CONTRIBUTIONS IN SCIENCE

A PHYLOGENETIC REASSESSMENT OF THISBE AND URANEIS BUTTERFLIES
(RIODINIDAE, NYMPHIIDINII)

C. M. PENZ AND P. J. DeVRIES
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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 Thyssanotha 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 Thyssanotha 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 biolo-

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gists 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-
tral and South America, all of which form apparent mimetic associations with butterflies or day-flying moths. Seitz (1916) stated that the genus *Thysbe* "is so much altered by mimicry that it is difficult to find out its real alliance," and he also noted that members of *Uranéis* 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 Lemonini. Recent phylogenetic analyses of DNA sequence (Campbell, 1998) and morphological characters (Penz and DeVries, 1999) indicate that *Thysbe* and *Uranéis* are sister genera and belong to the tribe Nymphidiini. Furthermore, morphological analysis of five species suggested that *Thysbe* was paraphyletic with respect to *Uranéis* (Penz and DeVries, 1999), and these observations provided the impetus for the present study.

This study examines all seven species currently classified in *Thysbe* and *Uranéis*. We use cladistic analyses of adult morphology to: (1) verify the systematic position of *T. fenesstrella* Lathy, 1932; (2) propose a phylogeny for the genera *Thysbe* and *Uranéis*; (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 *Thysbe lycorias* (Hewitson, 1852) to *Uranéis* and *Thysbe fenesstrella* to *Synargis* Hübner, 1819.

**METHODS**

**EXAMINED MATERIAL**


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 *Thysbe* and *Uranéis*, 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 *Thysbe* and *Uranéis*.

Morphology indicated that *Thysbe fenesstrella* 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): *Adelotypha alector* (Butler, 1867); *Ariocoris tutana*; *Andre domina* (Bates, 1864), *A. erostratus* (Westwood, 1851), and *Andre* sp.; *Calospila emlyus* (Cramer, 1775); *Eiseleta pinchonalis* Miller and Miller, 1972; *Ematurgina n. leucotopus*; *Juditha azan* (Stoll, 1780) and *J. molpe* (Hübner, 1808); *Lemonias caliginea* (Butler, 1867) and *L. zygia* (Hübner, 1806); *Nymphidium azanoides* Butler, 1867; *N. cacabres* (Fabricius, 1787); and *N. mantus* (Cramer, 1775); *Setabas lagus* (Cramer, 1777); *Synargis abaris* (Cramer, 1776), *S. mycone* (Hewitson, 1865), *S. orestes* (Cramer, 1780), and *S. palaeotis* (Hewitson, 1870c); *Theope pubius* Felder and Felder, 1861, and *T. virgillus* (Fabricius, 1793); *Thysbe irenea*, *T. molota* (Hewitson, 1865); *T. lycorias*, and *T. fenesstrella*; *Thysanota galena* (Bates, 1868); *Uranéis byalina* (Butler, 1867), *U. cucubis* Hewitson, 1870c, and *U. zamaro* (Thieme, 1907). *Stalacthis enterpe* (Linnaeus, 1758) (Stalacthim) 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 *Andre guttata* (Stichel, 1910), *Catocycloto aemulius* (Fabricius, 1793), and *Lemonias aegae* (Godman and Salvin, 1886). Our previous study (Penz and DeVries, 1999) showed that A.
guttata and L. agave were highly divergent from their con-
geners and that C. aemulus accumulated a large number of autapomorphies, therefore causing difficulties in estab-
lishing their systematic position. Because the analysis here centers on Thysanota fenestrella, the exclusion of these species is un-
likely to affect our conclusions.

Our second analysis is a preliminary attempt to assess phylogenetic relationships within Synarxis. Based on re-

sults from previous studies (Penz and DeVries, 1999; 

DeVries, unpublished), we examined Thysanota galena and 

nine species to represent the taxonomic diver-
sity of Synarxis: the type species S. tyta (Cramer, 
1777), S. abaris, S. ethelinda (Hewitson, 1870b), S. gela 
(Hewitson, 1853), S. mycone, S. orcesis, S. palaezite, S. 
phillone (Godart, 1824), and S. velabrum (Godman and 
Salvin, 1878). The outgroup included Audre domina and 

A. erosatus because they are considered closely related to

Synarxis (Hare, 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 Stalactis euterpe (vix a vix the 

first part of our study) plus Lemonia caliginea and L. 

zygae—species that are closely related to Thisbe and 

Uraneis (Hare, 1987; Penz and DeVries, 1999).

