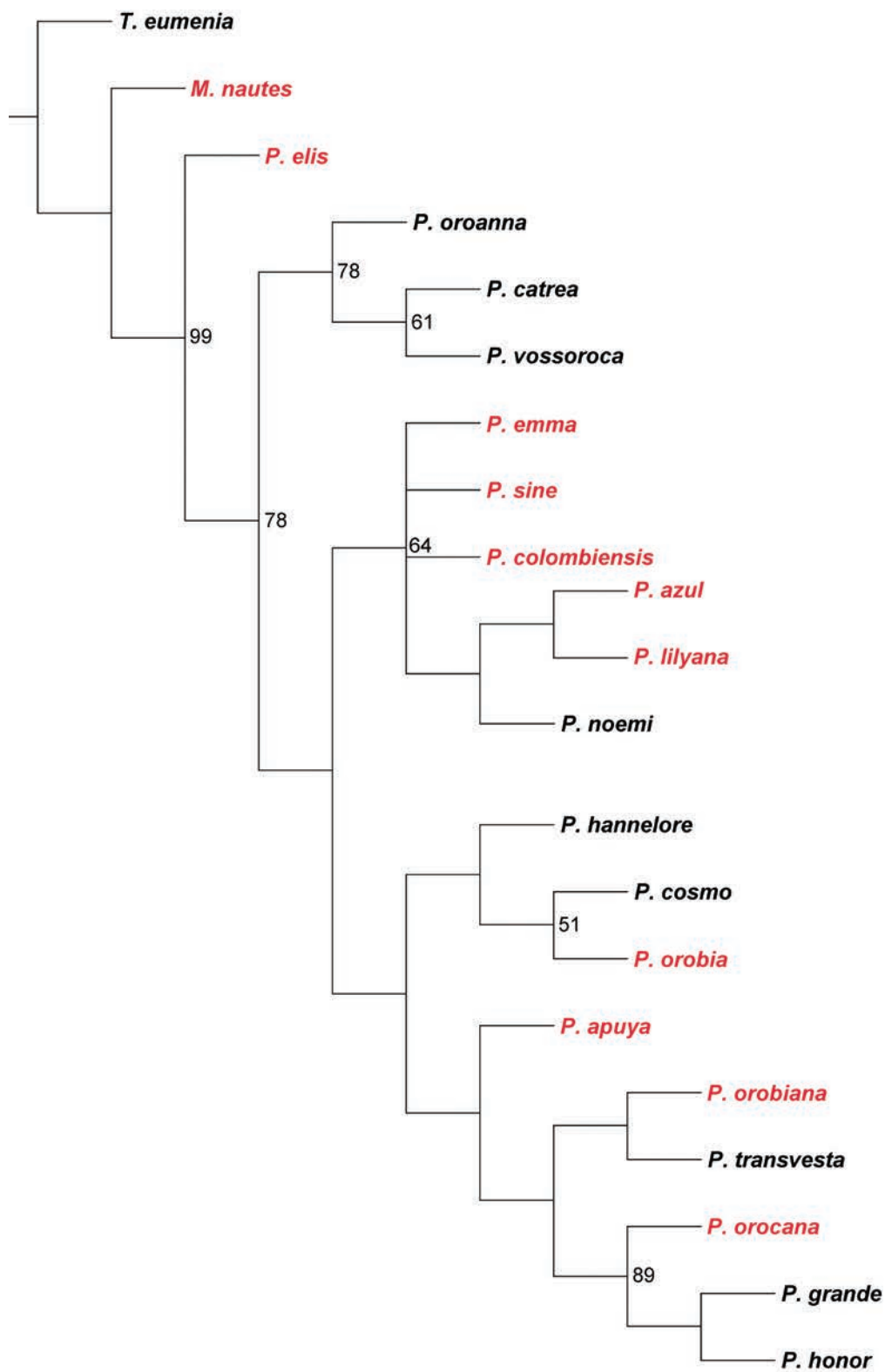


FIGURE 129. Most parsimonious implied-weight (default  $K = 3$ ) tree based on the combined morphological and molecular data set. The taxa in red are sympatric in the upper Amazon Basin below 1,250 m elevation. Bootstrap values noted.



male genitalic structures are interspecifically uniform in the Eumaeini, such as within the genus *Arcas* (Nicolay, 1971a), each species has a unique set of male secondary sexual traits as well as wing pattern/shape differences (Robbins et al., 2012). Finally, when sexual structures are uniform, as in the *Electrostrymon guzanta* species complex (Thompson and Robbins, 2016), males of each species can be distinguished by their wing pattern.

Analysis of DNA sequences provides an independent test of the traditional morphological character sets in the Eumaeini for biased selection and misinterpretation, especially as it relates to species delimitation. Mitochondrial CO1 barcode sequences have been widely adopted for species delimitation (Janzen et al., 2009). Discordance between species delimited by morphology and by CO1 sequences in the Lepidoptera is generally in the 10–15% range (Wiemers and Fiedler, 2007; Zahiri et al., 2014). The recent introduction of the barcode index number (BIN) (Ratnasingham and Hebert, 2013) makes the identification and measurement of discordance easier.

We determined species limits in *Paraspiculatus* based on male wing pattern and shape. We then determined species limits for each of the 17 *Paraspiculatus* species (Figure 113) for which we had data based on the clustering of CO1 barcode sequences. The morphological species determinations agreed with BINs in 92 of 95 males (3.2% discordance). Intraspecific CO1 sequences for *P. orobiana*, *P. apuya*, and *P. noemi* varied more than was recognized by the refined single linkage analysis that is used to determine BINs (Ratnasingham and Hebert, 2013). Geographical variation in DNA sequences is a likely explanation for this discordance. For each of the three species, the second BIN was assigned to a male from a different geographic area.

