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# Contributions in Science

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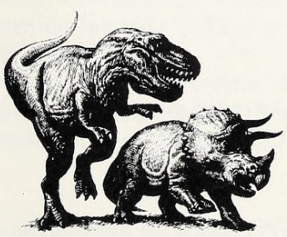

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# A Phylogenetic Reassessment of *Thisbe* and *Uraneis* Butterflies (Riodinidae, Nymphidiini)

C. M. Penz[1,2] and P. J. DeVries[1,3]



CONTENTS



**ABSTRACT.** This study addresses the phylogeny of the sister genera *Thisbe* and *Uraneis* using three separate phylogenetic analyses. An analysis of 97 characters showed that *Thisbe fenestrella* is more closely related to *Synargis* and *Thysanota* than to *Thisbe*. Second, cladistic analysis of 30 characters strongly supported the hypothesis that *T. fenestrella* is closely related to *Synargis velabrum* and *S. phillone*, and that both *T. fenestrella* and *Thysanota galena* are imbedded within *Synargis*. Third, cladistic analysis of 39 characters produced a well-resolved phylogeny for *Thisbe* and *Uraneis*, confirming a previous hypothesis that *Thisbe* was paraphyletic. Based on our phylogenetic analyses, *T. lycorias* is formally transferred to *Uraneis* and *T. fenestrella* is transferred to *Synargis*. Finally, in light of our analysis, *Thisbe* and *Uraneis* are redefined, and for each species studied we provide a diagnostic description, a summary of its geographic distribution and biology, and comments on subspecific taxa.

## INTRODUCTION

Over the last 10 years the riodinid genus *Thisbe* Hübner, 1819, has come to the attention of biologists through studies on *Thisbe irenea* (Stoll, 1780) that explore the ecology, evolution, and maintenance of caterpillar–ant symbioses (DeVries, 1988; 1990; 1991a,b,c; DeVries and Baker, 1989). However, almost no biological information is available for other *Thisbe* species or those in the closely related genus *Uraneis* Bates, 1868 (summarized in DeVries, 1997). Further, the patterns of diversification in these butterflies are poorly understood because the phylogenetic relationships among the species of *Thisbe* and *Uraneis* have never been assessed (see Penz and DeVries, 1999).

Together the genera *Thisbe* and *Uraneis* include seven species that occur from Mexico through Cen-

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tral and South America, all of which form apparent mimetic associations with butterflies or day-flying moths. Seitz (1916) stated that the genus *Thisbe* "is so much altered by mimicry that it is difficult to find out its real alliance," and he also noted that members of *Uraneis* mimic moths (see also DeVries, 1997). Stichel (1930, 1931) classified both genera in his tribe Ancyluridi, subtribe Emesini, and subsequently Harvey (1987) placed these genera in the *Lemonias* section of his Lemoniini. Recent phylogenetic analyses of DNA sequence (Campbell, 1998) and morphological characters (Penz and DeVries, 1999) indicate that *Thisbe* and *Uraneis* are sister genera and belong to the tribe Nymphidiini. Furthermore, morphological analysis of five species suggested that *Thisbe* was paraphyletic with respect to *Uraneis* (Penz and DeVries, 1999), and these observations provided the impetus for the present study.

This study examines all seven species currently classified in *Thisbe* and *Uraneis*. We use cladistic analyses of adult morphology to: (1) verify the systematic position of *T. fenestrella* Lathy, 1932; (2) propose a phylogeny for the genera *Thisbe* and *Uraneis*; (3) provide diagnostic descriptions for the genera and species; (4) discuss valid subspecies, and describe a new subspecies of *T. irenea*; and (5) formally transfer *Thisbe lycorias* (Hewitson, 1852) to *Uraneis* and *Thisbe fenestrella* to *Synargis* Hübner, 1819.

## METHODS

### EXAMINED MATERIAL

We examined four species of *Thisbe*, three of *Uraneis*, and also species in the genera *Adelotypa* Warren, 1895, *Aricoris* Westwood, 1851, *Audre* Hemming, 1934, *Calospila* Geyer, 1832, *Eiseleia* Miller and Miller, 1972, *Ematurgina* Röber, 1903, *Juditha* Hemming, 1964, *Lemonias* Hübner, 1806, *Nymphidum* Fabricius, 1807, *Setabis* Westwood, 1851, *Stalachtis* Hübner, 1818, *Synargis*, *Theope* Doubleday, 1847, and *Thysanota* Stichel, 1910. Females were not examined for *Thisbe fenestrella*, *Uraneis zamuro* (Thieme, 1907), *Ematurgina* nr. *leucotopus* Stichel, 1910, and *Aricoris tutana* (Godart, 1824). Examined specimens belong to the collections listed below:

| | |
|---|---|
| AME | Allyn Museum of Entomology, Florida Museum of Natural History, 3621 Bay Shore Road, Sarasota, Florida 34234, USA. |
| AMNH | Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024-5192, USA. |
| BH | Private collection of B. Harris. |
| BMNH | Department of Entomology, The Natural History Museum, Cromwell Road, London, SW7 5BD, UK. |
| GA | Private collection of G. Austin. |
| JH | Private collection of J. Hall. |
| LACM | Entomology Section, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, USA. |
| MPM | Milwaukee Public Museum, 800 West Wells Street, Milwaukee, Wisconsin 53233, USA. |
| PJD | Private collection of P. DeVries. |

### SPECIMEN PREPARATION

Dissections were performed using a standard treatment with 10% solution of potassium hydroxide, and stored and examined in glycerol using light microscopy (stereo- and compound microscope). Characters examined include external morphology and male and female genitalia as described in Penz and DeVries (1999).

### CHARACTERS AND TERMINOLOGY

Terminology for general adult morphology follows Scoble (1992) and Klots (1970) for male and female genitalia. We consider three character sets: (1) 97 previously studied adult morphology characters (an illustrated character list and data matrix are in Penz and DeVries (1999); a complete character matrix for the present analysis is in Appendix 1); (2) a selection of characters that were informative for *Synargis* and *Thysanota*, including 15 characters compiled from Penz and DeVries (1999) and 15 characters confined to male genitalia and examined here for the first time (Appendices 2 and 3); and (3) a selection of informative characters for assessing phylogenetic relationships among species of *Thisbe* and *Uraneis*, including 20 characters compiled from Penz and DeVries (1999) and 19 characters examined and described here for the first time (Appendices 4 and 5).

### PHYLOGENETIC ANALYSES

We used three separate analyses which address two complementary aspects of the systematics of *Thisbe* and *Uraneis*.

Morphology indicated that *Thisbe fenestrella* departed strongly from all other taxa within the genus. Therefore, to verify its generic position we performed two separate parsimony analyses. To elucidate its generic affinity we examined 97 characters for 30 species in 15 Nymphidiini genera (Appendix 1). To establish its generic position we focused on nine species of *Synargis* plus *Thysanota galena* for which 30 characters were assembled (Appendices 2 and 3).

The following taxa were included in the first analysis (illustrated in Penz and DeVries, 1999): *Adelotypa alector* (Butler, 1867); *Aricoris tutana*; *Audre domina* (Bates, 1864), *A. erostratus* (Westwood, 1851), and *Audre* sp.; *Calospila emylius* (Cramer, 1775); *Eiseleia pinchanalensis* Miller and Miller, 1972; *Ematurgina* nr. *leucotopus*; *Juditha azan* (Stoll, 1780) and *J. molpe* (Hübner, 1808); *Lemonias caliginea* (Butler, 1867) and *L. zygia* (Hübner, 1806); *Nymphidium azanoides* Butler, 1867, *N. cachrus* (Fabricius, 1787), and *N. mantus* (Cramer, 1775); *Setabis lagus* (Cramer, 1777); *Synargis abaris* (Cramer, 1776), *S. mycone* (Hewitson, 1865), *S. orestes* (Cramer, 1780), and *S. palaeste* (Hewitson, 1870c); *Theope publius* Felder and Felder, 1861, and *T. virgilus* (Fabricius, 1793); *Thisbe irenea*, *T. molela* (Hewitson, 1865), *T. lycorias*, and *T. fenestrella*; *Thysanota galena* (Bates, 1868); *Uraneis hyalina* (Butler, 1867), *U. ucubis* Hewitson, 1870c, and *U. zamuro* (Thieme, 1907). *Stalachtis euterpe* (Linnaeus, 1758) (Stalachtini) was selected as an outgroup species for rooting the tree because all evidence suggests that it belongs to a group separate from the Nymphidiini (Stichel, 1910, 1911, 1930, 1931; Harvey, 1987). For this part of our study we used the same characters as Penz and DeVries (1999), and the same set of taxa except for *Audre guttata* (Stichel, 1910), *Catocyclotis aemulius* (Fabricius, 1793), and *Lemonias agave* (Godman and Salvin, 1886). Our previous study (Penz and DeVries, 1999) showed that *A.*

*guttata* and *L. agave* were highly divergent from their congeners and that *C. aemulius* accumulated a large number of autapomorphies, therefore causing difficulties in establishing their systematic position. Because the analysis here centers on *Thisbe fenestrella,* the exclusion of these species is unlikely to affect our conclusions.

Our second analysis is a preliminary attempt to assess phylogenetic relationships within *Synargis.* Based on results from previous studies (Penz and DeVries, 1999; DeVries, unpublished), we examined *Thysanota galena* and nine species selected to represent the taxonomic diversity of *Synargis*: the type species *S. tytia* (Cramer, 1777), *S. abaris, S. ethelinda* (Hewitson, 1870b), *S. gela* (Hewitson, 1853), *S. mycone, S. orestes, S. palaeste, S. phillone* (Godart, 1824), and *S. velabrum* (Godman and Salvin, 1878). The outgroup included *Audre domina* and *A. erostratus* because they are considered closely related to *Synargis* (Harvey, 1987; Penz and DeVries, 1999).

The third part of this study involved an examination of six species in *Thisbe* and *Uraneis* to test the hypothesis that *Thisbe* is paraphyletic with respect to *Uraneis* (Penz and DeVries, 1999). To test this hypothesis we performed a parsimony analysis of 39 characters (Appendices 4 and 5). The outgroup included *Stalachtis euterpe* (*viz a viz* the first part of our study) plus *Lemonias caliginea* and *L. zygia*—species that are closely related to *Thisbe* and *Uraneis* (Harvey, 1987; Penz and DeVries, 1999).

For all phylogenetic analyses we performed a heuristic search with 20 tree bissection reconnection replicates as implemented in PAUP* 4.0 (Swofford, 1998), in which all characters were given equal weight, multistate characters were unordered, and polymorphic characters were treated as exhibiting both states. In all analyses we provide Bremer indices as estimates of branch support (Bremer, 1994).

## TAXON DESCRIPTIONS AND ILLUSTRATIONS

Descriptions and illustrations of adults and genitalia were based on male and female specimens, except for *Thisbe fenestrella* and *Uraneis zamuro* for which females were unavailable. Rather than providing complete descriptions for all taxa we focus on diagnostic characters, discuss characters defining subspecific taxa, and justify abandoning subspecies where appropriate.

# RESULTS

## PHYLOGENETIC RECONSTRUCTION

### Systematic Position of *Thisbe fenestrella*

Parsimony analysis of 97 characters for 30 species allowed us to verify the systematic position of *Thisbe fenestrella.* Eighty-nine equally parsimonious trees were produced (tree length = 351 steps, CI = 0.36, RI = 0.63), and the strict consensus of these trees is presented in Figure 1 (Analysis 1).

*Thisbe fenestrella* did not cluster with *Thisbe* or *Uraneis.* It emerged as a sister taxon to *Synargis* plus *Thysanota* (Fig. 1). Five characters support these relationships: (a) tip of bifurcated abdominal projection on male abdominal sternite 8 adorned with spines (Fig. 78); (b) posterior margin of uncus slightly concave (Fig. 77); (c) vinculum extending along entire anterior edge of tegumen; (d) in ventral view, distal end of aedeagus blunt (unique to this group, Fig. 76); (e) valvae fused ventrally (universal and unique to this group, Figs. 75–76). Based on the phylogenetic analysis here we concluded that *Thisbe fenestrella* is not a member of *Thisbe,* and therefore excluded it from our subsequent analysis of *Thisbe* and *Uraneis.*

Despite the exclusion of problematic taxa (see Methods, Phylogenetic Analyses) the tree in Figure 1 is less resolved than the one presented by Penz and DeVries (1999). This instability is likely due to the fact that ca. 90% of the characters used in the analyses were from male and female genitalia. Although genitalia characters are adequate to group species and closely related genera (Fig. 1), within Nymphidiini they appear too labile for resolving deep nodes of the tree (Penz and DeVries, 1999). Based on our experience we believe that alternative sources of characters (e.g., early stage morphology, DNA sequence data) will prove useful for tribal level studies within Riodinidae.

Parsimony analysis of 30 characters for 11 species allowed us to assess the phylogenetic relationships among *Thisbe fenestrella, Thysanota galena,* and species of *Synargis.* A single most parsimonious tree was produced (tree length = 68 steps, CI = 0.55, RI = 0.65) in which *T. fenestrella* appears as sister species to *S. velabrum* (Fig. 1, Analysis 2). Two characters justify grouping *T. fenestrella* with *S. velabrum*: character 3:0, abdominal projections asymmetrical (unique to this group), and character 29:0, coecum penis absent. Four characters suggest that *T. galena, T. fenestrella, S. velabrum,* and *S. phillone* form a monophyletic group: character 22: 0, tip of valva more heavily sclerotized than the base, pointed (unique to this group); character 23: 0, juxta joins valvae at base; character 26:1, dorsal bulge of aedeagus present (unique to this group); and character 28:0, distal opening of aedeagus dorsal (unique to this group). Since both *T. fenestrella* and *T. galena* are imbedded within *Synargis* (Fig. 1), this strongly suggests that *Synargis* is paraphyletic. Transferring *T. fenestrella* to *Synargis* resolves this problem in part (see Taxonomy section), and although the pattern of relationships in Figure 1 indicates that *T. galena* should be classified in *Synargis,* the relationships between these taxa will be addressed in a future study (DeVries and Penz, in preparation)

**EXAMINED SPECIMENS.** *Adelotypa alector*: ECUADOR, Sucumbios, Garza Cocha, 1 male, 1 female (PJD). *Aricoris tutana*: BRAZIL, Santa Catarina, Jaraguá do Sul, 1 male (AME); BRAZIL, Santa Catarina, São Bento do Sul, 1 male (AME). *Audre domina*: PANAMA, Panama, Pipeline Road, 1 male (PJD); PANAMA, Panama, Gamboa, 1 female (PJD). *Audre erostratus*: PANAMA, Panama, Corozal, 1 male (ANMH); PANAMA, Panama, Nueva Gorgona, 1 female (AMNH). *Audre* sp.: ARGENTINA, Mendoza, San Rafael, 1 male, 1 female (PJD). *Calospila emylius*: ECUADOR, Sucumbios, Garza Cocha, 1 male, 1 female (PJD). *Eiseleia pinchanalensis*: PARAGUAY, Cordillera San-

tíssima Trinidad, 1 male (AME); ARGENTINA, Salta, Pichanal, 1 female (AME). *Ematurgina* nr. *leucotopus*: ECUADOR, Sucumbios, Garza Cocha, 1 male (PJD). *Juditha azan*: ECUADOR, Sucumbios, Garza Cocha, 1 male, 1 female (PJD). *Juditha molpe*: COSTA RICA, Puntarenas, Parque Nacional Corcovado, 1 male, 1 female (PJD). *Lemonias caliginea*: MEXICO, Veracruz, 1 male, 1 female (LACM). *Lemonias zygia*: BRAZIL, Rondônia, Caucalândia, Fazenda Rancho Grande, 1 male, 1 female (LACM). *Nymphidium azanoides*: PANAMA, Darién, Cerro Pirre, 1 male (PJD); COSTA RICA, Heredia, La Selva, 1 male, 1 female (PJD). *Nymphidium cachrus*: ECUADOR, Sucumbios, Garza Cocha, 1 male, 1 female (PJD). *Nymphidium mantus*: ECUADOR, Sucumbios, Garza Cocha, 1 male (PJD); PANAMA, Darién, Cerro Pirre, 1 male (PJD); PANAMA, Panama, Barro Colorado Island, 1 male (PJD); PANAMA, Panama, Pipeline Road, 1 female (PJD). *Setabis lagus*: COSTA RICA, Puntarenas, Las Alturas, 1 male (PJD); COSTA RICA, Puntarenas, Las Cruces, 1 female (PJD). *Stalachtis euterpe*: ECUADOR, Sucumbios, Garza Cocha, 1 male, 1 female (PJD). *Synargis abaris*: PERU, Madre de Dios, Shintuya, 1 male (PJD); ECUADOR, Napo, Jatun Sacha, 1 female (PJD). *Synargis ethelinda*: COSTA RICA, Puntarenas, Barranca, 1 male (PJD); BELIZE, Orangewalk, Hillbank, 1 female (PJD). *Synargis gela*: no data, 1 male (MPM); BRAZIL, Amazonas, Borba, 1 female (MPM). *Synargis mycone*: COSTA RICA, Guanacaste, Parque Santa Rosa, 1 male (PJD); PANAMA, Panama, Barro Colorado Island, 1 male (PJD); COSTA RICA, Limon, Tortuguero, 1 female (PJD). *Synargis orestes*: ECUADOR, Sucumbios, Garza Cocha, 1 male, 1 female (PJD). *Synargis palaeste*: COSTA RICA, Puntarenas, Parque Nacional Corcovado, 1 male (PJD); COSTA RICA, Puntarenas, Rincón, 1 male (PJD); PANAMA, Darién, Pivesal, 1 female (PJD). *Synargis phillone*: BRAZIL, Rio de Janeiro, Pinheiral, 1 male (MPM); no data, 1 female (MPM). *Synargis tytia*: BRAZIL, Rondônia, Caucalândia, Fazenda Rancho Grande, 1 male (MPM); BRAZIL, Obidos, 1 female (MPM). *Synargis velabrum*: COSTA RICA, Heredia, Tirimbina, 1 male (MPM); COSTA RICA, Heredia, Tilamate, 1 female (PJD). *Theope publius*: COSTA RICA, Puntarenas, Punta Quepos, 1 male (PJD); COSTA RICA, Puntarenas, Corcovado, 1 female (PJD). *Theope virgilius*: COSTA RICA, Puntarenas, Isla del Caño, 1 male, 1 female (PJD). *Thisbe irenea*: COSTA RICA, Heredia, Chilamate, 1 male (PJD); PANAMA, Panama, Pipeline Road, 1 male (PJD); PANAMA, Panama, Barro Colorado Island, 1 female (PJD). *Thisbe lycorias*: COSTA RICA, Guanacaste, Parque Santa Rosa, 1 male (PJD); COSTA RICA, Heredia, Finca La Selva, 1 female (PJD). *Thisbe molela*: PERU, Madre de Dios, Shintuya, 1 male (PJD); VENEZUELA, Canaima, 1 female (LACM). *Thysanota galena*: BRAZIL, Rondônia, Caucalândia, Fazenda Rancho Grande, 1 male (MPM), 1 male, 1 female (AMNH). *Uraneis hyalina*: ECUADOR, Sucumbios, Garza Cocha, 1 male, 1 female (PJD). *Uraneis ucubis*: COSTA RICA, Heredia, Cariblanco, 1 male (PJD); COSTA RICA, Cartago, Turrialba, 1 female (PJD). *Uraneis zamuro*: ECUADOR, Tena-Loreto Road, 1 male (JH).