For all phylogenetic analyses we performed a heuristic 

search with 20 tree bissection connection replicates as 
implemented in PAUP* 4.0 (Swofford, 1998), in which 

all characters were given equal weight, multistate char-
acters were unordered, and polymorphic characters were 
treated as exhibiting both states. In all analyses we pro-

vide Bremer indices as estimates of branch support (Bre-
mer, 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 abandon-

ing 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 This-

be 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 (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 tegmen; (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 
Thysanota 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 lev-
el studies within Riodinidae.

Parsimony analysis of 30 characters for 11 spe-
cies allowed us to assess the phylogenetic relations-

ships among Thysanota fenestrella, Thysanota galena, 

and species of Synarxis. 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 dor-

sal (unique to this group). Since both T. fenestrella 

and T. galena are imbedded within Synarxis (Fig. 

1), this strongly suggests that Synarxis is parphy-

letic. Transferring T. fenestrella to Synarxis 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 Syn-

arxis, the relationships between these taxa will be 

addressed in a future study (DeVries and Penz, in 

preparation).

EXAMINED SPECIMENS. Adelotypha 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 erosatus: PANAMA, Panama, 

Corozal, 1 male (ANMH); PANAMA, Panama, 

Nueva Gorgona, 1 female (ANMH). Audre sp.: 

ARGENTINA, Mendoza, San Rafael, 1 male, 1 

female (PJD). Calopsis emylus: ECUADOR, Suc-

umbios, Garza Cocha, 1 male, 1 female (PJD). 

Ei-

seleia pinchacalensis: PARAGUAY, Cordillera San-
tissima 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 caliginosa*: MEXICO, Veracruz, 1 male, 1 female (LACM). *Lemonias zygia*: BRAZIL, Rondônia, Caucalândia, Fazenda Rancho Grande, 1 male, 1 female (LACM). *Nymphidium anzoides*: PANAMA, Darién, Cerro Pirre, 1 male (PJD); COSTA RICA, Heredia, La Selva, 1 male, 1 female (PJD). *Nymphidium cachrurus*: 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). *Setabiss lagus*: COSTA RICA, Puntarenas, Las Alturas, 1 male (PJD); COSTA RICA, Puntarenas, Las Cruces, 1 female (PJD). *Stalachis euterpe*: ECUADOR, Sucumbios, Garza Cocha, 1 male, 1 female (PJD). *Syngapsis abaris*: PERU, Madre de Dios, Shintuya, 1 male (PJD); ECUADOR, Napo, Jatun Sacha, 1 female (PJD). *Syngapsis ethelinda*: COSTA RICA, Puntarenas, Barranca, 1 male (PJD); BELIZE, Orangewalk, Hillbank, 1 female (PJD). *Syngapsis gela*: no data, 1 male (MMP); BRAZIL, Amazonas, Borba, 1 female (MMP). *Syngapsis 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). *Syngapsis orestes*: ECUADOR, Sucumbios, Garza Cocha, 1 male, 1 female (PJD). *Syngapsis palaesta*: COSTA RICA, Puntarenas, Parque Nacional Corcovado, 1 male (PJD); COSTA RICA, Puntarenas, Rincón, 1 male (PJD); PANAMA, Darién, Pivesal, 1 female (PJD). *Syngapsis phillone*: BRAZIL, Rio de Janeiro, Pinheiral, 1 male (MMP); no data, 1 female (MMP). *Syngapsis tytta*: BRAZIL, Rondônia, Caucalândia, Fazenda Rancho Grande, 1 male (MMP); BRAZIL, Obidos, 1 female (MMP). *Syngapsis velafram*: COSTA RICA, Heredia, Tirimbina, 1 male (MMP); 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). *Theope irina*: COSTA RICA, Heredia, Chilamate, 1 male (PJD); PANAMA, Panama, Pipeline Road, 1 male (PJD); PANAMA, Panama, Barro Colorado Island, 1 female (PJD). *Theope lycorias*: COSTA RICA, Guanacaste, Parque Santa Rosa, 1 male (PJD); COSTA RICA, Heredia, Finca La Selva, 1 female (PJD). *Theope molela*: PERU, Madre de Dios, Shintuya, 1 male (PJD); VENEZUELA, Canaima, 1 female (LACM). *Thysanota galena*: BRAZIL, Rondônia, Caucalândia, Fazenda Rancho Grande, 1 male (MMP); 1 male, 1 female (AMNH). *Uranies hyali-nda*: ECUADOR, Sucumbios, Garza Cocha, 1 male, 1 female (PJD). *Uranies ucubis*: COSTA RICA, Heredia, Cariblanco, 1 male (PJD); COSTA RICA, Cartago, Turrialba, 1 female (PJD). *Uranies zamuro*: ECUADOR, Tena-Loreto Road, 1 male (JH).