*Paraspiculatus* adds another piece of indirect evidence that some female eumaeines use wing pattern to recognize conspecific males. *Paraspiculatus* primary male sexual structures vary little interspecifically. Secondary male sexual structures are lacking. Presumably, females do not use sexual structures to recognize conspecific males. Alternatively, variation in male wing pattern is concordant with species delimitation by CO1 barcode sequences, so the hypothesis that females recognize males by wing pattern is plausible.

#### DOCUMENTING DIVERSITY

Robbins (2004a) noted that more than 25% of neotropical eumaeine species represented in museum collections were undescribed. In subsequent taxonomic revisions of *Timaeta* Johnson, Kruse, and Kroenlein, *Thepytus* Robbins, *Lathecla* Robbins, *Porthoecla* Robbins, and *Oenomaus*, more than 50% of the recognized species were newly described (Robbins and Busby, 2008, 2015; Robbins et al., 2010b; Faynel, 2006b, 2008; Faynel and Moser, 2008; Faynel et al., 2011, 2012). *Paraspiculatus* continues this trend, with 10 of 19 species treated newly described in this paper. Although butterflies are considered to be the best documented large group of insects (Robbins and Opler, 1997), there is still a significant proportion of undocumented diversity.

We noted in the introduction that a revision of *Paraspiculatus* was possible only because new sampling techniques using fish bait resulted in a fivefold increase in the number of specimens available for study. It would be hard to overemphasize the need for expanded and more intensive collecting of eumaeines, especially in South America.

#### ROTTING FISH, STRATIFICATION, AND NUTRITION

Rotting fish in a trap 10 m above the ground is not a “natural” food source for hairstreak butterflies. This collecting method has been used primarily to increase sample sizes of otherwise rare species and not as a way to study biology. Despite these limitations, the attraction to rotting fish is related to various biological aspects of *Paraspiculatus* and other eumaeines. The significance of adult male butterfly food sources has been discussed in the Lycaenidae and Riodinidae (Beck et al., 1999; Hall and Willmott, 2000), but needs to be expanded to account for variation in the attractiveness of rotting fish as a eumaeine bait depending upon geographic area, taxon, and sex. The purpose of this section is to summarize what we know about the attraction of adult eumaeines, especially *Paraspiculatus*, to rotting fish and to discuss how these observations may relate to *Paraspiculatus* biology.

The attractiveness of rotting fish bait to eumaeines is geographically variable. On the eastern slope of the Andes, especially in Ecuador, it has been effective at 200 to 1,800 m elevation. On the western slopes of the Ecuadorian Andes, it has been much less effective. In the mountains of northern Venezuela and in French Guiana, it did not attract eumaeines. We do not know whether these results are due to geographic variation in naturally occurring sources of adult nutrition or to other geographically variable factors, such as availability of larval food. Regardless, this geographic variability in the attractiveness of rotting fish to eumaeines is one reason for the limited number of records of *Paraspiculatus* in areas such as the northern parts of South America.

Trapping adult eumaeines with fish-baited traps is different from trapping other adult butterflies. Nymphalidae attracted to traps baited with fish usually land on the bait and fly up into the trap. Adult eumaeines apparently fly downward toward the fish (Robbins, 2001), and land on the top and sides of the trap, not on the bait dish. If the netting has rotting fish on it, the landed butterfly extends its proboscis, presumably feeding. If the trap is disturbed, it flies away. To sample these adult lycaenids, the trap has to be lowered carefully to the ground, where the butterflies are caught on the trap netting.

The efficacy of rotting fish bait for eumaeines depends upon taxon and sex. In *Paraspiculatus*, *Ocaria* Clench, and *Penaincisalia* Johnson, the ratio of baited males to females is almost 1:0 (the few female exceptions in *Paraspiculatus* have been noted). In *Ignata* Johnson, *Strephonota* Johnson, Austin, Le Crom, and Salazar, *Siderus* Kaye, and *Erora* Scudder, the ratio of baited individuals is reversed, close to 0:1 (again with a few exceptions, this time male). In the majority of Eumaeini, however, both sexes are attracted to rotting fish, although the sex ratio is variable from species to species. In contrast, the majority of riodinids

attracted to fish bait in the same area were males (Hall and Willmott, 2000). Finally, in some eumaeine genera, such as *Timaeta* and *Micandra* Staudinger, neither sex is attracted to rotting fish.

Adult butterflies and other animals may spend most of their time in a restricted stratum of the forest (cf. DeVries, 1988 and included references). For slow-flying butterflies, flight height above the ground can be recorded and has been shown to be a function of wing pattern and/or size (Papageorgis, 1975; Medina et al., 1996). For faster-flying butterflies, two methods have been used. A tower in tropical forest in Africa allowed observation and trapping of butterflies at different forest strata (Jackson, 1961). For Lycaenidae, this was apparently the first time that it was demonstrated that some species are frequent and active in the higher forest strata, but not at ground level. In other words, Lycaenidae may be rare to butterfly collectors on the ground, but are not necessarily rare in the forested habitats. Second, traps placed at the ground and in the upper forest strata may attract different sets of species. Those caught primarily in ground-level traps are presumed to be primarily active at ground level, not in the upper strata, and vice versa (DeVries, 1988; DeVries and Walla, 2001; DeVries et al., 2012; Alexander and DeVries, 2012; Fordyce and DeVries, 2016). Exceptions to this presumption were summarized in DeVries and Walla (2001).