## Phylogeny of *Thisbe* and *Uraneis*

Parsimony analysis of 39 characters for six species of *Thisbe* and *Uraneis* produced a single most parsimonious tree (tree length = 64 steps, CI = 0.72, RI = 0.77, Fig. 2). Our results indicated that *Thisbe irenea* and *T. molela* are sister species, and *T. lycorias* groups with *Uraneis hyalina, U. ucubis,* and *U. zamuro,* thus confirming the hypothesis that *Thisbe* is paraphyletic with respect to *Uraneis* (Penz and DeVries, 1999), and justifying the placement of *T. lycorias* in *Uraneis.* Characters that support groupings in Figure 2 are as follows.

***Thisbe* Plus *Uraneis.*** Five characters justify grouping *Thisbe* and *Uraneis* (Fig. 2): character 3: 0, hindwing A2 produced in at least one sex; character 9:0, connection of ductus bursa with corpus bursa narrow (Figs. 24, 35, 45, 55, 72); character 10:0, corpus bursa rounded (Figs. 24, 35, 45, 55, 72); character 12:1, spines that compose the sculpturing of corpus bursa clustered (not in *T. irenea*); character 17:0, in ventral view, uncus with a central depression (Figs. 19, 30, 40, 50, 67).

***Thisbe irenea* Plus *T. molela.*** Grouping of *Thisbe irenea* and *T. molela* (Fig. 2) was supported by nine characters: character 15:0, in dorsal view, shape of the uncus: pattern A (Figs. 20, 31); character 18:0, ventral depression of uncus narrow (Figs. 19, 30); character 19:0, distal portion of gnathos wide (Figs. 19, 30); character 22:1, posterior end of subscaphium broad (Figs. 19, 30); character 23:1, in ventral view, posterior end of the subscaphium not extended, ending before anterior edge of uncus (Figs. 19, 30); character 24:0, in lateral view, vinculum sharply bent immediately after tegumen (Figs. 18, 29, also in *Lemonias caliginea*); character 30:1, coecum penis present (Fig. 19, also in *Uraneis hyalina* and *L. caliginea*); character 32:1, lateral portion of valva weakly sclerotized (also in *L. zygia*); character 39:0, in lateral view, anterior base of valva conspicuously extending anteriorly beyond vinculum in an angle (Figs. 18, 29).

***Thisbe lycorias* Plus *Uraneis.*** Despite contrasting wing color pattern (Figs. 36–38, 46–48, 56–57, 62–65), *Thisbe lycorias* forms a monophyletic group with species of *Uraneis* (Fig. 2). Twelve characters justify this relationship: character 1:0, base of tegula bright orange or red, clearly contrasting with thorax; character 4:1, distribution of sensilla on first tarsomere of female foreleg: along the distal two-thirds (unknown for *U. zamuro*); character 14: 1, male abdominal sternite 8 lacking terminal projections; character 15:1, in dorsal view, shape of the uncus: pattern B (Figs. 41, 51, 61, 69); character 18:1, ventral depression of uncus broad (Figs. 40, 50, 67); character 20:0, distal and proximal por-

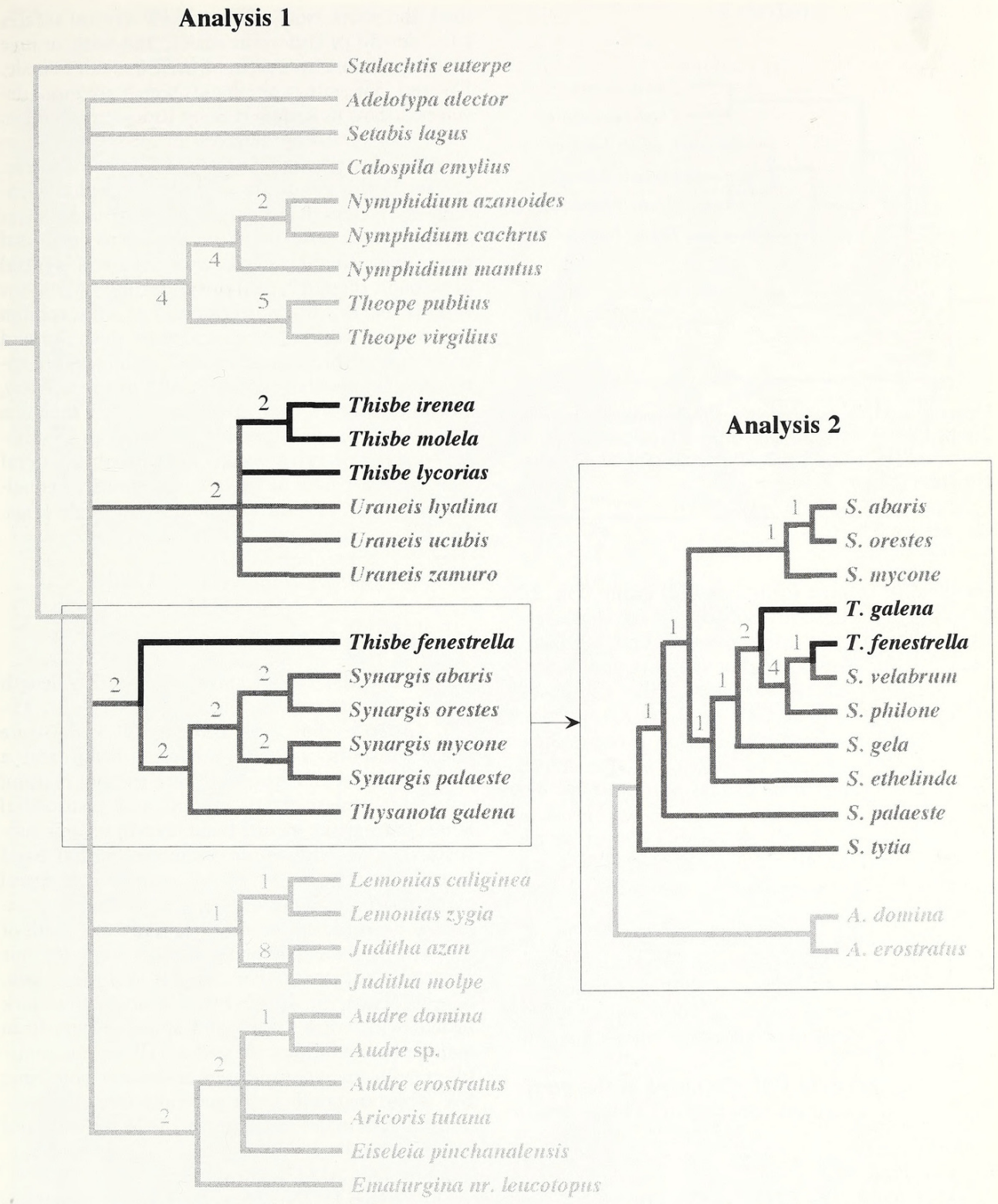



**Figure 1** Analysis 1—Strict consensus of two equally parsimonious trees from the analysis of 97 characters for 28 taxa (tree length = 351 steps, CI = 0.36, RI = 0.63). Analysis 2—Single most parsimonious tree from the analysis of 30 characters for 11 taxa (tree length = 68 steps, CI = 0.55, RI = 0.65). Numbers above branches are Bremer indices of support

tions of gnathos forming an angle (Figs. 39, 49, 58, 66); character 21:1, pedunculum reduced; character 25:2, in ventro-lateral view, vinculum narrow; character 27:0, cornuti absent; character 33:0, lateral portion of valva with a transversal window (Figs. 39, 49, 58, 66); character 34:0, valva with a lateral constriction (Figs. 40, 50, 59, 67); character 37:0, tip of valva adorned with spines (Figs. 40, 50, 59, 67).

***Uraneis hyalina, U. ucubis,*** **and** ***U. zamuro.*** Our analysis of characters independent from wing color pattern indicated that the three species currently

**Analysis 3**

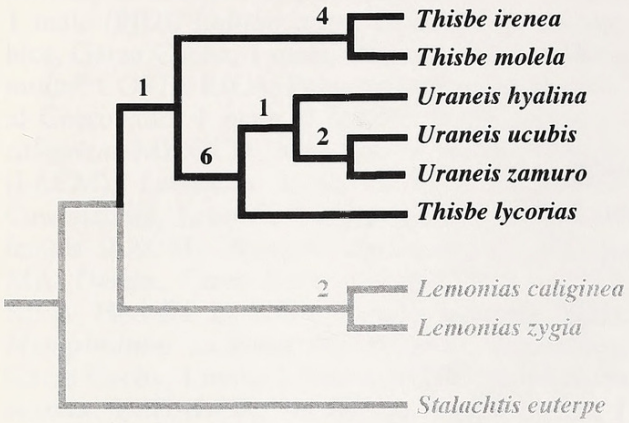



Figure 2 Analysis 3—Single most parsimonious tree from the analysis of 39 characters for nine taxa (tree length = 64 steps, CI = 0.72, RI = 0.77). Numbers above branches are Bremer indices of support

classified in *Uraneis* form a natural group (Fig. 2). These relationships are justified by seven characters (those of female *U. zamuro* are unknown): character 2:1, forewing R4 meets wing margin posteriorly to apex; character 7:1, genital plate composed of two units (Figs. 44, 53); character 8:1, portion of ductus bursa bordering antrum membranous; character 11:0, corpus bursa with a cone-shaped protrusion located in its medial portion (Figs. 45, 55); character 26:1, in ventral view, vinculum arched (Figs. 40, 50, 59); character 35:0, valva with a mild arch (Figs. 40, 50, 59); character 36:1, tip of valva similarly sclerotized to the remaining portion.

***Uraneis ucubis* Plus *U. zamuro*.** Two characters indicate that *Uraneis ucubis* and *U. zamuro* are sister species (Fig. 2): character 28:0, distal opening of aedeagus dorsal; character 38:0, tip of valva shaped as a hook that smoothly curves inwards (Figs. 50, 59).

**EXAMINED SPECIMENS.** Listed in the previous section, Systematic position of *Thisbe fenestrella*.

## TAXONOMY

### *Thisbe* Hübner, 1819
(Figs. 3–35)

*Thisbe* Hübner, 1819:24. Type species: *Papilio belise* Stoll, 1782, by monotypy.

**DESCRIPTION.** Male. FW dorsal surface: dark brown with marginal row of white spots (inconspicuous in some subspecies), and subapical and medial white bands; a broad band pale blue iridescent scales flank the white medial band (except for one subspecies). HW dorsal surface: medial/submedial white band (faint in males of *Thisbe molela*) on a dark brown background; iridescent scales flank the white band. FW and HW ventral suface: pale, devoid of iridescent scales, and with orange markings (more conspicuous in *T. irenea*). Female. FW and HW with white bands which are more developed than in males; lacking iridescent scales in the dorsal surface, except for an inconspicuous iridescent blue ring at tornus of HW in some forms. Species in this genus are sexually dimorphic. Genitalia characters that separate *Thisbe* from its sister genus *Uraneis* are: shape of the uncus in dorsal view (Figs. 20, 31); uncus with a narrow ventral depression (Figs. 19, 30); distal portion of gnathos wide (Figs. 19, 30); posterior end of subscaphium broad (Figs. 19, 30); in ventral view, posterior end of the subscaphium not extended, ending before anterior edge of uncus (Figs. 19, 30); in lateral view, vinculum sharply bent immediately after tegumen (Figs. 18, 29); coecum penis present (Fig. 19); lateral portion of valva weakly sclerotized; in lateral view, anterior base of valva conspicuously extending anteriorly beyond vinculum in an angle (Figs. 18, 29).

### *Thisbe irenea* (Stoll, 1780)
(Figs. 3–24)

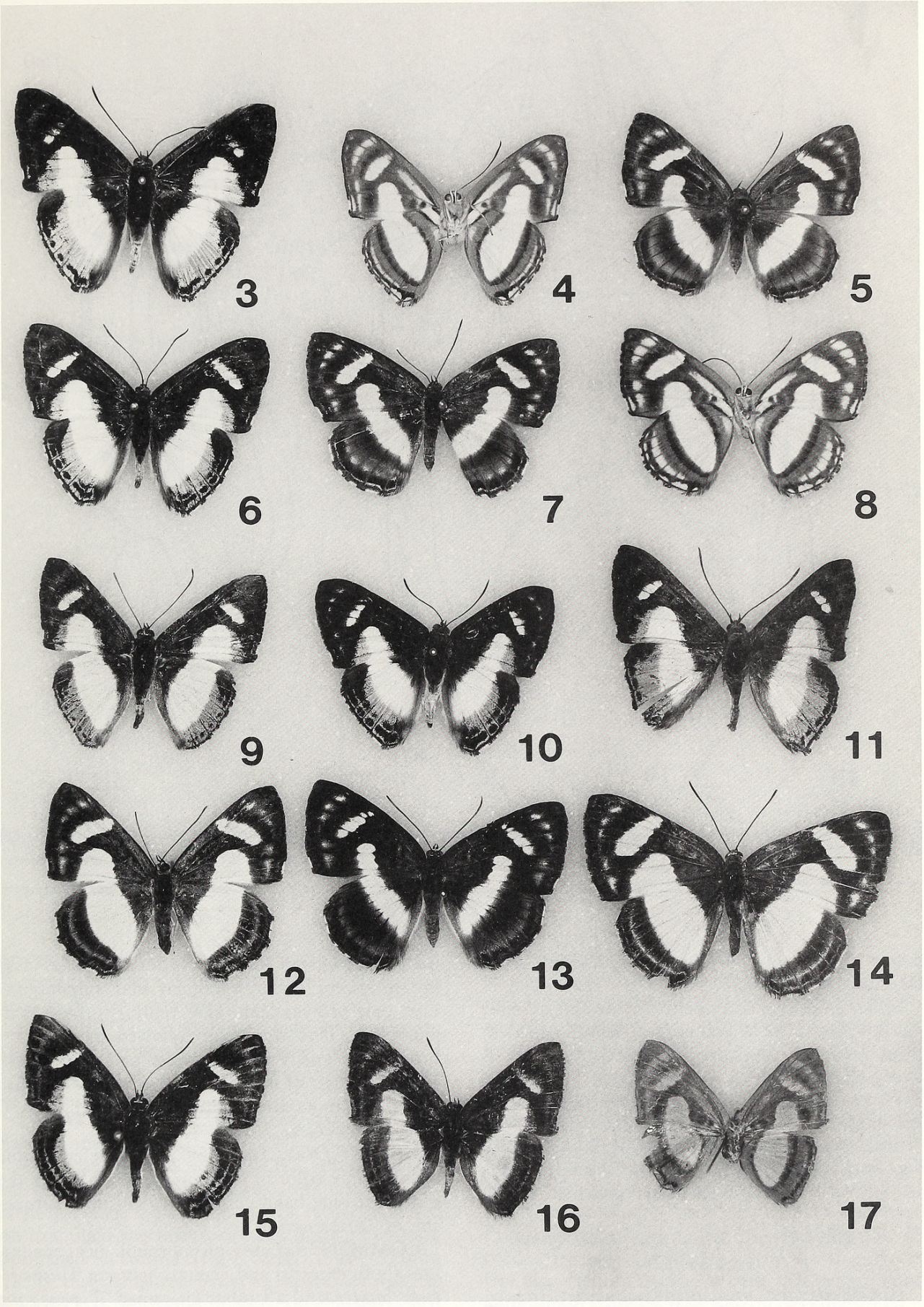
*Papilio irenea* Stoll, 1780:77.

**DIAGNOSIS.** Dorsal surface: Male (FW length 16.5–21.3 mm, n = 9) (Figs. 3–4, 6–7, 9–11, 15–17). Ground color dark brown; FW with white marginal spots, a white subapical band, and a white medial band from cell Cu1 to anal margin; pale blue iridescent submedial and postmedial bands flank white medial band (except for one subspecies). HW with white submedial/medial band from costal margin to cell 1A, expanded in discal area, and flanked by a pale blue iridescent postmedial band that is one-third or more the width of the white submedial/medial band (except for one subspecies). Female (FW length 18.3–22.5 mm, n = 6) (Figs. 5, 8, 12–14). Ground color dark brown with white bands and spots. Differs from male in lacking iridescent scales; HW tornus sometimes with an inconspicuous iridescent blue ring; FW white marginal spots generally more conspicuous than in males. See Figures 18–24 for male and female genitalia.