*Paraspiculatus* are rarely encountered in the forest understory in the eastern Andes, as determined by the paucity of net-collected individuals in museums. Less than 2% of the specimens in our study series from eastern Ecuador were collected with a net. Although we used rotting fish poured on leaves near ground level as well as in traps hung 7 to 20 m above the ground, the latter method was more than twice as productive in attracting male *Paraspiculatus*. Controlled experiments with paired traps near ground level and in the forest upper strata might be used to test the hypothesis that adult *Paraspiculatus* are rare in collections because they spend most of their time in the upper forest strata.

DeVries (1988:99) wrote “Excluding those species where males visit wet sand or plant material for non-nutritional resources . . . , any tropical forest community of butterflies can be divided into two adult feeding guilds: those species that obtain the bulk of their nutritional requirements from flower nectar (all Papilionidae, Pieridae, Lycaenidae, Riodinidae and some Nymphalidae), and those species that feed upon the juices of rotting fruits, fermenting sap, or animal waste (several subfamilies of the Nymphalidae . . .).” This guild partition needs modification, at least for Riodinidae (Hall and Willmott, 2000) and Lycaenidae in eastern Ecuador. Whereas many neotropical forest eumaeine lycaenids nectar at flowers seasonally, especially when certain species of *Cordia* (Boraginaceae) are flowering (Opler et al., 1975; Faynel, 2003, 2005, 2006a, 2010), it is premature to conclude that flower nectar makes up the bulk of adult eumaeine nutritional requirements. In our experience, adult eumaeines in wet forest feeding on flowers is a rarely observed occurrence. Adults of a Colombian eumaeine species feed on exudates from Hemiptera and on plant fluids oozing from wounds made by sucking insects (Heredia and Robbins, 2016). Nonfloral adult feeding behavior is widely observed in miletine lycaenids

(Lohman and Samarita, 2009 and included citations) and has recently been noted in North American eumaeines (Wagner and Gagliardi, 2015; Gagliardi and Wagner, 2016). Finally, many lycaenid adults are attracted to and eat liquefied decaying animals, such as rotting fish (and cow’s blood in one instance). The limited previous observations of this phenomenon may be due to the geographical and seasonal variation in its occurrence or due to the observation that lycaenid adults do not fly into traps, but land on the tops and sides. As noted, unless the trap is lowered with great care, such adults fly away and would not be recorded as being attracted to fish as bait (fish-bait).

Rotting fish attracts a significant proportion of the lycaenid fauna in eastern Ecuador. It may attract members of either sex, unlike previous work on non-nectar attractants (Beck et al., 1999; Hall and Willmott, 2000). Perhaps the most interesting and unusual observation is the intergeneric variation in sex ratio of adult eumaeines attracted to fish-bait. Adult male butterflies devote up to 10% of their adult weight to spermatophores transferred to females during mating (Rutowski et al., 1983; Caballero-Mendieta and Cordero, 2013). It might be reasonable to hypothesize that males in genera, such as *Paraspiculatus*, transfer the nutrition ingested to females in spermatophores. Alternately, in genera where females predominate at fish-bait, we might expect less nutritional transfer in spermatophores. Intergeneric variation in sex ratio of adult eumaeines attracted to fish-bait suggests that eumaeine reproductive biology is worth investigating.

## DISTRIBUTION

Based on current data, most *Paraspiculatus* species have restricted geographic distributions and occur over a relatively narrow range of elevations (Figure 130). Only *P. orobia* occurs in more than one of the major biogeographic regions of Brown (1982). Only three species (*P. orobia*, *P. colombiensis*, *P. catrea*) occur over an elevation range of more than 1,000 m (Figure 130). The wide elevational range of *P. transvesta* is an artifact of imprecise data, as noted in its species account. However, the use of traps baited with rotting fish in areas other than Ecuador may significantly expand current geographic distributions.

The most widespread *Paraspiculatus* species are those that occur in the lowlands, as seems generally true for Eumaeini (Robbins et al., 2010b; Robbins and Busby, 2015). *Paraspiculatus elis*, *P. orobia*, *P. noemi*, and *P. colombiensis* occur throughout their respective biogeographic region (Figures 114, 117, 122, 124) and inhabit lowlands. However, the distributions of these species are restricted when compared with species in some eumaeine genera, such as *Rekoa* Kaye in which four of the seven species range from Mexico to southern Brazil (Robbins, 1991).

## SYMPATRY AND DIVERSIFICATION

In the Introduction, we noted the high incidence of sympatry among *Paraspiculatus* species in the upper Amazon under 1,250 m elevation (10 of 19 species). The set of sympatric *Paraspiculatus* species could result from in situ diversification in the