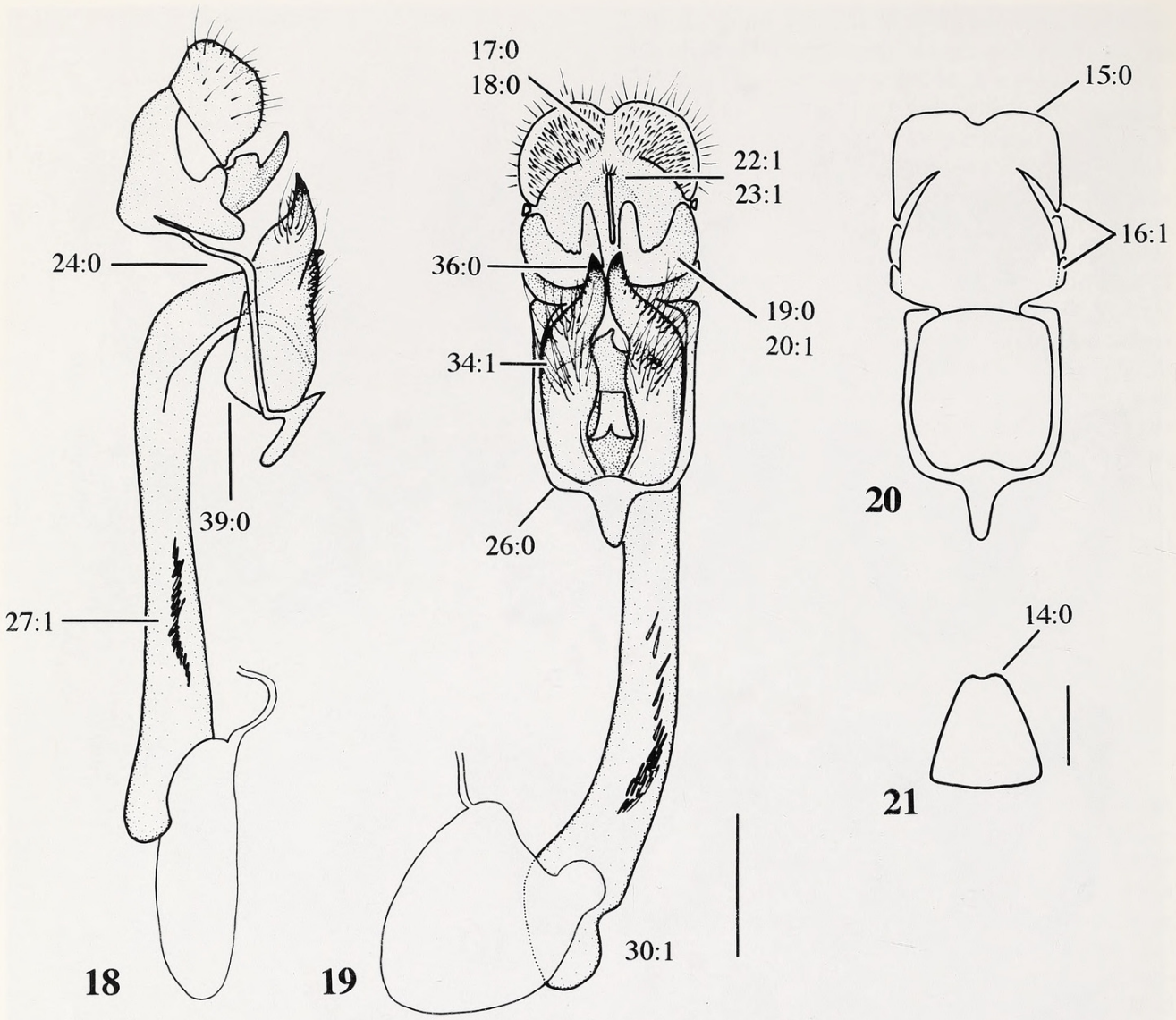
**TYPE LOCALITY.** Guyana.

**DISTRIBUTION.** Mexico, Central America, Guyana to Colombia, Ecuador, Peru, Venezuela, Trinidad, Brazil (Seitz, 1916; Stichel, 1930, 1931; DeVries, 1997).

**BIOLOGY.** In Belize, Costa Rica, Ecuador, and Peru caterpillars of *Thisbe irenea* feed on saplings of *Croton* spp. (Euphorbiaceae), and the caterpillars associate with a number of ant species (DeVries, 1988, 1997, and unpublished). In both sexes the color pattern of the hindwing underside resembles certain nymphalids (e.g., *Adelpha* Hübner, 1819; *Dynamine* Hübner, 1819; and *Eresia* Boisduval, 1836), and female *T. irenea* resemble certain *Dynamine* spp. and the melitaeine *Janatella leuco-*




**Figures 3–17** *Thisbe irenea* adults; **3,** *T. irenea irenea* male, dorsal (French Guyana); **4,** *T. irenea irenea* male, ventral (Panama); **5,** *T. irenea irenea* female, dorsal (Cayenne); **6,** *T. irenea belides* male, dorsal (Tefé, Brazil); **7,** *T. irenea belides* female, dorsal (Tefé, Brazil); **8,** *T. irenea irenea* female, ventral (Panama); **9,** *T. irenea atlantis* male, dorsal (Trinidad); **10,** *T. irenea interjecta* male, dorsal (Mato Grosso, Brazil); **11,** *T. irenea prodiga* male, dorsal (Minas Gerais, Brazil); **12,** *T. irenea atlantis* female, dorsal (Trinidad); **13,** *T. irenea interjecta* female, dorsal (Mato Grosso, Brazil); **14,** *T. irenea prodiga* female, dorsal (Jacarepaguá, Brazil); **15,** *T. irenea* male, dorsal (Madre de Dios, Peru); **16,** *T. irenea branca* new subspecies male, dorsal (Amazonas, Brazil); **17,** *T. irenea branca* new subspecies male, ventral (Amazonas, Brazil)




**Figures 18–21** *Thisbe irenea,* male genitalia; **18,** lateral view; **19,** ventral view; **20,** detail of the dorsal view; **21,** 8th sternite. Scale bars = 0.5 mm

*desma* (Felder and Felder, 1861) (Seitz, 1916; DeVries, 1987, 1997).

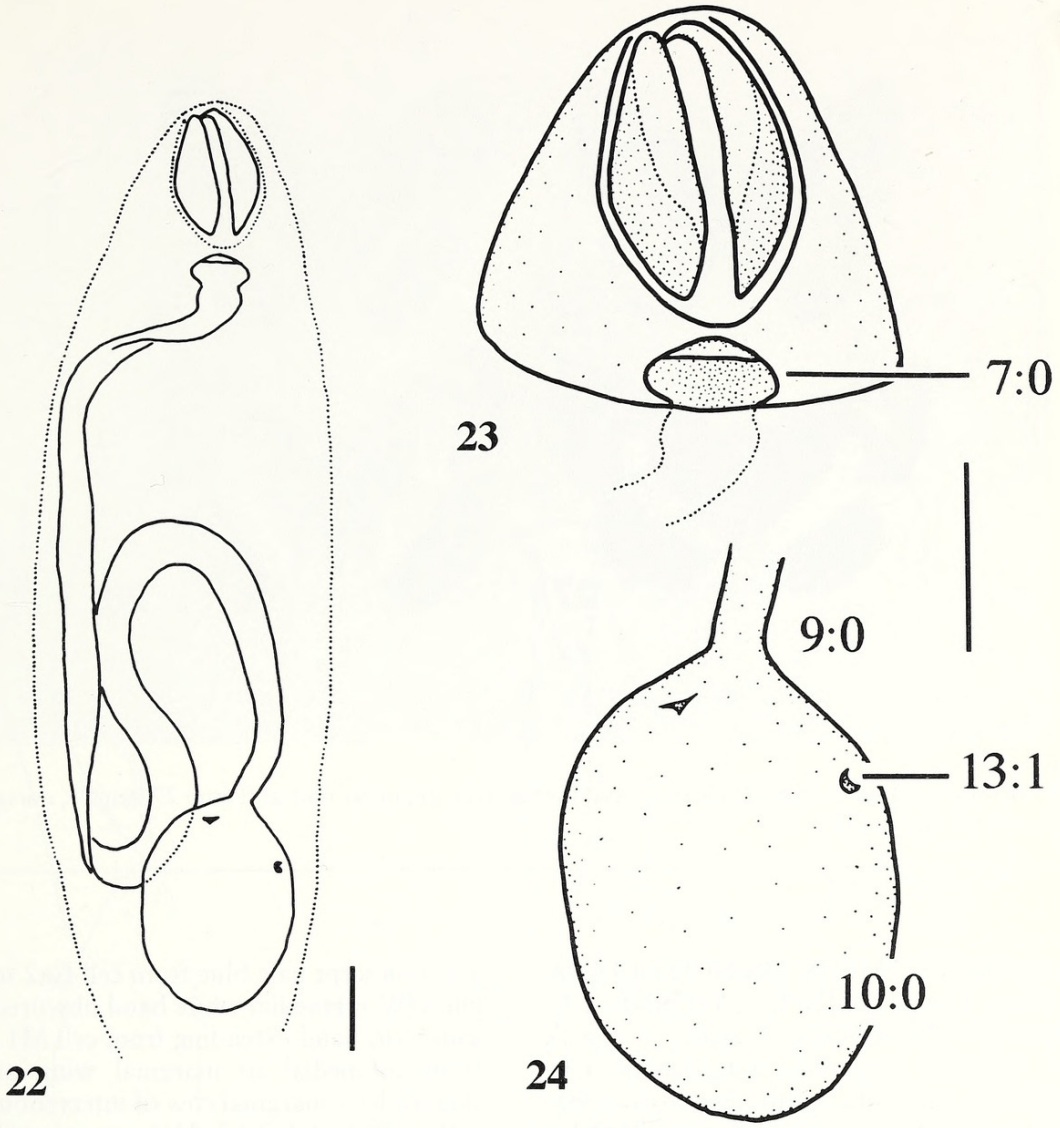
**SUBSPECIES.** In addition to *Thisbe irenea irenea* (Stoll, 1780) (Mexico and part of Central America) (Figs. 3–5), we recognize four other subspecies: *T. irenea atlantis* Stichel, 1910 (Trinidad) (Figs. 9, 12), *T. irenea belides* Stichel, 1910 (Costa Rica, Colombia) (Figs. 6–7), *T. irenea interjecta* Talbot, 1928 (Brazil, Mato Grosso) (Figs. 10, 13), *T. irenea prodiga* Stichel, 1929 (Brazil, Espirito Santo) (Figs. 11, 14), plus a new subspecies from Amazonas, Brazil.

### *Thisbe irenea branca* new subspecies
(Figs. 16–17)

**DESCRIPTION.** Male (FW length 17.3–18 mm, n = 2) (Figs. 16–17). FW dorsal surface: white marginal spots faint, submarginal band small; lacking iridescent scales. FW ventral surface: subapical, disco-cellular and submedial white bands encircled by pale brown scales (i.e., surface of the wing predominantly brown and white). HW dorsal surface: lacking iridescent scales; marginal and submarginal lines pale brown, faint. HW ventral surface: marginal white line very thin, followed by a thicker brown line and very thin white and pale brown lines. The lack of iridescent scales makes *T. irenea branca* the most distinct and easily recognizable *T. irenea* subspecies.

**ETYMOLOGY.** The name *branca* refers to the simple white color of the wing bands that lack the iridescent blue band common to all other subspecies of *Thisbe irenea.*

**COMMENTS.** Based on morphological similarities (both external and genital) between *Thisbe irenea branca* and all other examined *T. irenea* we conferred this new taxon subspecific status. However, our assessment should be confirmed though examination of more specimens from the type locality and neighboring populations—not available at present. Should *T. irenea* males possessing iri-




**Figures 22–24** *Thisbe irenea,* female genitalia; **22,** outline of the abdomen; **23,** detail of the ostium bursa; **24,** detail of the corpus bursa. Scale bars = 0.5 mm

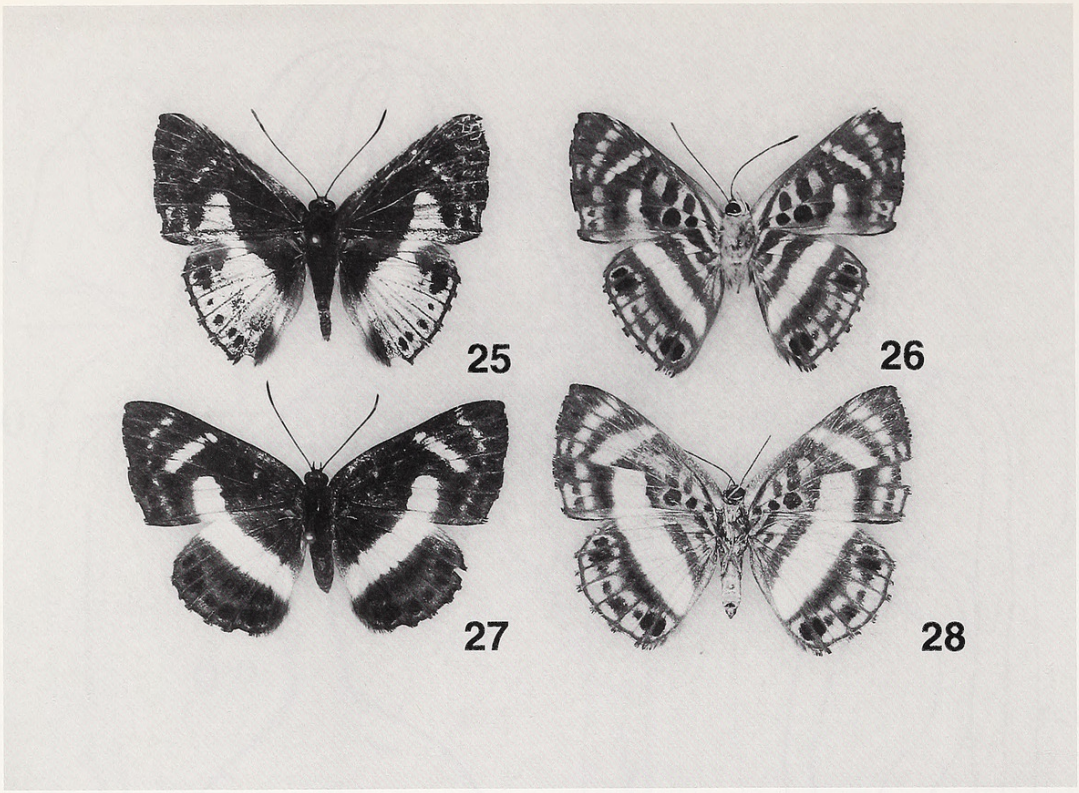
descent blue bands occur in the same locality with *T. irenea branca,* the rank of this new taxon will need to be reevaluated.

**DISTRIBUTION.** Only two male specimens are known, both from the same locality in Brazil.

**HOLOTYPE.** BRAZIL, Amazonas, Carauari Road, 1 male (LACM).

**PARATYPE.** BRAZIL, Amazonas, Carauari Road, 1 male (LACM).

**COMMENTS ON SUBSPECIES.** Among all species we studied, geographic variation was most evident in *Thisbe irenea* (Figs. 3–17). However, based on examined specimens, original descriptions, and published accounts (e.g., Seitz, 1916; Talbot, 1928), discrimination between subspecies was not always clear. We found that certain characters varied both between and within subspecies (e.g., darkening of the ventral side of the forewing), and that characters used to define subspecies were, at times, of questionable use because color pattern may overlap (e.g., width of the male HW dorsal iridescent postmedial band; see also Seitz, 1916). With respect to wing color pattern, we found that males of the subspecies *T. i. irenea* (Fig. 3), *T. i. belides* (Fig. 6), and *T. i. interjecta* (Fig. 10) were almost indistinguishable (see also Talbot, 1928), and males of *T. i. atlantis* (Fig. 9) and *T. i. prodiga* (Fig. 11) were very similar. Except for *T. i. branca,* males of all subspecies had a relatively broad and well-defined hindwing dorsal iridescent postmedial band. However, we found that in specimens from Barro Colorado Island, Panama, and Madre de Dios, Peru, this band is slightly narrower than in specimens from other localities (Fig. 15), something also recorded by Seitz (1916) for Costa Rican material (see also Talbot, 1928). We note that geographical variation in color pattern was more pronounced in females than in males in our sample, and females of *T. i. belides* and *T. i. prodiga* can easily be distinguished (Figs. 7, 14). Nevertheless, we feel that critical evaluation of all currently valid subspecies will require examination of many more specimens.




Figures 25–28 *Thisbe molela* adults; **25**, male, dorsal (Venezuela); **26**, male, ventral (Peru); **27**, female, dorsal (Cayenne); **28**, female, ventral (Venezuela)

**EXAMINED SPECIMENS.** FRENCH GUIANA, Maroni River, 1 male (BMNH); CAYENNE, 1 female (BMNH); TRINIDAD, 1 male, 1 female (BMNH); BRAZIL, Amazonas, Tefé, 1 male, 1 female (BMNH); BRAZIL, Mato Grosso, Cuiabá–Corumbá River system, 1 male, 1 female (BMNH); BRAZIL, Rondônia, Caucalândia, Fazenda Rancho Grande, 1 male, 1 female (GA); BRAZIL, Rondônia, Caucalândia, Fazenda Rancho Grande, 1 male (LACM); BRAZIL, Rondônia, Caucalândia, Fazenda Rancho Grande, 1 female (BH); BRAZIL, Amazonas, Carauari Road, 2 males (LACM); COSTA RICA, Heredia, Chilamate, 1 male (PJD); PANAMA, Panama, Pipeline Road, 1 male (PJD); PANAMA, Panama, Barro Colorado Island, 1 male, 1 female (PJD); BELIZE, Punta Gorda, 1 female (LACM); PERU, Madre de Dios, 1 male (PJD); BRAZIL, Minas Gerais, Belo Horizonte, 1 male (BMNH); BRAZIL, São Paulo, Jacarepaguá (*sic*), 1 female (BMNH).