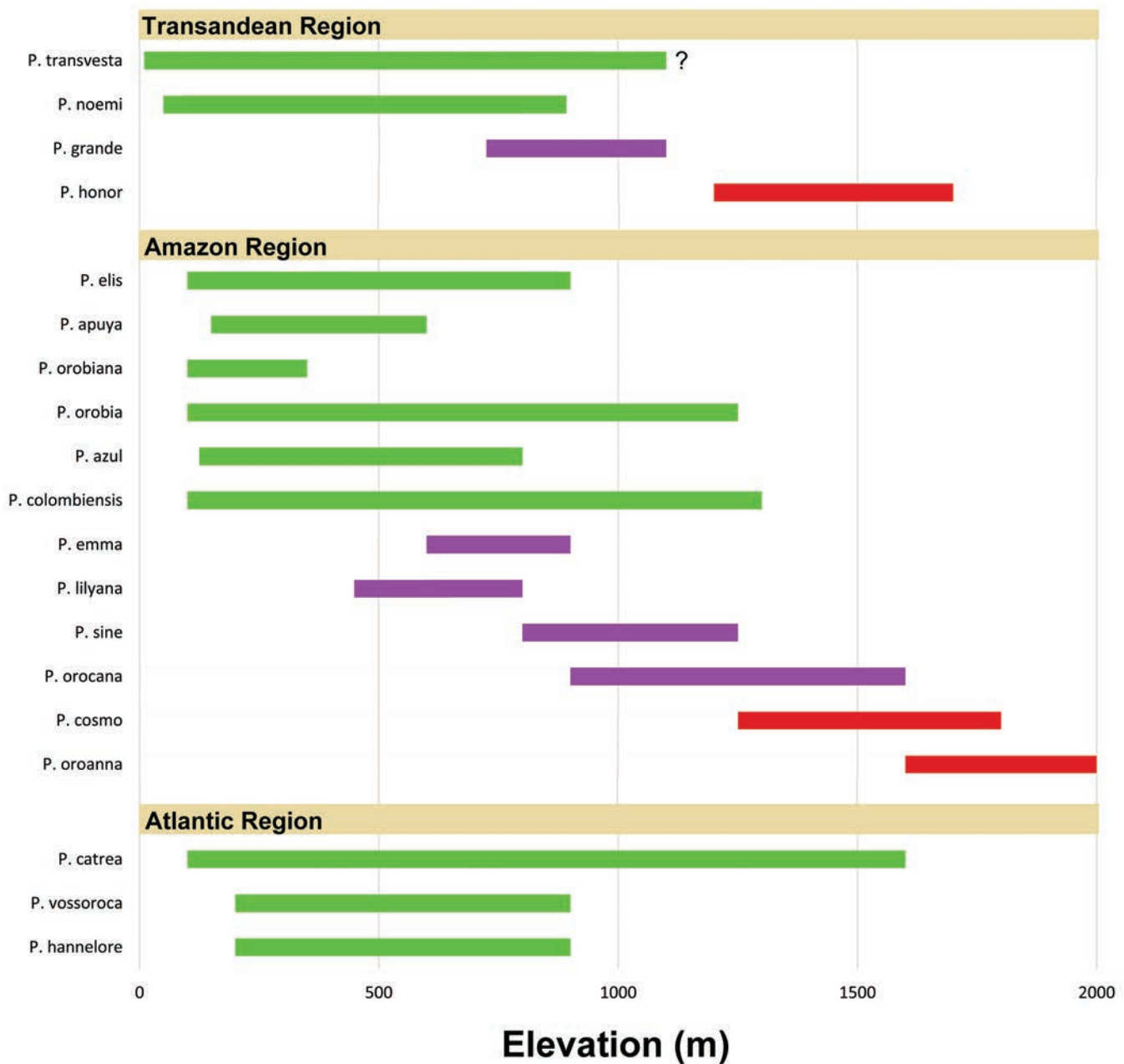


FIGURE 130. Biogeographic regions and elevation zones for each *Paraspiculatus* species. *Paraspiculatus orobia* also occurs in the northern part of the Atlantic Region. Green bars represent lowland species, violet are lower montane species, and red are montane species. *Paraspiculatus catrea* is an elevational generalist over its entire range, but this may be an artifact because it occurs at higher elevations in the northern part of its range and at lower ones in the southern part.

upper Amazon, from the diversification of clades, each with one Amazonian representative, or a combination of these processes. Although a comprehensive explanation for the high frequency of sympatry in *Paraspiculatus* is beyond the scope of this paper, revising the genus is a first step.

According to our results, the 10 *Paraspiculatus* species that occur in the upper Amazon under 1,250 m elevation represent all three possibilities. Three species (*P. elis*, *P. apuya*, and *P. orobiana*) belong to single species complexes because they have no evident very close relative within the genus. The *P. orobia*



and *P. orocana* species groups fit the traditional “superspecies” concept of Mayr (1963), in which no two component species are sympatric. Each of these superspecies has one species in the upper Amazon Basin under 1,250 m elevation (*P. orobia* and *P. orocana*). Finally, five of the six species in the *P. colombiensis* species complex (*P. colombiensis*, *P. lilyana*, *P. azul*, *P. emma*, and *P. sine*) are sympatric at 800 m elevation in eastern Ecuador. This species complex is the main reason for the original observation

of a high incidence of sympatry in the upper Amazon Basin. In situ diversification is usually examined on ecological or physical islands (Simon et al., 2009; Gómez-Díaz et al., 2012; Pante et al., 2012; Blaimer et al., 2015), but perhaps it is also relevant to biogeographic areas. A comprehensive explanation for the high frequency of sympatry in *Paraspiculatus* would undoubtedly focus on this lineage.



# Acknowledgments

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For allowing us to examine specimens in collections under their care, we are grateful to Mirna Casagrande (DZUP), David Grimaldi (AMNH), Blanca Huertas (BMNH), Gerardo Lamas (MUSM), Olaf Mielke (DZUP), Jacques Pierre (MNHN), and Wolfgang Nassig (SMF). For giving us access to their private collection and providing specimens for DNA sequencing, we thank Jason Hall and Keith Willmott. For providing photographs, specimens, or other data, we are grateful to Pierre Boyer, Michael Büche, Mauro Costa, Will and Gill Carter, Jose Cerdeña, Jean-Yves Gallard, Kim Garwood, Jean-François Le Crom, Jean-Claude Petit, Thibault Rosant, and Rob Westerduijn. For illustrative and technical help at Smithsonian, we are indebted to Karie Darrow, Brian Harris, and Vichai Malikul. We thank Gerardo Lamas for information on the history of collecting in Balsapuerto, Peru. We thank two anonymous reviewers, who made numerous suggestions and corrections, for their time-consuming contributions. For help dealing with the BOLD database and sequencing at the Canadian Centre for DNA Barcoding, we thank Jeremy DeWaard, Vlad Dinca, Evgeny V. Zakharov, and their many coworkers. For facilitating specimen loans among the authors, we thank Helena Romanowski and Vanessa Schaeffer at the federal university (UFRGS) in Porto Alegre, Brazil. For supporting the project “Diversidad y Biología de Lepidopteros en el Ecuador,” we thank the Museo Ecuatoriano de Ciencias Naturales, especially Santiago Villamarín-Cortez, Curador de Invertebrados, who has provided valuable assistance in obtaining permits for our fieldwork in Ecuador. Faynel expresses his appreciation to the Smithsonian Institution Short-Term Visitor Program, which facilitated this project. To all, we are grateful.





# Appendix A: CO1 DNA Sequence Information

TABLE A.1. The CO1 sequence samples listed alphabetically by genus, species, sex, and country of origin, with collection voucher numbers for the U.S. National Museum (USNM) and the private collection of Christophe Faynel (CF); and online BOLD database–assigned process identification numbers.

Species, sex, country	Voucher number	BOLD ID
<i>Mithras nautes</i> , f, French Guiana	CF-LYC-162	NLYCA162-12
<i>Mithras nautes</i> , m, Ecuador	USNM ENT 00180865	EUM070-13
<i>Mithras nautes</i> , m, Peru	CF-LYC-161	NLYCA161-12
<i>Paraspiculatus apuya</i> , m, Brazil	USNM ENT 00180888	EUM081-13
<i>Paraspiculatus apuya</i> , m, Ecuador	USNM ENT 00180817	EUM027-13
<i>Paraspiculatus apuya</i> , m, Ecuador	USNM ENT 00180818	EUM028-13
<i>Paraspiculatus apuya</i> , m, Ecuador	USNM ENT 00181672	EUM116-14
<i>Paraspiculatus apuya</i> , m, Ecuador	USNM ENT 00181767	EUM301-15
<i>Paraspiculatus azul</i> , f, Peru	USNM ENT 00180894	EUM087-13
<i>Paraspiculatus azul</i> , m, Ecuador	USNM ENT 00180848	EUM052-13
<i>Paraspiculatus azul</i> , m, Ecuador	USNM ENT 00180871	EUM056-13
<i>Paraspiculatus azul</i> , m, Ecuador	USNM ENT 00180878	EUM102-14
<i>Paraspiculatus azul</i> , m, Ecuador	USNM ENT 00181669	EUM113-14
<i>Paraspiculatus azul</i> , m, Ecuador	USNM ENT 00181671	EUM115-14
<i>Paraspiculatus azul</i> , m, Ecuador	USNM ENT 00181700	EUM118-14
<i>Paraspiculatus azul</i> , m, Ecuador	USNM ENT 00181701	EUM119-14
<i>Paraspiculatus azul</i> , m, Ecuador	USNM ENT 00181702	EUM120-14
<i>Paraspiculatus azul</i> , m, Ecuador	USNM ENT 00181703	EUM121-14
<i>Paraspiculatus azul</i> , m, Ecuador	USNM ENT 00181704	EUM122-14
<i>Paraspiculatus azul</i> , m, Ecuador	USNM ENT 00181706	EUM124-14
<i>Paraspiculatus azul</i> , m, Peru	CF-LYC-158	NLYCA158-12
<i>Paraspiculatus catrea</i> , f, Brazil	USNM ENT 00181667	EUM111-14
<i>Paraspiculatus catrea</i> , f, Brazil	USNM ENT 00181668	EUM112-14
<i>Paraspiculatus catrea</i> , m, Brazil	USNM ENT 00179443	EUM089-13

TABLE A.1. (Continued)