## *Thisbe molela* (Hewitson, 1865)
(Figs. 25–35)

*Nymphidium molela* Hewitson, 1865:14.
*Thisbe molela palilis* Stichel, 1910:87;
**new synonymy**

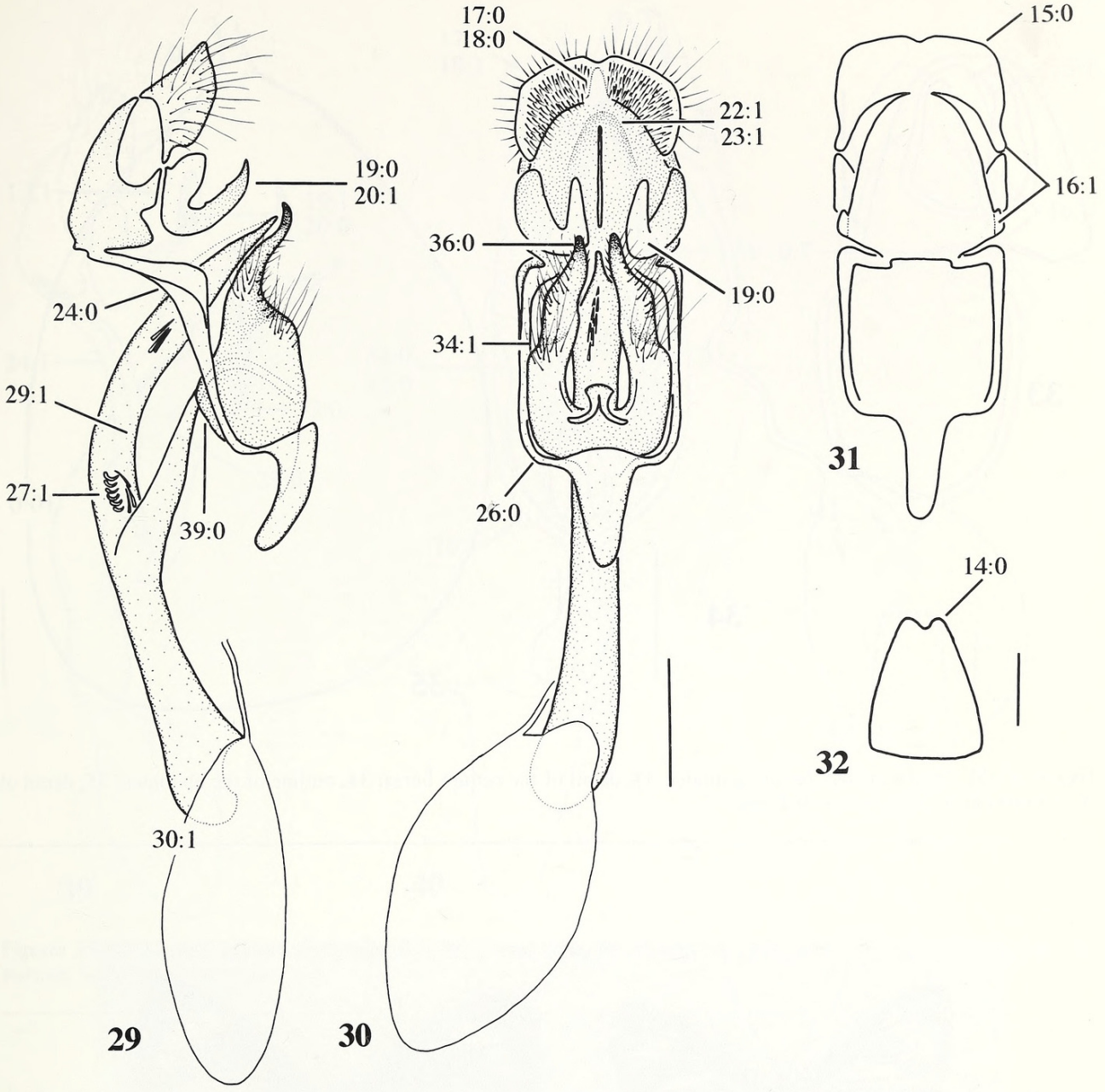
**DIAGNOSIS.** Dorsal surface: Male (FW length 17.5–19.4 mm, n = 5) (Figs. 25–26). Ground color dark brown; FW with faint marginal series of white spots; subapical row of white spots on cells R2, R5, M1, and M2; submedial band white on cell Cu1 and iridescent pale blue from cell Cu2 to anal margin. HW submedial white band obscured by a large iridescent band extending from cell M1 to 1A, and from submedial to marginal wing areas, interspersed by a marginal row of intervenous spots. Female (FW length 20.3–21.3 mm, n = 5) (Figs. 27–28). Lacking iridescence; FW marginal row of white spots more conspicuous than in males; subapical white band well developed; submedial white band more developed than in males; HW with a well-developed submedial white band; HW faint white marginal bands are interspersed by a marginal row of intervenous spots. See Figures 29–35 for male and female genitalia. Note that there were two different types of cornuti (Fig. 29).

**TYPE LOCALITY.** Amazonas.

**DISTRIBUTION.** Guyana, Venezuela, Amazonas, Peru, Pará (Brazil) (Seitz, 1916; Stichel, 1930, 1931; DeVries, personal observations).

**BIOLOGY.** Host plants and early stages unknown. Although *Thisbe molela* bears superficial resemblance to *T. irenea* on the dorsal surface (females in particular), the ventral surface of the wings is remarkably different between these species. The ventral pattern of *T. molela* is spotted and superficially similar to that of small satyrines (e.g., *Euptychia* Hübner, 1818, and *Cissia* Doubleday, 1848).

**COMMENTS ON SUBSPECIES.** Males of *Thisbe molela molela* (Hewitson, 1865) and *T. molela palilis* Stichel, 1910, are very similar except for a slightly more developed HW white submedial band




**Figures 29–32** *Thisbe molela,* male genitalia; **29,** lateral view; **30,** ventral view; **31,** detail of the dorsal view; **32,** 8th sternite. Scale bars = 0.5 mm

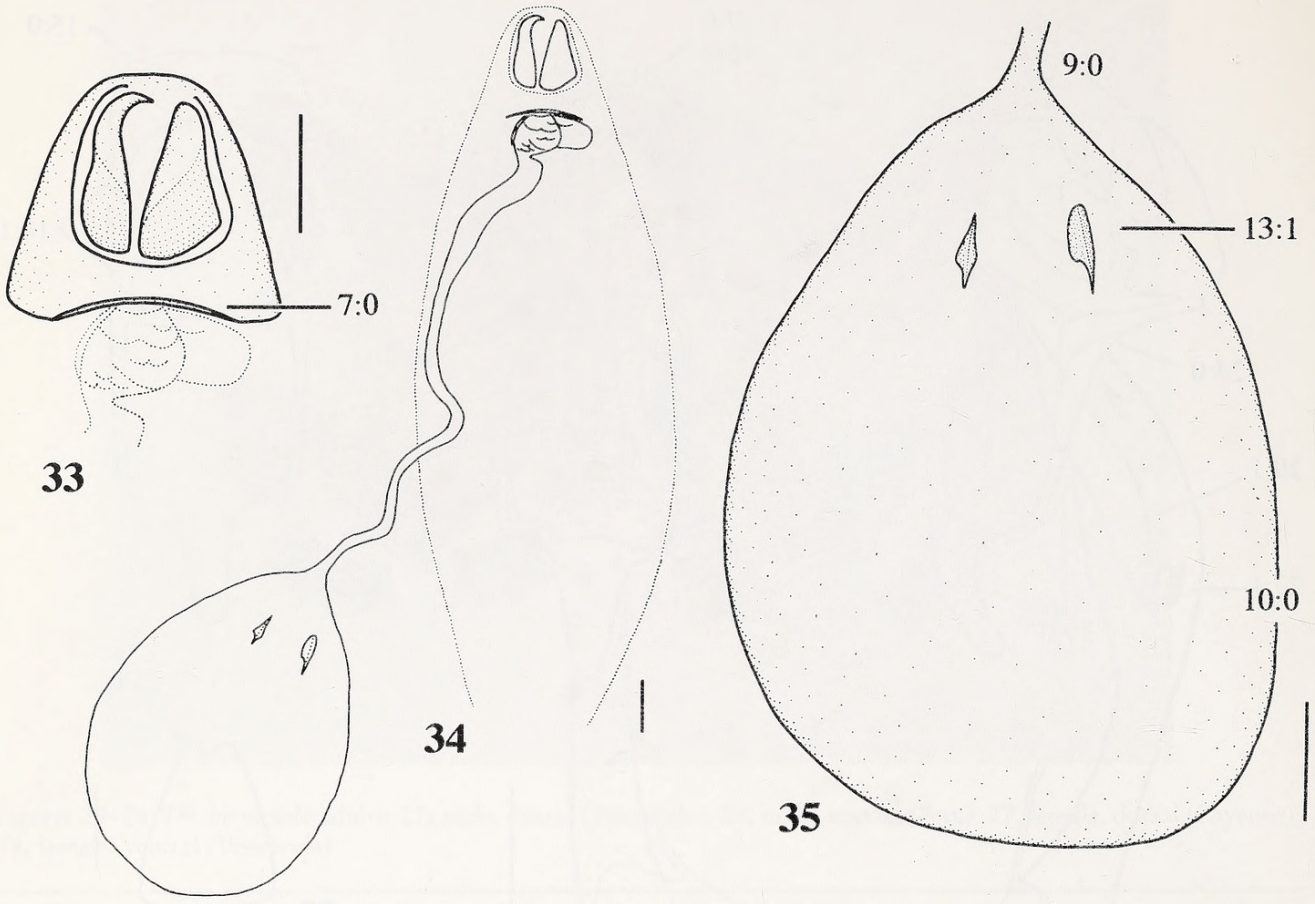
in *T. m. palilis.* Examined females from distant localities (and supposedly representing different subspecies) were indistinguishable to us. We therefore conclude that the subspecies designation *palilis* should be abandoned.

**EXAMINED SPECIMENS.** PERU, Madre de Dios, Shintuya, 1 male (PJD); BRAZIL, Rondônia, Caucalândia, Fazenda Rancho Grande, 1 male, 1 female (GA); BRAZIL, 1 male, 1 female (LACM); CAYENNE, 1 male, 1 female (BMNH); VENEZUELA, Canaima, 1 male, 2 females (LACM).

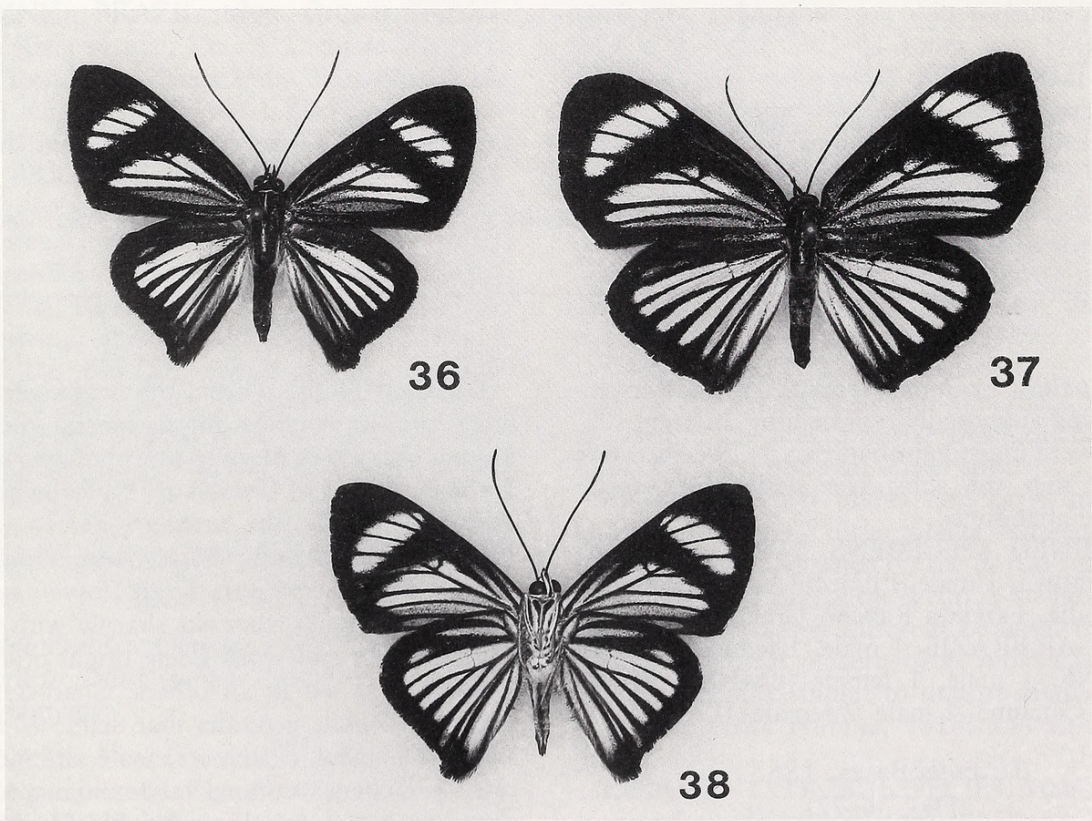
## *Uraneis* Bates, 1868
(Figs. 36–72)

*Uraneis* Bates, 1868:411. Type species: *Tharops hyalina* Butler 1867, by monotypy.

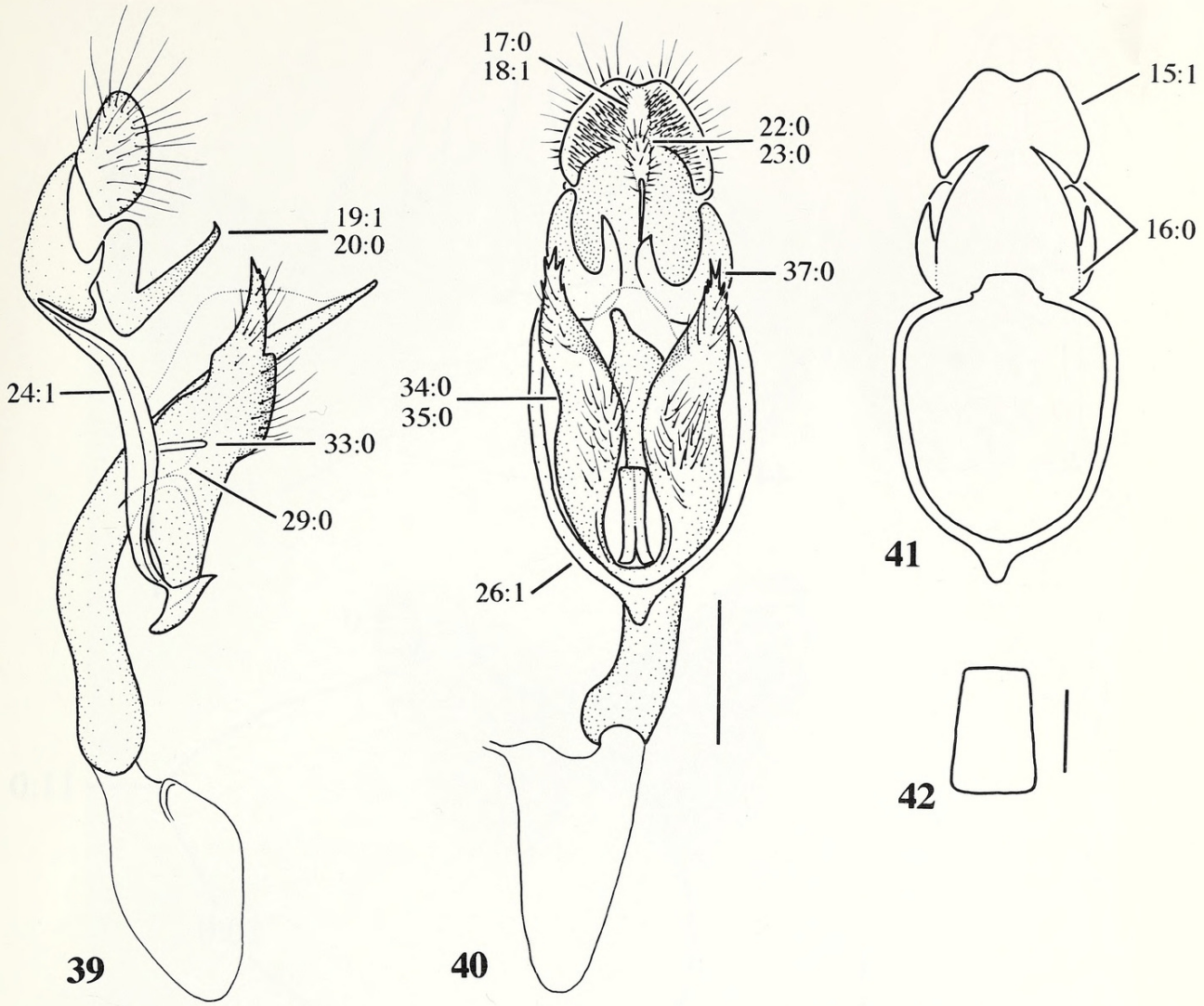
**DESCRIPTION.** Given the wide variation in wing color or venation among species, there are no unique characters of wing morphology that define *Uraneis.* Species of *Uraneis* are typically larger than species in *Thisbe,* the sexes are nearly monomorphic, and both the dorsal and ventral wing surfaces display a similar pattern. In all *Uraneis* species the base of the tegula contrasts sharply with the color of the thorax and wing, being bright orange in *U. lycorias,* and red in all others. Characters of the male and female genitalia that define *Uraneis* and separate it from *Thisbe* are: male abdominal sternite 8 lacking terminal abdominal projections; shape of the uncus (Figs. 41, 51, 61, 69); uncus with a broad ventral depression (Figs. 40, 50, 67); distal and proximal portions of gnathos forming an




**Figures 33–35** *Thisbe molela,* female genitalia; **33,** detail of the ostium bursa; **34,** outline of the abdomen; **35,** detail of the corpus bursa. Scale bars = 0.5 mm




**Figures 36–38** *Uraneis hyalina* adults; **36,** male dorsal (Ecuador); **37,** female, dorsal (Ecuador); **38,** male, ventral (Ecuador)




**Figures 39–42** *Uraneis hyalina,* male genitalia; **39,** lateral view; **40,** ventral view; **41,** detail of the dorsal view; **42,** 8th sternite. Scale bars = 0.5 mm

angle (Figs. 39, 49, 58, 66); pedunculum reduced; in ventro-lateral view, vinculum narrow; cornuti absent; lateral portion of valva with a transversal window (Figs. 39, 49, 58, 66); valva with a lateral constriction (Figs. 40, 50, 59, 67); tip of valva adorned with spines (Figs. 40, 50, 59, 67).

### *Uraneis hyalina* (Butler, 1867)
(Figs. 36–45)

*Tharops hyalina* Butler, 1867:225.