Species, sex, country	Voucher number	BOLD ID
<i>Paraspiculatus colombiensis</i> , f, Ecuador	USNM ENT 00179432	EUM074-13
<i>Paraspiculatus colombiensis</i> , f, Ecuador	USNM ENT 00180840	EUM045-13
<i>Paraspiculatus colombiensis</i> , f, Ecuador	USNM ENT 00180877	EUM036-13
<i>Paraspiculatus colombiensis</i> , f, Ecuador	USNM ENT 00181768	EUM302-15
<i>Paraspiculatus colombiensis</i> , f, Ecuador	USNM ENT 00181769	EUM303-15
<i>Paraspiculatus colombiensis</i> , m, Ecuador	USNM ENT 00180841	EUM046-13
<i>Paraspiculatus colombiensis</i> , m, Ecuador	USNM ENT 00180842	EUM047-13
<i>Paraspiculatus colombiensis</i> , m, Ecuador	USNM ENT 00180843	EUM048-13
<i>Paraspiculatus colombiensis</i> , m, Ecuador	USNM ENT 00180844	EUM050-13
<i>Paraspiculatus colombiensis</i> , m, Ecuador	USNM ENT 00180847	EUM051-13
<i>Paraspiculatus colombiensis</i> , m, Ecuador	USNM ENT 00180872	EUM049-13
<i>Paraspiculatus colombiensis</i> , m, Ecuador	USNM ENT 00181670	EUM114-14
<i>Paraspiculatus colombiensis</i> , m, Peru	CF-LYC-157	NLYCA157-12
<i>Paraspiculatus colombiensis</i> , m, Peru	CF-LYC-159	NLYCA159-12
<i>Paraspiculatus cosmo</i> , f, Ecuador	USNM ENT 00180806	EUM018-13
<i>Paraspiculatus cosmo</i> , m, Ecuador	USNM ENT 00180798	EUM012-13
<i>Paraspiculatus cosmo</i> , m, Ecuador	USNM ENT 00180799	EUM013-13
<i>Paraspiculatus cosmo</i> , m, Ecuador	USNM ENT 00180800	EUM014-13
<i>Paraspiculatus cosmo</i> , m, Ecuador	USNM ENT 00180804	EUM016-13
<i>Paraspiculatus cosmo</i> , m, Ecuador	USNM ENT 00180805	EUM017-13
<i>Paraspiculatus cosmo</i> , m, Peru	CF-LYC-156	NLYCA156-12
<i>Paraspiculatus elis</i> , m, Ecuador	USNM ENT 00180863	EUM069-13
<i>Paraspiculatus elis</i> , m, Peru	CF-LYC-163	NLYCA163-12
<i>Paraspiculatus emma</i> , m, Ecuador	USNM ENT 00180807	EUM019-13
<i>Paraspiculatus emma</i> , m, Ecuador	USNM ENT 00180808	EUM020-13
<i>Paraspiculatus emma</i> , m, Ecuador	USNM ENT 00180809	EUM021-13
<i>Paraspiculatus emma</i> , m, Ecuador	USNM ENT 00180811	EUM022-13
<i>Paraspiculatus emma</i> , m, Ecuador	USNM ENT 00180812	EUM023-13
<i>Paraspiculatus emma</i> , m, Ecuador	USNM ENT 00180813	EUM024-13
<i>Paraspiculatus emma</i> , m, Ecuador	USNM ENT 00180815	EUM025-13
<i>Paraspiculatus grande</i> , f, Panama	USNM ENT 00179438	EUM078-13
<i>Paraspiculatus grande</i> , m, Ecuador	CF-LYC-425	NLYCA425-13
<i>Paraspiculatus grande</i> , m, Ecuador	USNM ENT 00180788	EUM002-13
<i>Paraspiculatus grande</i> , m, Ecuador	USNM ENT 00180789	EUM003-13
<i>Paraspiculatus grande</i> , m, Ecuador	USNM ENT 00180790	EUM004-13
<i>Paraspiculatus grande</i> , m, Ecuador	USNM ENT 00180791	EUM005-13
<i>Paraspiculatus grande</i> , m, Ecuador	USNM ENT 00180792	EUM006-13
<i>Paraspiculatus grande</i> , m, Ecuador	USNM ENT 00180793	EUM007-13
<i>Paraspiculatus hannelore</i> , f, Brazil	USNM ENT 00181663	EUM107-14
<i>Paraspiculatus hannelore</i> , m, Brazil	USNM ENT 00181664	EUM108-14
<i>Paraspiculatus hannelore</i> , m, Brazil	USNM ENT 00181665	EUM109-14
<i>Paraspiculatus hannelore</i> , m, Brazil	USNM ENT 00181666	EUM110-14
<i>Paraspiculatus honor</i> , f, Ecuador	USNM ENT 00180862	EUM068-13
<i>Paraspiculatus honor</i> , m, Ecuador	USNM ENT 00181673	EUM117-14



TABLE A.1. (Continued)

Species, sex, country	Voucher number	BOLD ID
<i>Paraspiculatus lilyana</i> , m, Ecuador	USNM ENT 00180831	EUM037-13
<i>Paraspiculatus lilyana</i> , m, Ecuador	USNM ENT 00180832	EUM038-13
<i>Paraspiculatus lilyana</i> , m, Ecuador	USNM ENT 00180833	EUM039-13
<i>Paraspiculatus lilyana</i> , m, Ecuador	USNM ENT 00180834	EUM040-13
<i>Paraspiculatus lilyana</i> , m, Ecuador	USNM ENT 00180835	EUM042-13
<i>Paraspiculatus lilyana</i> , m, Ecuador	USNM ENT 00180838	EUM043-13
<i>Paraspiculatus lilyana</i> , m, Ecuador	USNM ENT 00180839	EUM044-13
<i>Paraspiculatus noemi</i> , m, Ecuador	USNM ENT 00180855	EUM063-13
<i>Paraspiculatus noemi</i> , m, Ecuador	USNM ENT 00180857	EUM064-13
<i>Paraspiculatus noemi</i> , m, Ecuador	USNM ENT 00180858	EUM065-13
<i>Paraspiculatus noemi</i> , m, Ecuador	USNM ENT 00180859	EUM066-13
<i>Paraspiculatus noemi</i> , m, Ecuador	USNM ENT 00180860	EUM067-13
<i>Paraspiculatus noemi</i> , m, Mexico	USNM ENT 00180898	EUM093-13
<i>Paraspiculatus oroanna</i> , m, Ecuador	CF-LYC-151	NLYCA151-12
<i>Paraspiculatus oroanna</i> , m, Ecuador	USNM ENT 00180787	EUM001-13
<i>Paraspiculatus oroanna</i> , m, Peru	CF-LYC-152	NLYCA152-12
<i>Paraspiculatus orobia</i> , f, French Guiana	CF-LYC-150	NLYCA150-12
<i>Paraspiculatus orobia</i> , f, Peru	USNM ENT 00181972	EUM380-15
<i>Paraspiculatus orobia</i> , f, Peru	USNM ENT 00180889	EUM082-13
<i>Paraspiculatus orobia</i> , m, Brazil	USNM ENT 00179431	EUM073-13
<i>Paraspiculatus orobia</i> , m, Ecuador	USNM ENT 00180819	EUM029-13
<i>Paraspiculatus orobia</i> , m, Ecuador	USNM ENT 00180821	EUM030-13
<i>Paraspiculatus orobia</i> , m, Ecuador	USNM ENT 00180823	EUM031-13
<i>Paraspiculatus orobia</i> , m, Ecuador	USNM ENT 00180825	EUM032-13
<i>Paraspiculatus orobia</i> , m, Ecuador	USNM ENT 00180826	EUM033-13
<i>Paraspiculatus orobia</i> , m, Ecuador	USNM ENT 00181997	EUM188-14
<i>Paraspiculatus orobia</i> , m, Ecuador	USNM ENT 00181998	EUM189-14
<i>Paraspiculatus orobia</i> , m, Ecuador	USNM ENT 00181999	EUM190-14
<i>Paraspiculatus orobia</i> , m, Peru	CF-LYC-160	NLYCA160-12
<i>Paraspiculatus orobiana</i> , f, Peru	USNM ENT 00180901	EUM095-13
<i>Paraspiculatus orobiana</i> , m, Brazil	USNM ENT 00179441	EUM096-14
<i>Paraspiculatus orobiana</i> , m, Ecuador	USNM ENT 00181753	EUM287-15
<i>Paraspiculatus orobiana</i> , m, Peru	CF-LYC-155	NLYCA155-12
<i>Paraspiculatus orocana</i> , m, Ecuador	CF-LYC-154	NLYCA154-12
<i>Paraspiculatus orocana</i> , m, Ecuador	USNM ENT 00180794	EUM008-13
<i>Paraspiculatus orocana</i> , m, Ecuador	USNM ENT 00180795	EUM009-13
<i>Paraspiculatus orocana</i> , m, Ecuador	USNM ENT 00180796	EUM010-13
<i>Paraspiculatus orocana</i> , m, Ecuador	USNM ENT 00180797	EUM011-13
<i>Paraspiculatus orocana</i> , m, Peru	CF-LYC-153	NLYCA153-12
<i>Paraspiculatus sine</i> , m, Ecuador	USNM ENT 00180830	EUM035-13
<i>Paraspiculatus sine</i> , m, Ecuador	USNM ENT 00180849	EUM057-13
<i>Paraspiculatus sine</i> , m, Ecuador	USNM ENT 00180851	EUM059-13
<i>Paraspiculatus sine</i> , m, Ecuador	USNM ENT 00180852	EUM060-13
<i>Paraspiculatus sine</i> , m, Ecuador	USNM ENT 00180853	EUM061-13
<i>Paraspiculatus sine</i> , m, Ecuador	USNM ENT 00180854	EUM062-13

TABLE A.1. (Continued)

Species, sex, country	Voucher number	BOLD ID
<i>Theorema eumenia</i> , m, Costa Rica	15-SRNP-30546	MHMYK7751-15
<i>Theorema eumenia</i> , m, Costa Rica	09-SRNP-30866	MHMYC1167-09
<i>Theorema eumenia</i> , m, Costa Rica	12-SRNP-31404	BLPEF1814-13
<i>Theorema eumenia</i> , m, Costa Rica	09-SRNP-30865	MHMYC1168-09
<i>Theorema eumenia</i> , f, Costa Rica	09-SRNP-30789	MHMYC1175-09
<i>Theorema eumenia</i> , f, Costa Rica	09-SRNP-30787	MHMYC1176-09
<i>Theorema eumenia</i> , f, Costa Rica	09-SRNP-32018	MHMYH037-10
<i>Theorema eumenia</i> , f, Costa Rica	09-SRNP-3212	MHMYH038-10
<i>Theorema eumenia</i> , f, Costa Rica	11-SRNP-30697	MHMYM1434-11
<i>Theorema eumenia</i> , f, Costa Rica	11-SRNP-30696	MHMYM1435-11

# Appendix B. *Paraspiculatus* Genitalic Dissections

TABLE B.1. Genitalic dissections of *Paraspiculatus* with dissection number, country (and province if known) where the specimen was collected, and museum in which it is deposited (with barcode identifier if available). An asterisk (\*) indicates a genitalic photograph was used for comparison of structures; a hashtag (#) indicates the specimen was drawn and is illustrated herein. Museum abbreviations are defined in text under “Materials and Methods” (ENT is part of the USNM barcode number).