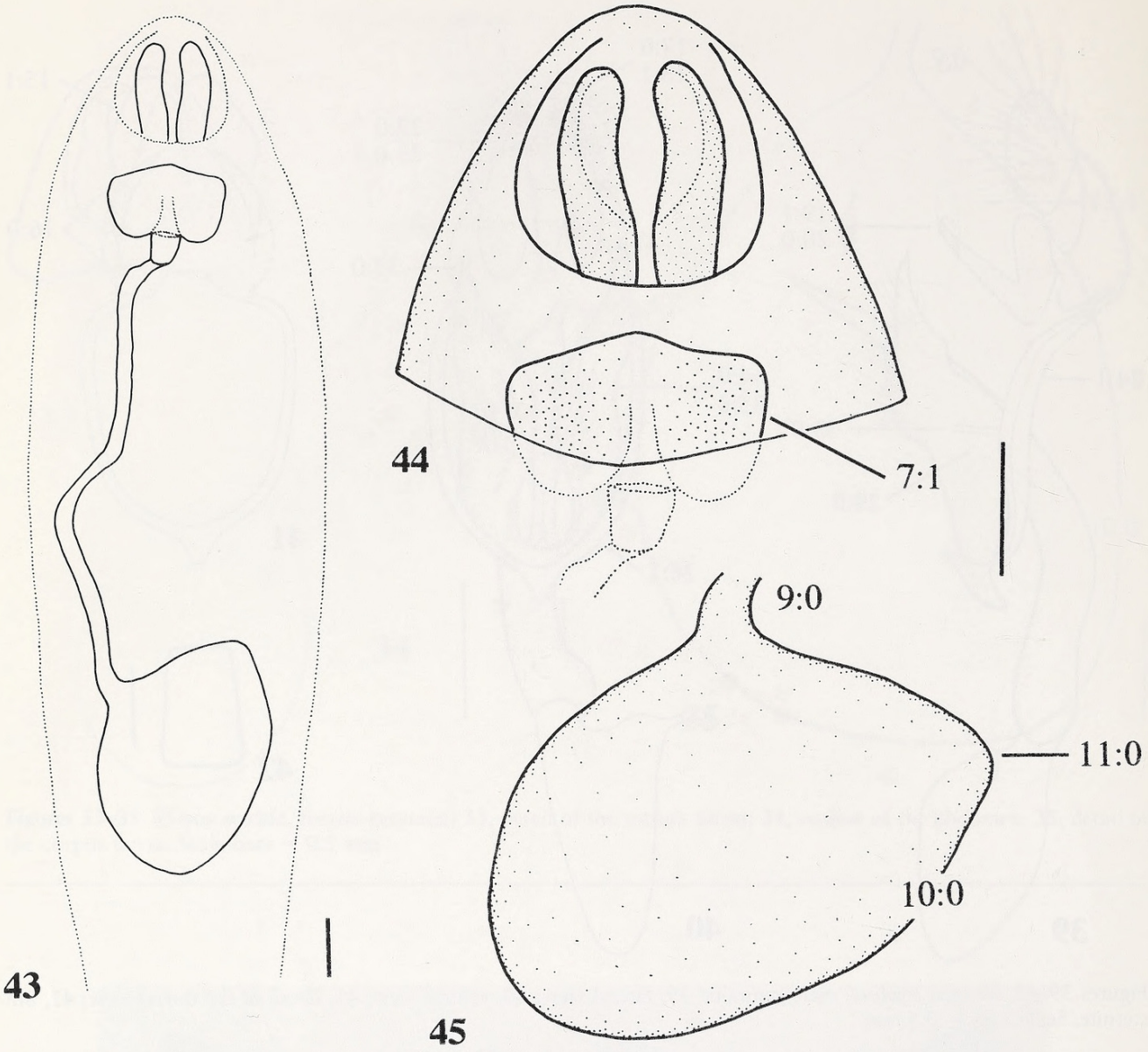
**DIAGNOSIS.** Dorsal surface: Male (FW length 21.9–24.2 mm, n = 4) (Figs. 36, 38). Ground color black; FW with white stripes, subapical white band, broad white stripes on discal cell, and cells Cu1 and Cu2; white stripe on cell Cu2 obscured from basal to medial portion by pale blue iridescent scales and divided longitudinally by a thin black line. HW with broad white intervenous stripes from basal to subapical areas covering most of its surface; broad white intervenous stripes on posterior half of discal cell, and cells M1, M2, M3, Cu1, Cu2, 1A+2A, and 3A. Female (FW length 26–27.3 mm, n = 2) (Fig. 37). Color almost identical to male; FW subapical white band slightly larger than in males; iridescent scales less conspicuous than in males. See Figures 39–45 for male and female genitalia.

**TYPE LOCALITY.** Amazonas.

**DISTRIBUTION.** Amazonas, Peru, Bolivia (Seitz, 1916; Stichel, 1930, 1931).

**BIOLOGY.** DeVries (1997) describes the larval biology from specimens reared in Ecuador. Adults resemble *Isostola* spp. (Arctiidae), *Phanoptis* spp. (Notodontidae), and the riodinids, *Lepricornis strigosa* (Staudinger, 1876) and *Esthemopsis colaxes* Hewitson, 1870a (see DeVries, 1997, for illustrations).

**SUBSPECIES.** There are no described subspecies. We found specimens from Rondônia, Brazil and Garza Cocha, Ecuador to be indistinguishable, and a single male from Peru, Pumayacu displayed an iridescent blue submarginal band from apex to tornus of the HW.




Figures 43–45 *Uraneis hyalina*, female genitalia; 43, outline of the abdomen; 44, detail of the ostium bursa; 45, detail of the corpus bursa. Scale bars = 0.5 mm

**EXAMINED SPECIMENS.** BRAZIL, Rondônia, Caucalândia, Fazenda Rancho Grande, 1 male (GA); BRAZIL, Rondônia, Caucalândia, Fazenda Rancho Grande, 1 male (BH); ECUADOR, Sucumbios, Garza Cocha, 5 males, 3 females (PJD); PERU, Pumayacu, 1 male (LACM).

## *Uraneis ucubis* Hewitson, 1870
(Figs. 46–55)

*Uraneis ucubis* Hewitson, 1870c:4.

**DIAGNOSIS.** Dorsal surface: Male (FW length 24.1 mm, n = 1) (Figs. 46, 48). Ground color black; FW with iridescent dark blue scales and a series of short longitudinal marginal stripes from cell R2 to Cu2. HW with iridescent dark blue scales and a series of short marginal white drop-shaped stripes from cell Rs to 1A+2A. Female (FW length 28 mm, n = 1) (Fig. 47). Dorsal surface dark brown; iridescence restricted to FW medial and postmedial areas of cells Cu1 and Cu2, almost not perceptible on HW, and absent in the ventral surface. See Figures 49–55 for male and female genitalia.

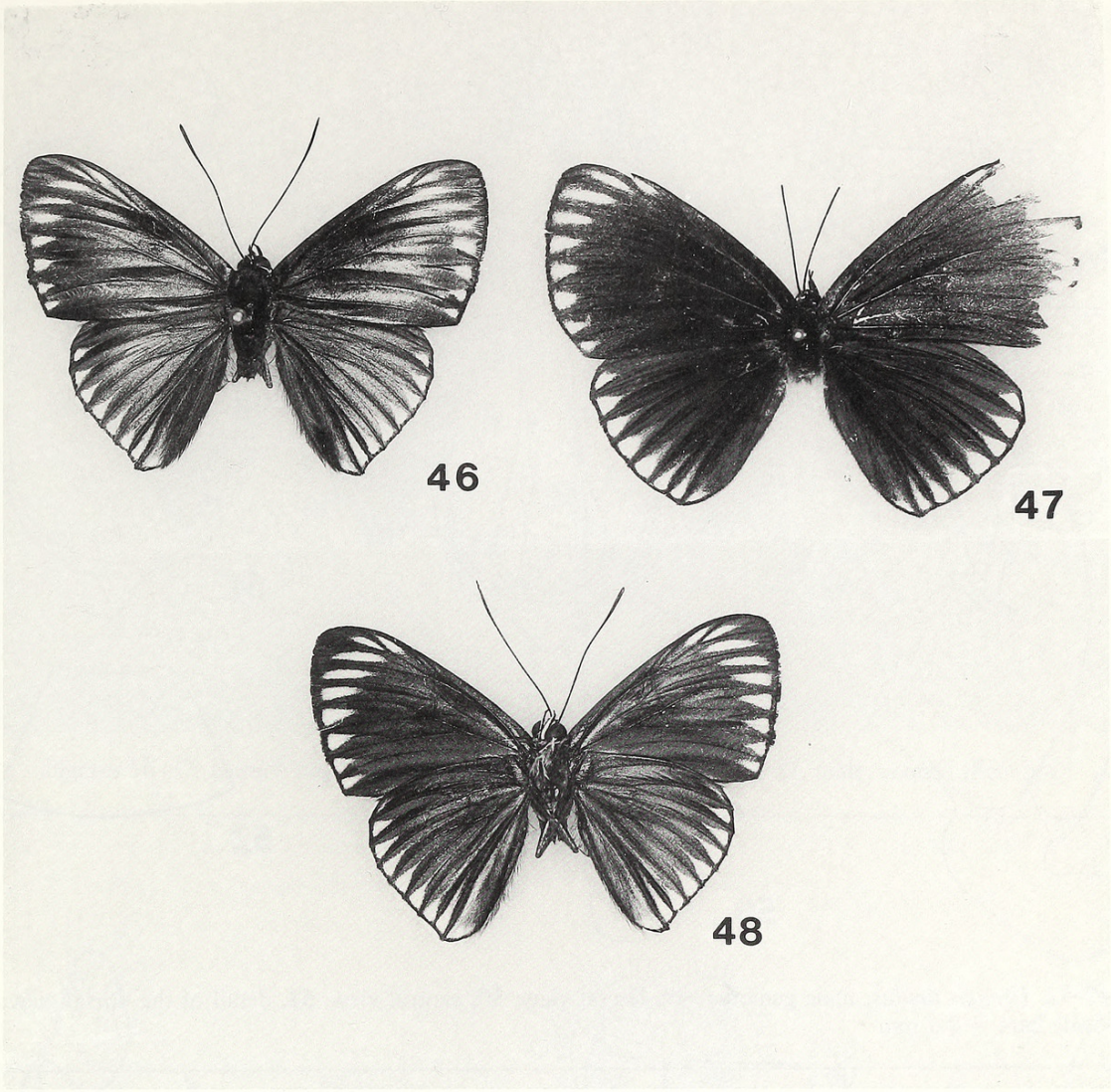
**TYPE LOCALITY.** Colombia.

**DISTRIBUTION.** Costa Rica to Colombia, Ecuador (DeVries, 1997), and possibly Pará, Brazil (Stichel, 1930, 1931).

**BIOLOGY.** Hostplants and early stages unknown. Adults resemble certain day-flying arctiid moths (DeVries, 1997).

**SUBSPECIES OR FORMS.** *Uraneis ucubis* form *lamprolenis* (Röber, 1903), described from West Colombia, was not examined.

**EXAMINED SPECIMENS.** COSTA RICA, Heredia, Cariblanco, 1 male (PJD); COSTA RICA, Cartago, Turrialba, 1 female (PJD).




**Figures 46–48** *Uraneis ucubis*, adults; **46**, male dorsal (Costa Rica); **47**, female dorsal (Costa Rica); **48**, male ventral (Costa Rica)

## *Uraneis zamuro* (Thieme, 1907)
(Figs. 56–61)

*Esthemopsis zamuro* Thieme, 1907:1, 11.

**DIAGNOSIS.** Dorsal surface: Male (FW length 23.2 mm, n = 1) (Figs. 56–57). Ground color dark brown to black; FW with large subapical white band; dark blue iridescence from basal to medial area. HW with narrow faint intervenous stripes from cell Sc+R1 to 1A+2A, entire wing dorsal surface iridescent dark blue. Females unknown to us. Male genitalia in Figs. 58–61.

**TYPE LOCALITY.** Ecuador.

**DISTRIBUTION.** Ecuador (Stichel, 1930, 1931).

**BIOLOGY.** Hostplants and early stages unknown. Like its congener, this species also appears to resemble certain day-flying arctiid moths.

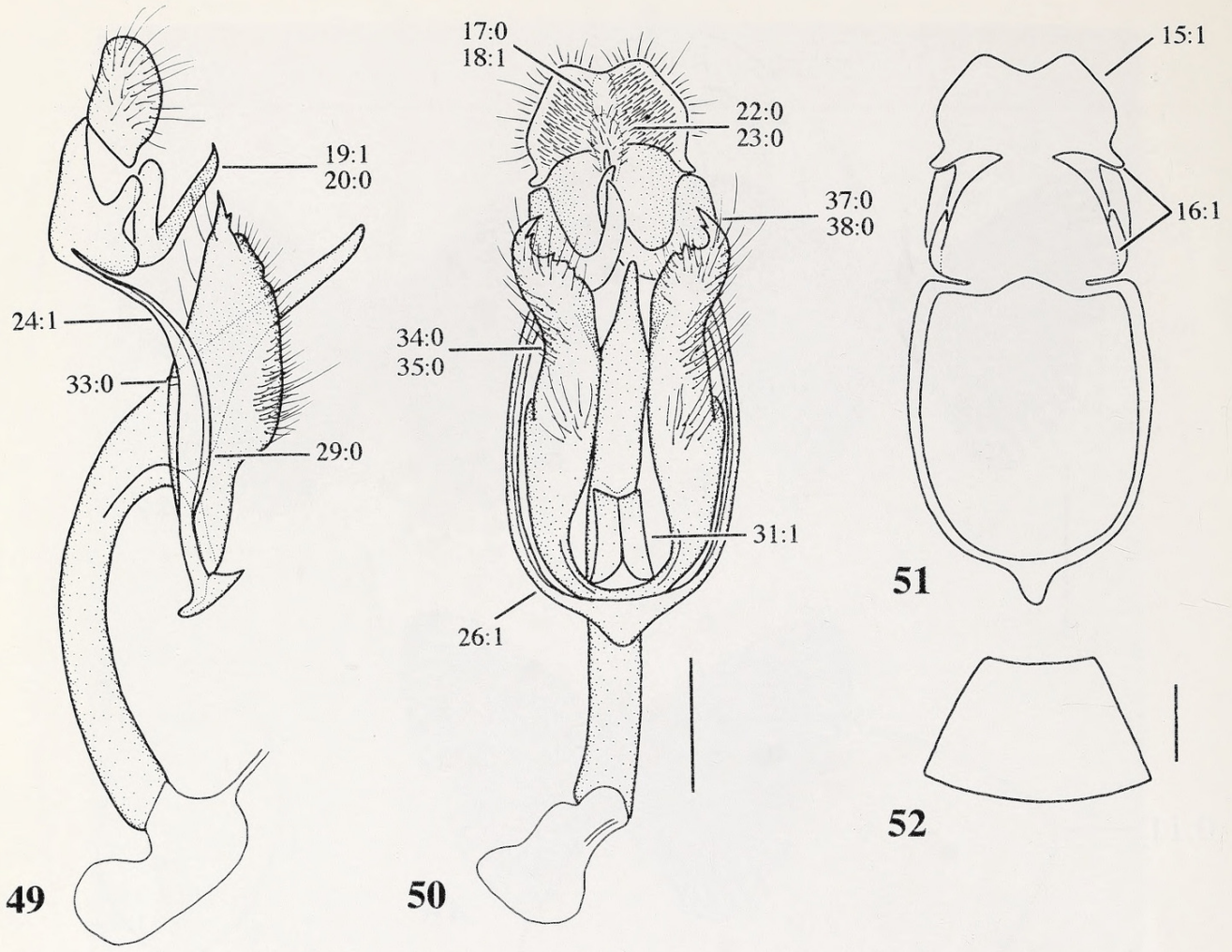
**SUBSPECIES.** None.

**EXAMINED SPECIMENS.** ECUADOR, Napo, Tena-Loreto Road, 1 male (JH); PERU, Pumayacu, 1 male (LACM).

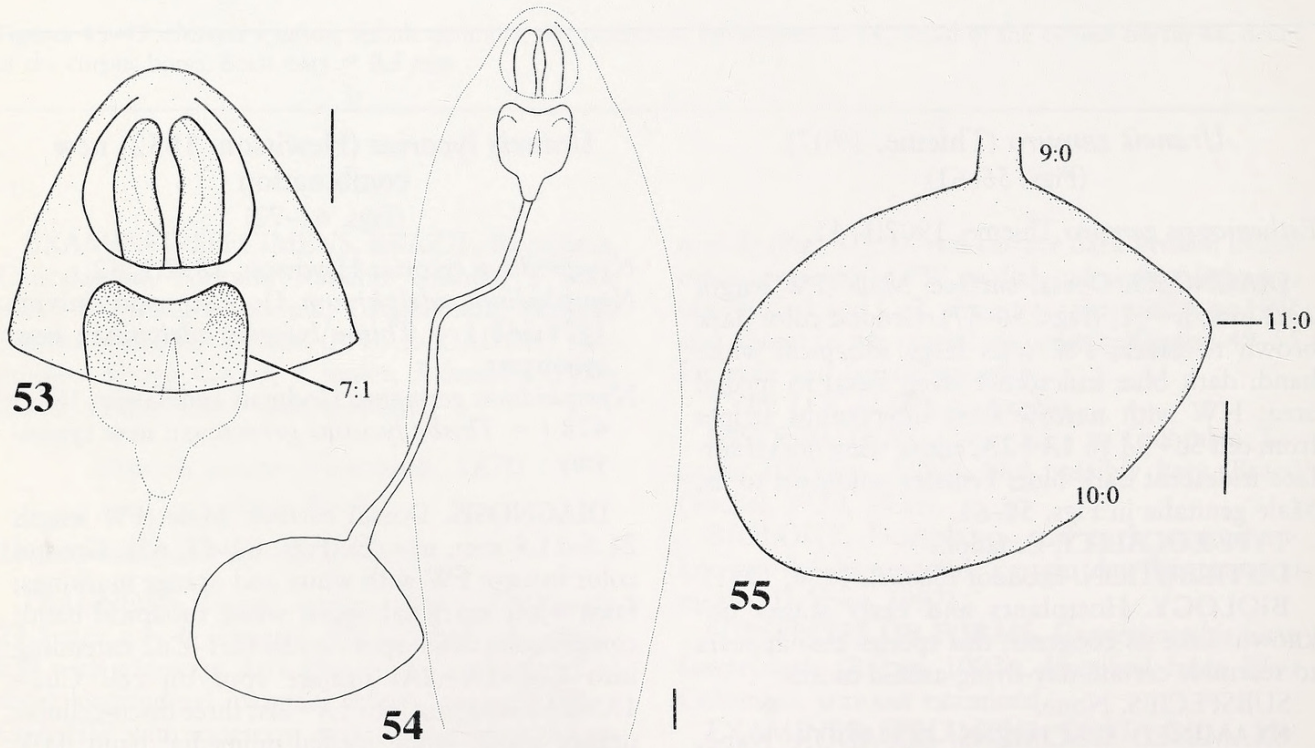
## *Uraneis lycorias* (Hewitson, 1852) new combination
(Figs. 62–72)

*Nymphidium lycorias* Hewitson, 1852:1, 12.
*Nymphidium adelphinum* Godman and Salvin, 1878:368 ( = *Thisbe lycorias adelphina*); **new synonymy**
*Nymphidium germanus* Godman and Salvin, 1886: 478 ( = *Thisbe lycorias germanus*); **new synonymy**

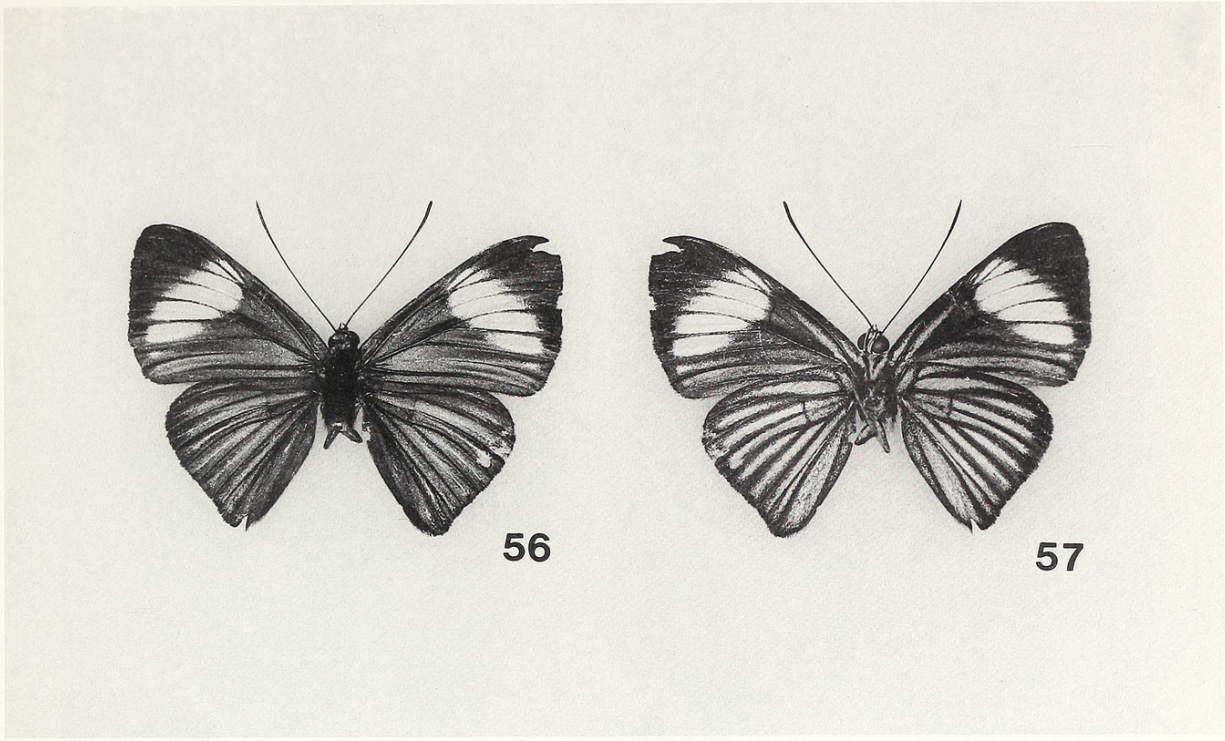
**DIAGNOSIS.** Dorsal surface: Male (FW length 21.6–21.8 mm, n = 2) (Figs. 62–63, 65). Ground color brown; FW with white and orange markings; faint white marginal spots; white subapical band; conspicuous white spot on cell Cu1–Cu2 extending into Cu2–1A+2A; orange spot on cell Cu2–1A+2A extending into 1A+2A; three disco-cellular orange spots; white medial/submedial band. HW dorsal surface: thin marginal and submarginal bands from apex to tornus, interspersed by brown



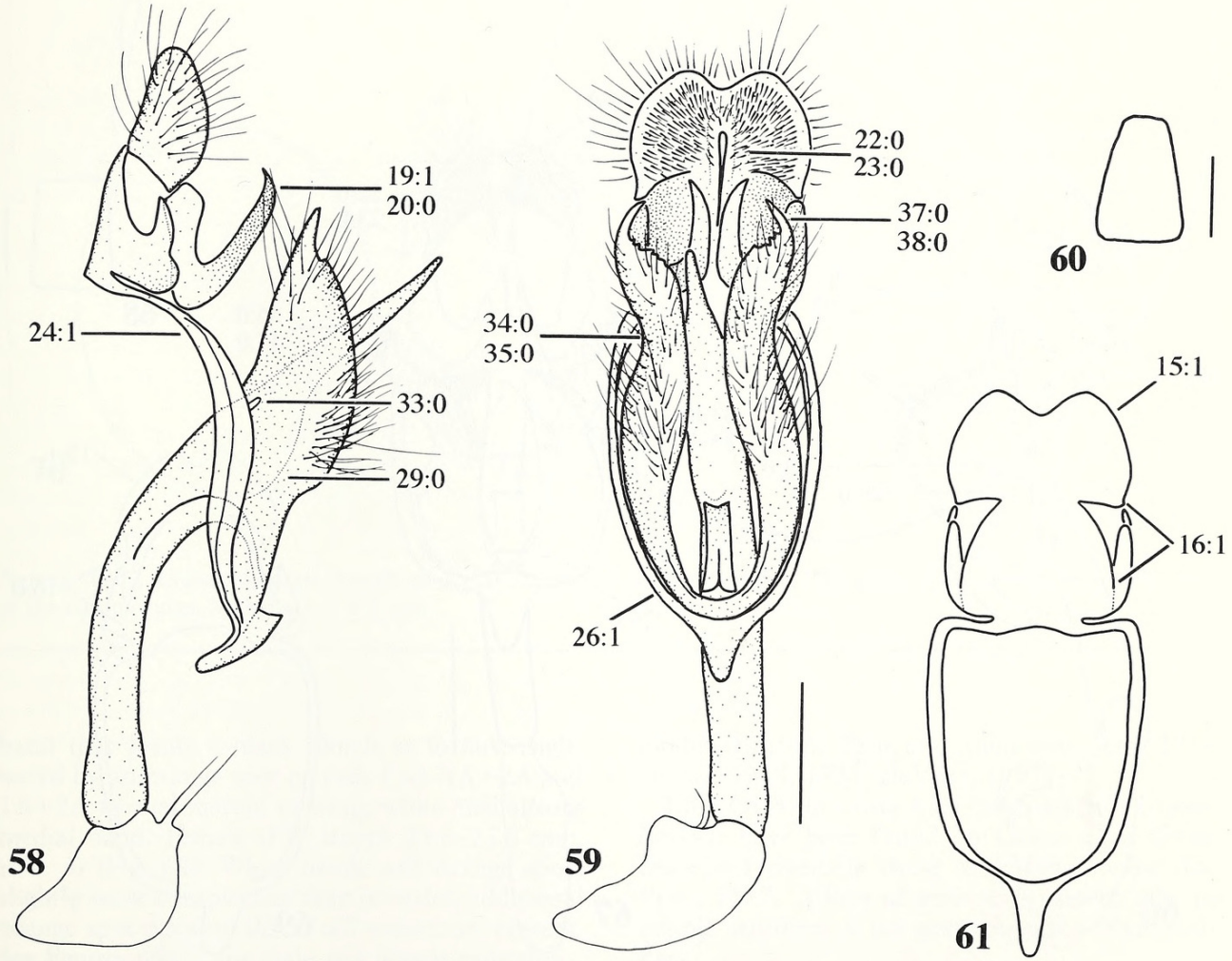

Figures 49–52 *Uraneis ucubis*, male genitalia; 49, lateral view; 50, ventral view; 51, detail of the dorsal view; 52, 8th sternite. Scale bars = 0.5 mm



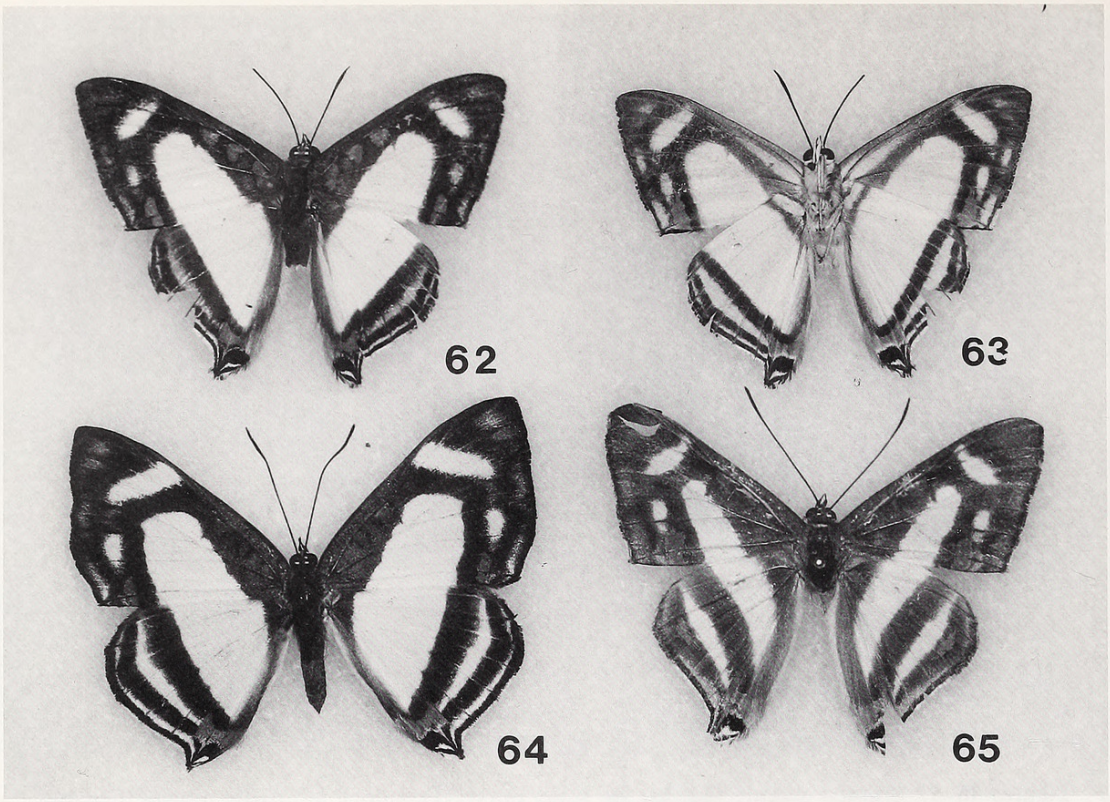

Figures 53–55 *Uraneis ucubis*, female genitalia; 53, detail of the ostium bursa; 54, outline of the abdomen; 55, detail of the corpus bursa. Scale bars = 0.5 mm



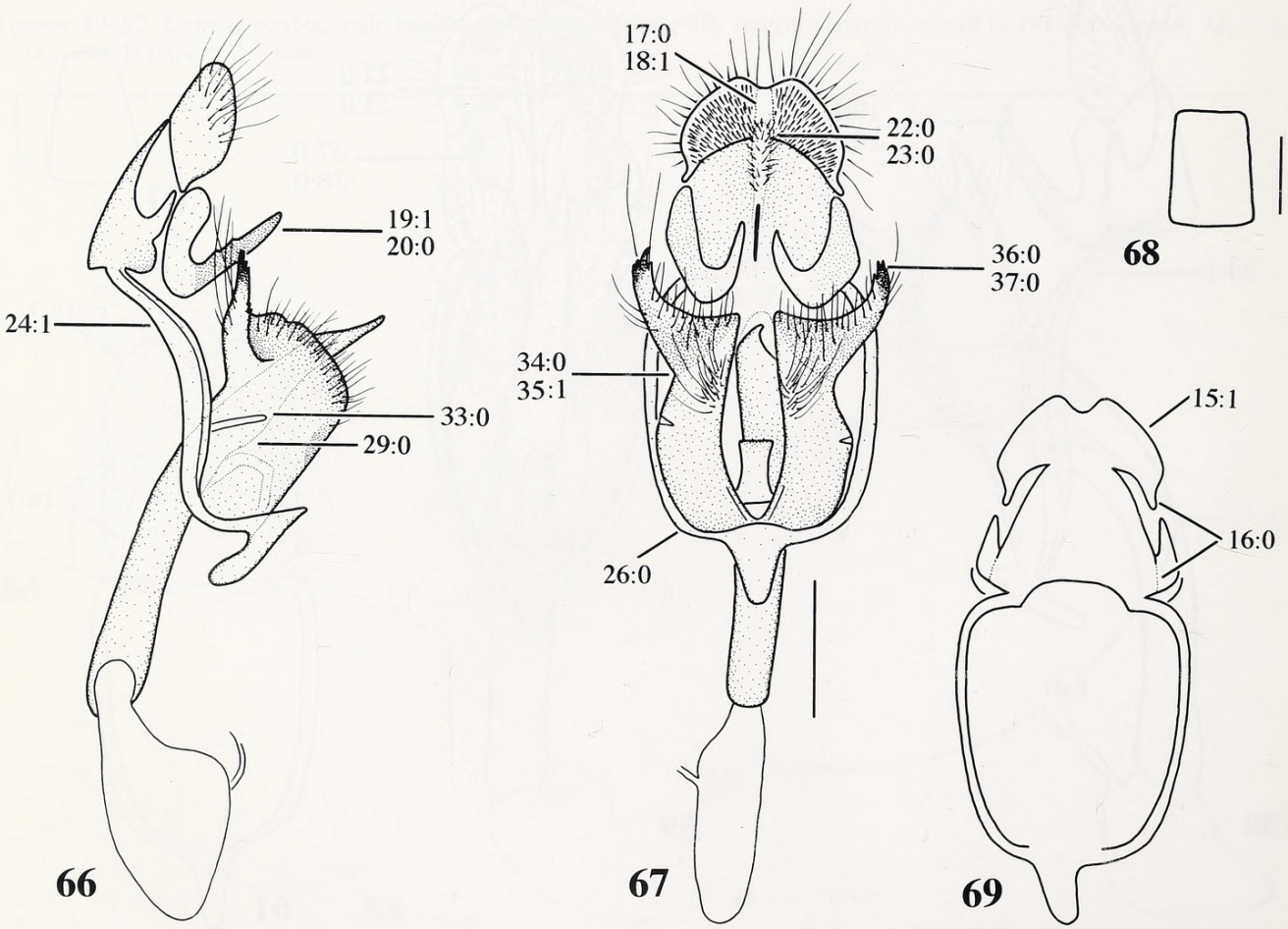

**Figures 56–57** *Uraneis zamuro*, adults; **56,** male, dorsal (Ecuador); **57,** male, ventral (Ecuador)



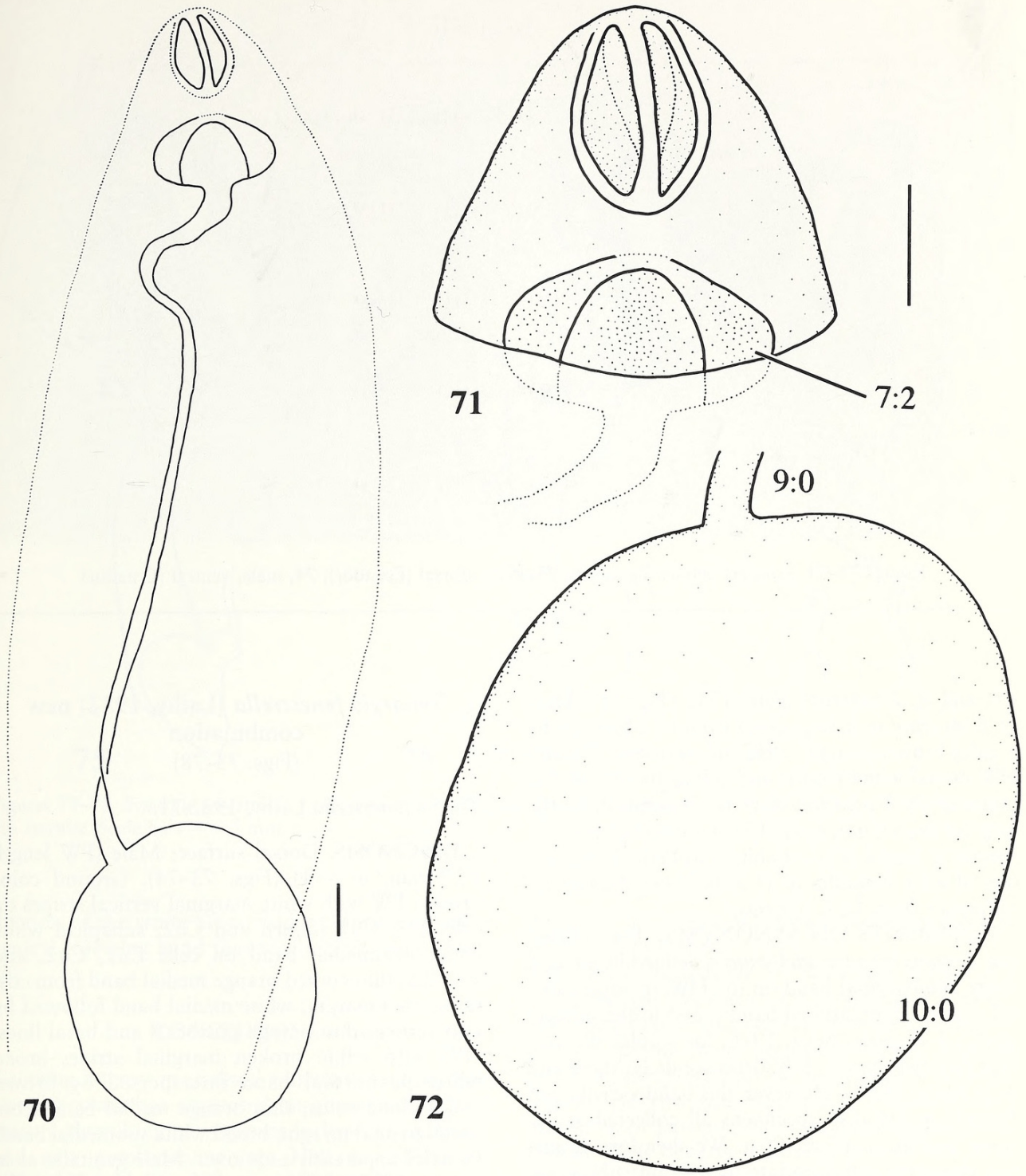

**Figures 58–61** *Uraneis zamuro*, male genitalia; **58,** lateral view; **59,** ventral view; **60,** 8th sternite; **61,** detail of the dorsal view. Scale bars = 0.5 mm