Sex, species	Dissection number	Locality	Museum, with barcode if available
♂ <i>P. apuya</i>	CF71*#	Napo, Ecuador	USNM ENT 00180817
♂ <i>P. apuya</i>	CF72*	Napo, Ecuador	USNM ENT 00180818
♂ <i>P. apuya</i>	CF73*	Rondonia, Brazil	USNM ENT 00180888
♂ <i>P. azul</i>	CF54*#	Napo, Ecuador	USNM ENT 00180848
♂ <i>P. azul</i>	CF55*	Napo, Ecuador	USNM ENT 00180871
♀ <i>P. azul</i>	CF56*#	Madre de Dios, Peru	USNM ENT 00180894
♂ <i>P. catrea</i>	1982:74*#	Santa Catarina, Brazil	USNM ENT 00181696
♀ <i>P. catrea</i>	WDF2411	Rio de Janeiro, Brazil	USNM
♀ <i>P. catrea</i>	1982:75#	Paraná, Brazil	USNM
♂ <i>P. catrea</i>	2013:68	Rio Grande do Sul, Brazil	USNM
♂ <i>P. catrea</i>	2013:69	Santa Catarina, Brazil	USNM ENT 00179443
♂ <i>P. colombiensis</i>	CF50*#	Morona Santiago, Ecuador	USNM ENT 00180842
♂ <i>P. colombiensis</i>	CF51*	Morona Santiago, Ecuador	USNM ENT 00180843
♂ <i>P. colombiensis</i>	CF52*	Pastaza, Ecuador	USNM ENT 00180847
♀ <i>P. colombiensis</i>	CF53*	Pastaza, Ecuador	USNM ENT 00179432
♀ <i>P. colombiensis</i>	CF49*#	Morona Santiago, Ecuador	USNM ENT 00180840
♂ <i>P. colombiensis</i>	CF 504	Colombia	MNHN
♂ <i>P. cosmo</i>	CF78*	Morona Santiago, Ecuador	USNM ENT 00180798
♂ <i>P. cosmo</i>	CF79*#	Morona Santiago, Ecuador	USNM ENT 00180800
♂ <i>P. cosmo</i>	CF80*	Morona Santiago, Ecuador	USNM ENT 00180804
♀ <i>P. cosmo</i>	CF81*#	Morona Santiago, Ecuador	USNM ENT 00180806
♀ <i>P. cosmo</i>	1982:312	Peru	USNM ENT 00179440



TABLE B.1. (Continued)

Sex, species	Dissection number	Locality	Museum, with barcode if available
♂ <i>P. elis</i>	1982:208#	Peru	USNM ENT 00181697
♂ <i>P. elis</i>	1983:135	Peru	USNM
♀ <i>P. elis</i>	1983:136#	Peru	USNM ENT 00179430
♂ <i>P. emma</i>	CF68*	Napo, Ecuador	USNM ENT 00180807
♂ <i>P. emma</i>	CF69*#	Napo, Ecuador	USNM ENT 00180812
♂ <i>P. emma</i>	CF70*	Napo, Ecuador	USNM ENT 00180813
♂ <i>P. emma</i>	CF509	Peru	USNM ENT 00180813
♂ <i>P. grande</i>	CF85*	Esmeraldas, Ecuador	USNM ENT 00180788
♂ <i>P. grande</i>	CF86*#	Esmeraldas, Ecuador	USNM ENT 00180789
♀ <i>P. grande</i>	CF87*#	Panama	USNM ENT 00179438
♂ <i>P. hannelore</i>	CF63	Santa Catarina, Brazil	USNM ENT 00180895
♂ <i>P. hannelore</i>	CF64*#	Santa Catarina, Brazil	USNM ENT 00180896
♀ <i>P. hannelore</i>	CF65*#	Santa Catarina, Brazil	USNM ENT 00180897
♂ <i>P. honor</i>	1982:311	Colombia	USNM ENT 00179442
♂ <i>P. honor</i>	2013:71#	Ecuador	RCB
♀ <i>P. honor</i>	CF84*#	Pichincha, Ecuador	USNM ENT 00180862
♂ <i>P. lilyana</i>	CF66*	Napo, Ecuador	USNM ENT 00180831
♂ <i>P. lilyana</i>	CF67*#	Napo, Ecuador	USNM ENT 00180832
♂ <i>P. noemi</i>	CF60*#	Pichincha, Ecuador	USNM ENT 00180855
♂ <i>P. noemi</i>	CF61*	Esmeraldas, Ecuador	USNM ENT 00180858
♂ <i>P. noemi</i>	CF62*	Mexico	USNM ENT 00180898
♀ <i>P. noemi</i>	2013:74#	Costa Rica	USNM ENT 00180899
♂ <i>P. oroanna</i>	2013:40#	Ecuador	USNM ENT 00180787
♂ <i>P. orobia</i>	CF74*#	Napo, Ecuador	USNM ENT 00180819
♂ <i>P. orobia</i>	CF75*	Napo, Ecuador	USNM ENT 00180821
♂ <i>P. orobia</i>	CF53145	Bolivia	CMNH
♂ <i>P. orobia</i>	CF209	Bolivia	USNM
♂ <i>P. orobia</i>	CF76*	Rondonia, Brazil	USNM ENT 00179431
♂ <i>P. orobia</i>	CF501	Peru	MNHN
♂ <i>P. orobia</i>	CF502	Bolivia	MNHN
♂ <i>P. orobia</i>	CF503	Amazonas, Brazil	MNHN
♂ <i>P. orobia</i>	CF507	Colombia	MNHN
♀ <i>P. orobia</i>	CF77*#	Peru	USNM ENT 00180889
♂ <i>P. orobiana</i>	1982:313*#	Amazonas, Brazil	USNM ENT 00179441
♀ <i>P. orobiana</i>	CF2013:28#	Peru	USNM ENT 00181901
♂ <i>P. orocana</i>	CF82*#	Zamora Chinchipe, Ecuador	USNM ENT 00180794
♂ <i>P. orocana</i>	CF83*	Morona Santiago, Ecuador	USNM ENT 00180795
♂ <i>P. sine</i>	CF57*	Napo, Ecuador	USNM ENT 00180849
♂ <i>P. sine</i>	CF58*#	Morona Santiago, Ecuador	USNM ENT 00180851
♂ <i>P. sine</i>	CF59*	Napo, Ecuador	USNM ENT 00180830
♂ <i>P. transvesta</i>	1982:210*#	Guatemala	USNM ENT 00179436
♀ <i>P. transvesta</i>	2013:70#	Mexico	MGCL
♀ <i>P. vossoroca</i>	CF88*#	Santa Catarina, Brazil	USNM ENT 00179437

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