**Figures 62–65** *Uraneis lycorias,* adults; **62,** *U. lycorias lycorias* male, dorsal (Costa Rica); **63,** *U. lycorias lycorias* male, ventral (Costa Rica); **64,** *U. lycorias lycorias* female, dorsal (Costa Rica); **65,** *U. lycorias incarum* male, dorsal (no data)




**Figures 66–69** *Uraneis lycorias,* male genitalia; **66,** lateral view; **67,** ventral view; **68,** 8th sternite; **69,** detail of the dorsal view. Scale bars = 0.5 mm




**Figures 70–72** *Uraneis lycorias*, female genitalia; **70,** outline of the abdomen; **71,** detail of the ostium bursa; **72,** detail of the corpus bursa. Scale bars = 0.5 mm

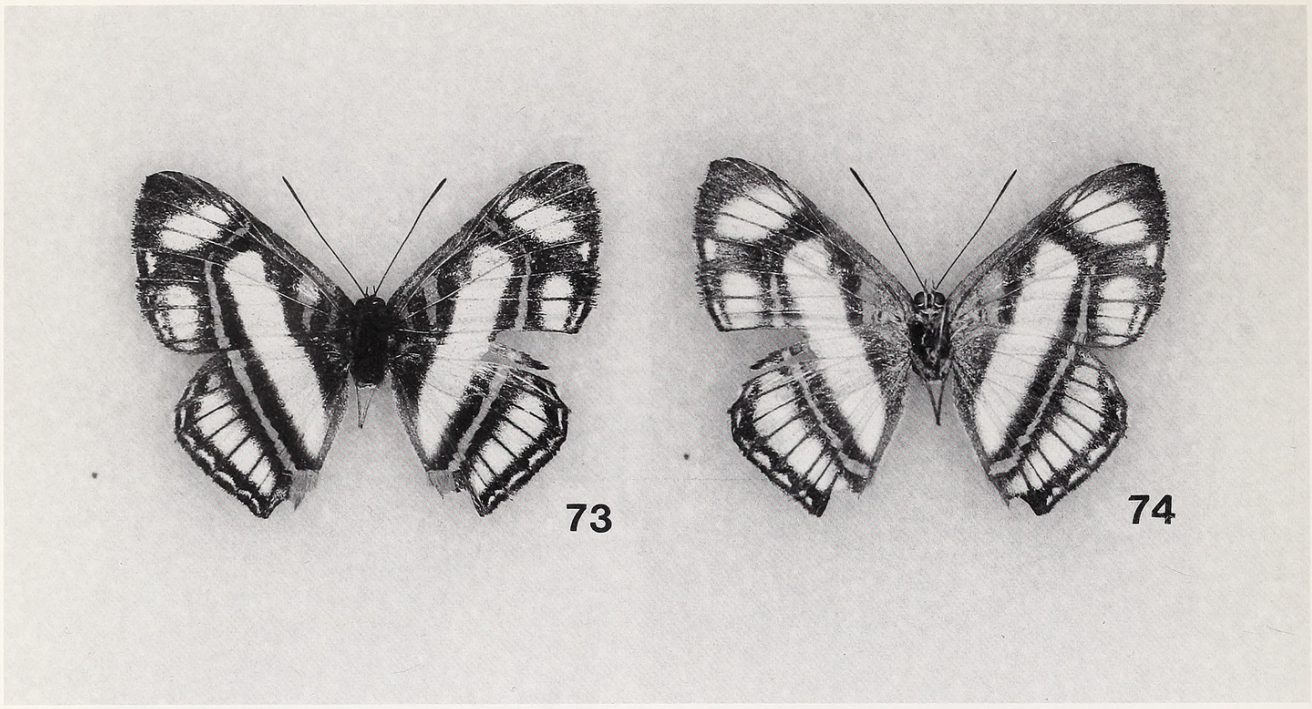
band that forms a black blotch at tornus neighbored by an orange spot on cells Cu2–1A+2A and 1A+2A to anal margin of wing; white medial/submedial band. Female (FW length 23.6–25.8 mm, n = 3) (Fig. 64). White bands and orange spots slightly more conspicuous than in males; additional orange spot distal to discal cell sometimes present. See Figures 66–72 for male and female genitalia.

**TYPE LOCALITY.** Honduras.

**DISTRIBUTION.** Mexico, Central America, Colombia, Ecuador, Peru, and Amazonas (Seitz, 1916; Stichel, 1930, 1931; DeVries, 1997).

**BIOLOGY.** In Costa Rica caterpillars of *Uraneis lycorias* have been found on *Cassia alata* (Fabaceae) and resemble those of *Juditha molpe* (DeVries, 1997). Adults of both sexes superficially resemble members of the genus *Adelpha* (Nymphalidae).

**SUBSPECIES.** We recognize two subspecies: *Uraneis lycorias lycorias* (Hewitson, 1852) (Figs. 62–




**Figures 73–74** *Synargis fenestrella,* adults; **73,** male, dorsal (Ecuador); **74,** male, ventral (Ecuador)

64) and *U. l. incarum* Seitz, 1916 (Fig. 65). Male *U. l. incarum* is distinguished from *U. l. lycorias* by a paler brown ground color, and narrower FW and HW dorsal white medial and submedial bands. Females of *U. l. incarum* were not examined. In the original description Seitz (1916) notes that this subspecies is found in dry habitats in Peru. Morphology of male genitalia of *U. l. incarum* showed no difference from *U. l. lycorias.*

**COMMENTS ON SYNONYMY.** The subspecies *Uraneis lycorias adelphina* is defined by a faded white submarginal band on the HW, in contrast to the discrete submarginal band found in the subspecies *U. l. lycorias* (Seitz, 1916; for a color illustration of subspecies *U. l. lycorias* see de la Maza and de la Maza, 1993). However, this band varied from discrete to faded in specimens all collected at the same locality in Costa Rica. We therefore regard this character inappropriate to warrant subspecific status, and consider *U. l. adelphina* a synonym of *U. l. lycorias. Uraneis lycorias germanus* is defined by a faded white submarginal band on the HW (similar to *U. l. adelphina*) and smaller orange spots in the forewing than the remaining subspecies (Seitz, 1916), as evident from the type specimen. However, in specimens from Costa Rica the orange spots in the disco-cellular region varied in size and number. We conclude that this character is inadequate to justify the subspecies *U. l. germanus,* and consider it a synonym of *U. l. lycorias.*

**EXAMINED SPECIMENS.** COSTA RICA, Guanacaste, Parque Santa Rosa, 1 male (PJD); COSTA RICA, Heredia, Finca La Selva, 3 females (PJD); no data (supposedly Peru), 1 male (BMNH).

### *Synargis fenestrella* (Lathy, 1932) new combination

(Figs. 73–78)

*Thisbe fenestrella* Lathy, 1932:71.

**DIAGNOSIS.** Dorsal surface: Male (FW length 18.7 mm, n = 1) (Figs. 73–74). Ground color brown; FW with white marginal vertical stripes on cells M3, Cu1 (faint), and Cu2; subapical white band; postmedial band on cells Cu1, Cu2, and 1A+2A; thin curved orange medial band from costal to anal margin; white medial band followed by two vertical thin orange postbasal and basal lines. HW with white broken marginal stripe; broad white postmedial band interspersed by brown scales along veins; thin orange medial band from costal to anal margin; broad white submedial band. Females apparently unknown. Male genitalia as in Figures 75–78.

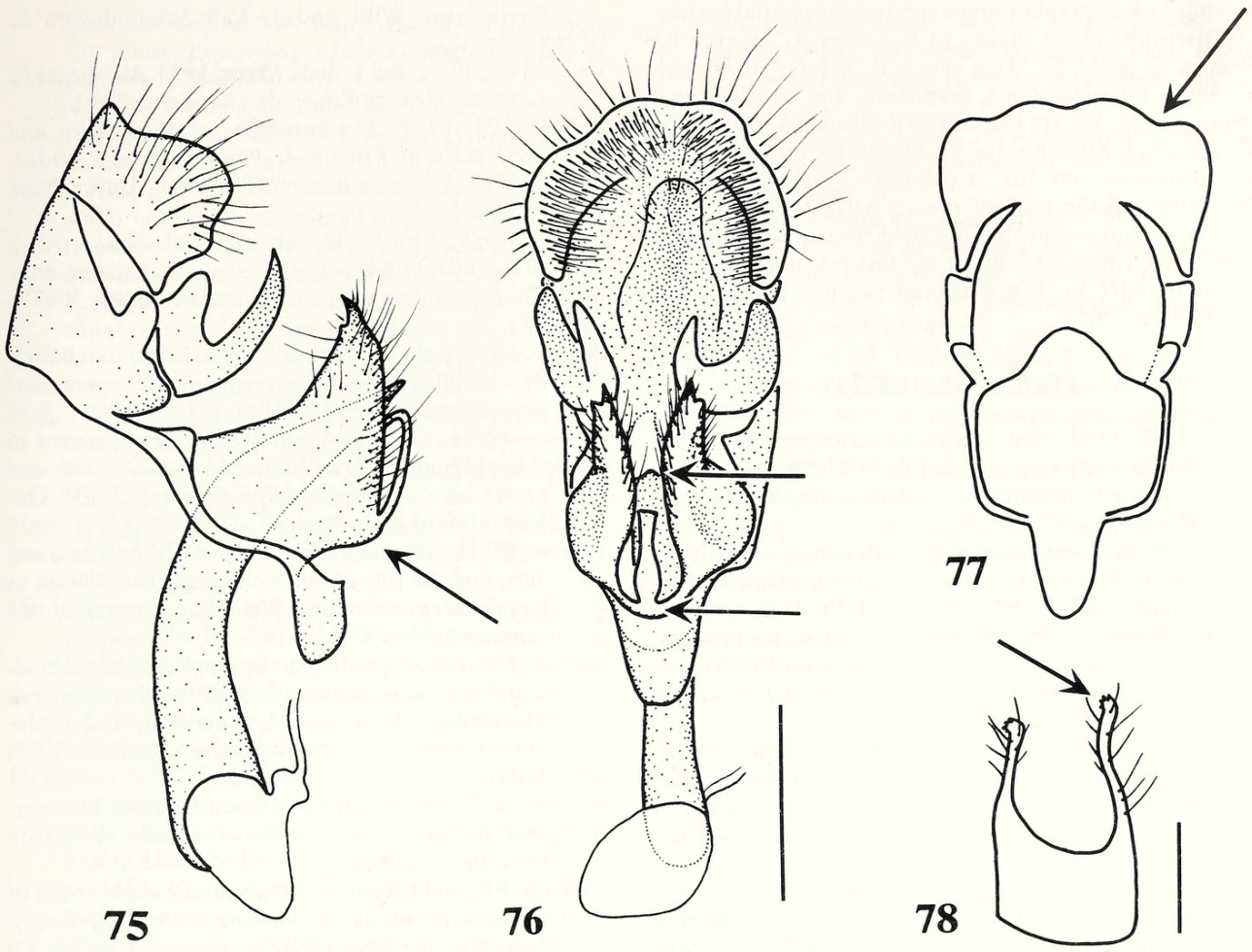
**TYPE LOCALITY.** Ecuador.

**DISTRIBUTION.** Ecuador to French Guyana.

**BIOLOGY.** Host plant, early stages, and females unknown.

**COMMENTS.** Lathy (1932:71) justified placing this species in *Thisbe* based on a "general pattern similar to that of *lycorias* Hew." However, examination of male genitalia indicated that *fenestrella* is closely related to *Thysanota* and *Synargis.*

**SUBSPECIES.** Specimens *Thisbe fenestrella cayennensis* (Brevignon and Gallard, 1992) described from French Guyana were not examined. According to Brevignon and Gallard (1992) *T. f. cayennensis* is distinguished from the nominate subspecies by having broader dark wing bands (i.e., a re-




**Figures 75–78** *Synargis fenestrella,* male genitalia; 75, lateral view; 76, ventral view; 77, detail of the dorsal view; 78, 8th sternite. Scale bars = 0.5 mm

duction of the white areas) and a complete orange ventral forewing band that reaches the costal margin.

## CONCLUSIONS

Growing interest in riodinid systematics during the last five years has generated an abundance of literature describing new species, subspecies, genera, and new combinations (see Hall and Wilmott, 1995, 1996; Hall and Harvey, 1998, and references therein). However, it is unfortunate that none of these recent studies have provided formal cladistic methods and analyses to justify proposed new taxa or combinations. Here, phylogenetic analyses allowed us to verify the systematic position of *Thisbe fenestrella* and reassess the sister genera *Thisbe* and *Uraneis*. Parsimony analysis of 97 characters showed that *T. fenestrella* is most closely related to *Synargis* and *Thysanota,* not *Thisbe*. Our analysis of 30 characters from male genitalia indicated that both *T. fenestrella* and *Thysanota galena* are imbedded within *Synargis,* thus suggesting that *Synargis* is paraphyletic. Transferring *T. fenestrella* to *Synargis* partly resolves this problem, but available evidence suggests that a complete revision of *Synargis* will be necessary before adjusting taxonomic status of *Thysanota*.

Cladistic analysis of 39 characters produced a fully resolved phylogeny for *Thisbe* and *Uraneis*. We found that *Thisbe lycorias* formed a monophyletic group with three species of *Uraneis,* therefore justifying the placement of *T. lycorias* in *Uraneis*. *Uraneis lycorias* and members of *Thisbe* share a similar color pattern (white bands on brown background) that departs dramatically from the other species of *Uraneis* which form mimetic complexes with day-flying moths. However, in contrast to *Thisbe,* species of *Uraneis* (including *U. lycorias*) are typically larger insects, and have the sexes nearly monomorphic.

This study shows that even familiar taxa of riodinids like *Thisbe* and *Uraneis* are poorly understood taxonomically and biologically, and serves to demonstrate how phylogenetic methods may help elucidate patterns of species diversification within the riodinid butterflies.

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# APPENDICES

## Appendix 1

Matrix of 97 characters used to evaluate the systematic position of *Thisbe fenestrella*.
See Penz and DeVries (1999) for the character list. Character states in parentheses indicate polymorphism.

| | | | | | |
|---|---|---|---|---|---|
| *Stalachtis euterpe* | 0111101010 | 1001100100 | 0102111101 | 1012000102 | 0101?????1 |
| *Adelotypa alector* | 0110121111 | ?????00102 | 1111011101 | 1010011000 | 010001?011 |
| *Setabis lagus* | 0110120210 | 1011000100 | 1111111011 | 1112011000 | 010001?011 |
| *Calospila emylius* | 0110121210 | 1011010100 | 1000111010 | ??????1000 | 110001?011 |
| *Nymphidium azanoides* | 0010121210 | 1001001101 | 1111101011 | 1110111000 | 111000?111 |
| *Nymphidium cachrus* | 0010111110 | 1001001101 | 1001101001 | 1010111000 | 211000?111 |
| *Nymphidium mantus* | 0110120210 | 1011003?00 | 1111101001 | 1110111000 | 211000?111 |
| *Theope publius* | 0110131210 | 0001003?01 | 0111101101 | 1110011010 | 100001?011 |
| *Theope virgilius* | 0110131210 | 2001003?00 | 1112101011 | 1110001010 | 200001?011 |
| *Thisbe irenea* | 0010(01)31210 | 1001000100 | 0012001001 | 00??001002 | 2100110011 |
| *Thisbe lycorias* | 0000020110 | 1201000100 | 0011101200 | ??????1001 | 1101?????1 |
| *Thisbe molela* | 0010030310 | 0001000100 | 0011101201 | 1010001002 | 1100110011 |
| *Thisbe fenestrella* | ?1100????? | ?????????? | ?????????? | ????????02 | 0100100101 |
| *Uraneis zamuro* | ?0010????? | ?????????? | ?????????? | ????????02 | 1101?????1 |
| *Uraneis hyalina* | 0001031110 | 1101000100 | 1011101200 | ??????1002 | 0101?????1 |
| *Uraneis ucubis* | 0001031110 | 1101010100 | 1011101201 | 00??011002 | 0101?????1 |
| *Lemonias caliginea* | 0110120300 | 0000000010 | 0110111101 | 1110011001 | 0100111011 |
| *Lemonias zygia* | 0010120200 | 0000000010 | 0111111101 | 1110011002 | 0100111111 |
| *Juditha azan* | 0110120300 | 0000000011 | 1110111101 | 1010111002 | 0100110011 |
| *Juditha molpe* | 0110120300 | 0000000012 | 1110111101 | 1010111002 | 0100110011 |
| *Synargis abaris* | 0110110211 | ??????03?00 | 0110111101 | 1101111002 | 1100110101 |
| *Synargis mycone* | 0110120310 | 1001100000 | 0100111001 | 11012?1001 | 2100110101 |
| *Synargis orestes* | 0110131211 | ?????00000 | 0110111101 | 1111111002 | 2100110101 |
| *Synargis palaeste* | 0110131310 | 1001100000 | 0100111001 | 1111011002 | 1100110111 |
| *Thysanota galena* | 111013?200 | 0001000000 | 1100111101 | 1101011002 | 2100110101 |
| *Audre domina* | 1110130211 | ?????02111 | 1111110??1 | 1110011002 | 0100110110 |
| *Audre erostratus* | 1110130111 | ?????12011 | 1????????? | ??????1001 | 1100110110 |
| *Audre* sp. | 1110130210 | 1001002011 | 1110110??1 | 1110011001 | 1101?????0 |
| *Aricoris tutana* | 11101????? | ?????????? | ?????????? | ????????02 | 0101?????0 |
| *Eiseleia pinchanalensis* | 1110120311 | ?????10011 | 1110111101 | 11102?1002 | 0101?????0 |
| *Ematurgina* nr. *leucotopus* | 01101????? | ?????????? | ?????????? | ????????0? | 0100110110 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Stalachtis euterpe* | 0??0110111 | 0001121021 | 0021111112 | 10??200001 | 1?10100 | |
| *Adelotypa alector* | 0??0110102 | 1001021000 | 0000131110 | 10??2001?0 | 1?11111 | |
| *Setabis lagus* | 0??1110102 | 1001020110 | 0001101110 | 10???001?0 | 1?10111 | |
| *Calospila emylius* | 0??0110102 | 1011020010 | 1100121111 | 10???001?0 | 1?10111 | |
| *Nymphidium azanoides* | 0??0112002 | 0010200021 | 2201101010 | 1111200001 | 1?10100 | |
| *Nymphidium cachrus* | 0??0112012 | 00?0100010 | 2201000010 | 1111200001 | 1?10110 | |
| *Nymphidium mantus* | 0??0112002 | 01?1021021 | 2201031010 | 1112200001 | 1?10110 | |
| *Theope publius* | 0??0111011 | 0010210000 | 2211011012 | 1100221??1 | ??100?? | |
| *Theope virgilius* | 0??0111011 | 0000010000 | 2201001011 | 10??221??1 | ??1?0?? | |
| *Thisbe irenea* | 0??0110101 | 1011020000 | 1110120011 | 0101100?1 | 1?10111 | |
| *Thisbe lycorias* | 0??0110101 | 1001020010 | 1120101111 | 00??2101?1 | 1?10111 | |
| *Thisbe molela* | 0??0110101 | 1011020000 | 1110121011 | 1100110?1 | 1?10111 | |
| *Thisbe fenestrella* | 0??0111101 | 1011111010 | 0110102?10 | 10???101?1 | 0111110 | |
| *Uraneis zamuro* | 0??0110101 | 1011020010 | 0120101110 | 00??1001?1 | 1?10111 | |
| *Uraneis hyalina* | 0??0110101 | 1011020010 | 1120101111 | 0100110?1 | 1?10111 | |
| *Uraneis ucubis* | 0??0110101 | 1011020010 | 1120101110 | 00??1101?1 | 1?10111 | |
| *Lemonias caliginea* | 0??0110101 | 1001021010 | 1110120001 | 1100110?1 | 1?10110 | |
| *Lemonias zygia* | 0??0110101 | 1001020010 | 1110120001 | 10??1101?1 | 1?10110 | |
| *Juditha azan* | 1101111102 | 1001021010 | 1220100011 | 10???10011 | 1?01101 | |
| *Juditha molpe* | 1101110102 | 1001021010 | 1220100011 | 10??210011 | 1?01101 | |
| *Synargis abaris* | 1010011001 | 0011311000 | 0100102011 | 1102?001?0 | 0011100 | |
| *Synargis mycone* | 1010112001 | 1011311000 | 1100102011 | 1102?101?1 | 0011100 | |
| *Synargis orestes* | 1010011001 | 0011321000 | 0100102011 | 1102?101?1 | 0011100 | |
| *Synargis palaeste* | 1000111011 | 0011301000 | 0100102011 | 1102?101?0 | 0011100 | |
| *Thysanota galena* | 1010001101 | 0011010000 | 0100102010 | 1102?101?1 | 0111110 | |
| *Audre domina* | 11011100?1 | 1011130011 | 1120101111 | 10??2001?0 | 1?11100 | |
| *Audre erostratus* | 11011101?1 | 1011030021 | 1120131111 | 10??0101?1 | 1?11100 | |
| *Audre* sp. | 10011100?1 | 1011130011 | 1120131111 | 1100100?0 | 1?11100 | |
| *Aricoris tutana* | 10011100?1 | 1011030021 | 0120131111 | 10??1101?1 | 1?11100 | |
| *Eiseleia pinchanalensis* | 1101?100?1 | 1011010021 | 1220131111 | 10???001?1 | 1?11100 | |
| *Ematurgina* nr. *leucotopus* | 0?00110002 | 1011210011 | 2020131010 | 10??2001?1 | 1?11100 | |

## Appendix 2

### List of characters included in the preliminary analysis of *Synargis*.

Fifteen of these characters have been included in a previous analysis (original character numbers are indicated), and 15 characters are new (marked with an asterisk). Comments are presented when appropriate. We use the following abbreviations: Ae, aedeagus; Coe, coecum penis; Jx, juxta (= pedicel *sensu* Harvey, 1987); Ped, pedunculum; Ssca, subscaphium; Stn, sternite (numbers may follow abbreviation; e.g., Stn7, seventh sternite); Teg, tegumen; Tg, tergite (numbers may follow abbreviation; e.g., Tg7, seventh tergite), Un, uncus; Va, valva; Vin, vinculum.

1. Male Tg8: similar in length to Tg7 (0); about 1.5 times as long as Tg7 (1); about twice as long as Tg7 (2). Character 41 in Penz and DeVries (1999).
2*. Bifurcated abdominal projections on male Stn8: uniform in width, narrowing at tip to form a sharp point (0); uniform in width, rounded at tip (1); bulging near distal end, narrowing at tip (2).
3*. Bifurcated abdominal projections on male Stn8: asymmetrical (0); symmetrical (1).
4. Posteromedial margin of male Stn8: well sclerotized (0); weakly sclerotized (1). Character 51 in Penz and DeVries (1999).
5. Tip of bifurcated abdominal projection on male Stn8: adorned with spines (0); devoid of spines (1). Character 49 in Penz and DeVries (1999).
6. Weakly sclerotized posteromedial margin of male Stn8: extending to reach anterior edge of Stn8 (0); anterior edge of Stn8 well sclerotized (1). Character 52 in Penz and DeVries (1999).
7. Un: entire (0); split (1). Character 54 in Penz and DeVries (1999).
8. Posterior margin of Un: adorned with spiny projections (0); devoid of spiny projections (1). Character 56 in Penz and DeVries (1999).
9. Posterior margin of Un: convex or straight (0); slightly concave (1); strongly concave, Un apparently four-lobed (2). Character 57 in Penz and DeVries (1999).
10*. Un: lateral lobes with a point (0); smoothly rounded (1).
11*. Posterior lobes of Un equal or more developed than lateral lobes (0); less developed than lateral lobes (1).
12*. Posterior lobes of Un: rounded (0); pointed (1).
13. In ventral view, lateral margins of Un: widened (0); not widened (1). Character 58 in Penz and DeVries (1999).
14*. In lateral view, Ped + Vin: forming angles (0); straight (1).
15. Ssca: uniformly narrow (0); uniformly broad (1); broad posteriorly and narrowed anteriorly (2); broad anteriorly and narrowed posteriorly (3). Character 65 in Penz and DeVries (1999).
16. In lateral view, Ssca: depressed (0); flat (1); sharp, bladelike protrusion (2); rounded protrusion (3). Character 66 in Penz and DeVries (1999).
17*. Setae on membranous region lateral to Ssca: absent (0); present (1).
18. Va: fused ventrally (0); not fused ventrally (1). Character 91 in Penz and DeVries (1999).
19*. Setae on ventral weakly sclerotized ventral "bridge" between fused Va: distributed along entire "bridge" (0); restricted to the posterior portion of "bridge" (1).
20*. In lateral view, dorsal, subapical pointed process of Va: absent (0); present (1).
21*. In lateral view, Va: with a ventral, subapical pointed process (0); smoothly rounded (1).
22*. Sclerotization of Va tip: heavier than base, pointed (0); similar to base, adorned with a rounded nub (1); similar to base, blunt (2); similar to base, pointed (3).
23*. Jx: joins Va at base (0); terminating before ventral, anterior edge of Va (1).
24*. In lateral view, Jx extended beyond ventral edge of Va (0); not extended beyond ventral edge of Va (1).
25*. In lateral view, Jx midlength bend: reaches or surpasses the posterior edge of Va (0); does not reach posterior edge of Va (1).
26*. Dorsal bulge of Ae: absent (0); present (1).
27. Distal end of Ae: acute (0); intermediate (1); blunt (2). Character 77 in Penz and DeVries (1999).
28. Distal opening of Ae: dorsal (0); dorsolateral or lateral (1); ventral (2). Character 80 in Penz and DeVries (1999).
29. Coe: absent (0); present (1). Character 82 in Penz and DeVries (1999).
30. Coe: ⅔ or more the length of bulbus ejaculatorius (0); ⅓ or less (1). Adapted from character 84 in Penz and DeVries (1999).

## Appendix 3

Character matrix including 30 characters listed in Appendix 2 and used in the preliminary analysis of *Synargis*.

| | | | |
|---|---|---|---|
| *Audre domina* | 001111110? | ??01130l?0 | 0201101l0? |
| *Audre erostratus* | 1?11111l0? | ??10030l?0 | 0201101l0? |
| *Thisbe fenestrella* | 21000?0110 | 1011300011 | 1000112002 |
| *Thysanota galena* | 2011000011 | 0110011000 | 1001112010 |
| *Synargis abaris* | 1011000110 | 0100311000 | 0110002110 |
| *Synargis ethelinda* | 2111000120 | 0010301000 | 1111101l0? |
| *Synargis gela* | 1211100110 | 0110301000 | 1111102110 |
| *Synargis mycone* | 2111000120 | 0000310000 | 1110001110 |
| *Synargis orestes* | 2011000110 | 0000321000 | 1310102110 |
| *Synargis palaeste* | 1111100111 | 0000301000 | 1111001110 |
| *Synargis phillone* | 21100?0110 | 1011300011 | 0000112011 |
| *Synargis tytia* | 2211100121 | 0000300000 | 0111001110 |
| *Synargis velabrum* | 21000?0110 | 1011310011 | 0000111002 |

## Appendix 4

### List of characters included in the species-level analysis of *Thisbe* and *Uraneis*.

Twenty of these characters have been included in a previous analysis (original character numbers are indicated), and 19 characters are new (marked with an asterisk). Comments are presented when appropriate. We use the following abbreviations: Ae, aedeagus; Antr, antrum; Coe, coecum penis; Crn, cornuti; Crp.bu, corpus bursa; Du.bu, ductus bursa; Gn, gnathos (= brachia *sensu* Muschamp in Ogata et al., 1957; falci *sensu* Bethune-Baker, 1910); Jx, juxta (= pedicel *sensu* Harvey, 1987); L1, foreleg; Ob, ostium bursae; Ped, pedunculum; Sa, saccus; Sig, signum; Ssca, subscaphium; Stn, sternite (numbers may follow abbreviation; e.g., Stn7, seventh sternite); Teg, tegumen; Tsm, tarsomere; Un, uncus; Va, valva; Vin, vinculum.

1. Base of tegula: bright orange or red, clearly contrasting with thorax (0); devoid of such a pattern (1). Character 3 in Penz and DeVries (1999).
2. Forewing R4: meets wing margin slightly anteriorly to apex or at apex (0); posteriorly to apex (1). Character 4 in Penz and DeVries (1999).
3. Hindwing A2: produced in at least one sex (0); not produced (1). Character 5 in Penz and DeVries (1999).
4. Distribution of sensilla on last Tsm of female L1: along the distal four-fifths (0); along the distal two-thirds (1); along the distal half (2); distributed over less than one-half of the length of last Tsm (3). No measurements were taken, and character states were determined arbitrarily based on observed patterns. Character 8 in Penz and DeVries (1999).
5. Female Stn7: elongated posteriorly to cover Ob (0); devoid of such a pattern (1). Character 9 in Penz and DeVries (1999).
6. Genital plate: equally well developed anteriorly and posteriorly (0); more developed posteriorly than anteriorly (1); more developed anteriorly than posteriorly (2). Character 11 in Penz and DeVries (1999).
7. Genital plate composed of: a single unit (0); two units (1); three units (2). Character 12 in Penz and DeVries (1999). Figs. 23, 34, 44, 54, 71.
8. Portion of Du.bu bordering Antr: well sclerotized (0); membranous (1). Character 21 in Penz and DeVries (1999).
9. Connection of Du.bu with Crp.bu: narrow (0); broad (1). Character 22 in Penz and DeVries (1999). Figs. 24, 35, 45, 55, 72.
10. Crp.bu: rounded (0); elongated (1). Character 26 in Penz and DeVries (1999). Figs. 24, 35, 45, 55, 72.

11*. Crp.bu: with a cone-shaped protrusion located in its medial portion (0); devoid of such a pattern (1). Figs. 45, 55.

12. Spines that compose the sculpturing of Crp.bu: aligned in rows (0); clustered (1). Adapted from character 28 in Penz and DeVries (1999).
13. Sig: absent (0); present (1). Character 30 in Penz and DeVries (1999). Figs. 24, 35.
14. Stn8: with terminal abdominal projections extending beyond edge of pleural membrane (0); devoid of such a pattern (1). Character 44 in Penz and DeVries (1999). Figs. 21, 32.

15*. In dorsal view, shape of the Un: pattern A (0); pattern B (1). Figs. 20, 31, 41, 51, 60, 68.

16*. In dorsal view, Un: similar in width to base of Teg (0); broader than base of Teg (1). Figs. 20, 31, 41, 51, 60, 68.

17*. In ventral view, Un with a central depression (0); devoid of such a pattern (1). Figs. 19, 30, 40, 50, 67.

18*. Ventral depression of Un: narrow (0); broad (1). Figs. 19, 30, 40, 50, 67.

19. Distal portion of Gn: wide (0); intermediate (1); narrow (2). No measurements were taken, and character states were determined based on observed patterns. Character 69 in Penz and DeVries (1999). Figs. 19, 29, 30, 39, 49, 58, 66.

20*. Distal and proximal portions of Gn: forming an angle (0); forming an arch (1). Figs. 19, 29, 39, 49, 58, 66.

21*. Ped: prominent (0); reduced (1). The illustrations presented here do not give an accurate representation of this character because the pedunculum bends internally. To score this character, specimens should be examined in ventro-lateral view.

22. Posterior end of Ssca: narrow (0); broad (1). Character 63 in Penz and DeVries (1999). Figs. 19, 30, 40, 50, 59, 67.

23*. In ventral view, posterior end of the Ssca: extended underneath Un (0); not extended, ending before anterior edge of Un (1). Figs. 19, 30, 40, 50, 59, 67.

24*. In lateral view, Vin: sharply bent immediately after Teg (0); arched (1). Figs. 18, 29, 39, 49, 58, 66.

25. In ventro-lateral view, Vin: laterally widened to form a blade (0); widened below Teg and sharply decreasing in width (1); narrow (2). Character 73 in Penz and DeVries (1999).

26*. In ventral view, Vin: sharply bent immediately before Sa (0); arched (1). Figs. 19, 30, 40, 50, 59, 67.

27. Crn: absent (0); present (1). Adapted from character 76 in Penz and DeVries (1999). Figs. 18, 29.

28. Distal opening of Ae: dorsal (0); dorso-lateral or lateral (1); ventral (2). Character 80 in Penz and DeVries (1999).

29. Ae: with a ventral swelling immediately distal to Jx (0); devoid of such a pattern (1). Character 81 in Penz and DeVries (1999). Figs. 29, 39, 49, 58, 66.

30. Coe: absent (0); present (1). Character 82 in Penz and DeVries (1999). Figs. 19, 29.

31*. Ventral portion of Jx: narrower than Ae (0); similar in width to Ae (1). Fig. 50. Note that this character is not clearly visible in Fig. 64 (*U. lycorias*) due to the angle in which the specimen was portrayed.

32*. Lateral portion of Va: well sclerotized (0); weakly sclerotized (1).

33*. Lateral portion of Va: with a transversal window (0); devoid of such a pattern (1). Figs. 39, 49, 58, 66.

34*. Va: arched outward (0); devoid of such a pattern (1). Figs. 19, 30, 40, 50, 59, 67.

35*. Va: with a mild arch (0); prominent arch (1). Figs 40, 50, 59, 67.

36*. Tip of Va: more heavily sclerotized than the remaining portion (0); deviod of such a pattern (1). Figs. 19, 30, 67.

37*. Tip of Va: adorned with spines (0); devoid of spines (1). Figs. 40, 50, 59, 67.

38*. Tip of Va: shaped as a hook that smoothly curves inwards (0); devoid of such pattern (1). Figs. 50, 59.

39*. In lateral view, base of Va: conspicuously extending anteriorly beyond Vin in an angle (0); devoid of such a pattern (1).

## Appendix 5

Character matrix including 39 characters listed in Appendix 4 and used in the species level analysis of *Thisbe* and *Uraneis*. Character states in parentheses indicate polymorphism.

| | | | | |
|---|---|---|---|---|
| *Stalachtis euterpe* | 1110120011 | 1011?11?21 | 1001211210 | 1011?1111 |
| *Lemonias caliginea* | 1013000011 | 0010??1?11 | 00?0101111 | 0011?0111 |
| *Lemonias zygia* | 1012000011 | 0010??1?11 | 00?1101110 | 0111?0111 |
| *Thisbe irenea* | 10(01)2110000 | 1?10010001 | 0110101101 | 0111?0110 |
| *Thisbe molela* | 1003100000 | 1110010001 | 0110101111 | 0111?0110 |
| *Uraneis zamuro* | 010??????? | ???1110110 | 1001210000 | 000011001 |
| *Uraneis hyalina* | 0101111100 | 0101100110 | 1001210101 | 000001011 |
| *Uraneis ucubis* | 0101111100 | 0111110110 | 1001210000 | 100011001 |
| *Uraneis lycorias* | 0001112000 | 1101100110 | 1001200100 | 100010011 |

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