**Phylogeny of Thisbe and Uranes**

Parsimony analysis of 39 characters for six species of *Thisbe* and *Uranes* 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 *Uranes hyalina, U. ucubis, and U. zamuro*, thus confirming the hypothesis that *Thisbe* is paraphyletic with respect to *Uranes* (Penz and DeVries, 1999), and justifying the placement of *T. lycorias* in *Uranes*. Characters that support groupings in Figure 2 are as follows.

**Thisbe Plus Uranes**. Five characters justify grouping *Thisbe* and *Uranes* (Fig. 2): character 3: 0, hindwing A2 produced in at least one sex; character 9: 0, connection of ducus 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 caliginosa*); character 30: 0, coecum penis present (Fig. 19, also in *Uranes hyalina* and *L. caliginosa*); 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 Uranes**. Despite contrasting wing color pattern (Figs. 36–38, 46–48, 56–57, 62–65), *Thisbe lycorias* forms a monophyletic group with species of *Uranes* (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-
Figures 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.

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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
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 bursae bordering antrum membranous; character 11-0, corpus bursae 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 ucubicus Plus U. zamuro. Two characters indicate that Uraneis ucubicus 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 fenes-trella.

TAXONOMY

Thisbe Hübner, 1819
(Figs. 3-35)

Thisbe Hübner, 1819:24. Type species: Papilio be-lise 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/sub- 
medial white band (faint in males of Thisbe molela) on a dark brown background; iridescent scales flap the white band. FW and HW ventral surface: 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 subcapshium broad (Figs. 19, 30); in ventral view, posterior end of the subcapshium not extended, ending before an-terior 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. Differes 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 (De-Vries, 1988, 1997, and unpublished). In both sexes the color pattern of the hindwing undersides resembles certain nymphaids (e.g., Adelpha Hübner, 1819; Dynamine Hübner, 1819; and Eresia Boisduval, 1836), and female T. irenea resemble certain Dynamine spp. and the melitaene 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 helides* male, dorsal (Tefe, Brazil); 7, *T. irenea helides* female, dorsal (Tefe, 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)
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.

COMMENT. 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-
descent blue bands occur in the same locality with *T. irenae 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 irenae* (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 character used to define subspecies were, at times, of questionable use because color patterns 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. irenae* (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. prodigia* (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. prodigia* 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.
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, Caucaulândia, Fazenda Rancho Grande, 1 male, 1 female (GA); BRAZIL, Rondônia, Caucaulândia, Fazenda Rancho Grande, 1 male (LACM); BRAZIL, Rondônia, Caucaulândia, 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 palidis* 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 satyrides (e.g., *Euptychia* Hübner, 1818, and *Cissia* Doubleday, 1848).

COMMENTS ON SUBSPECIES. Males of *Thisbe molela molela* (Hewitson, 1865) and *T. molela palidis* Stichel, 1910, are very similar except for a slightly more developed HW white submedial band.
in T. m. pulilis. Examined females from distant localities (and supposedly representing different subspecies) were indistinguishable to us. We therefore conclude that the subspecies designation pulilis 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)


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 norela*, 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 kyalina* adults; 36, male dorsal (Ecuador); 37, female, dorsal (Ecuador); 38, male, ventral (Ecuador)
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 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), _Phaenopsis_ spp. (Nolodontidae), and the riodinids, _Lepricornis striogosa_ (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, Pumaycu displayed an iridescent blue submarginal band from apex to tornus of the HW.
EXAMINED SPECIMENS. BRAZIL, Rondônia, Caucaalândia, Fazenda Rancho Grande, 1 male (GA); BRAZIL, Rondônia, Caucaalândia, Fazenda Rancho Grande, 1 male (BH); ECUADOR, Sucumbios, Garza Cocha, 5 males, 3 females (PJD); PERU, Pumayacu, 1 male (LACM).

_Uraneis ucbis_ Hewitson, 1870

_Uraneis ucbis_ 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 ucbis_ 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).
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 adelphinus); 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 rubris*, 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 rubris*, 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 incaranum* 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
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–
64) and U. l. incaram Seitz, 1916 (Fig. 65). Male U. l. incaram 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. incaram 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. incaram showed no difference from U. l. lycorias.

COMMENTS ON SYNONYMY. The subspecies Uranis 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. Uranis 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).

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

**Synargis fenestrella (Lathy, 1932) new combination**  
(Figs. 73–78)


**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; postmedian 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 Guiana.

**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 Guiana 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-
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 Thyasanota, not Thisbe. Our analysis of 30 characters from male genitalia indicated that both T. fenestrella and Thyasanota galena are embedded 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 Thyasanota.

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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Contributions in Science, Number 485
Penz and DeVries: Thsibe and Uranets
### 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.

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The characters used to evaluate the systematic position of *Thisbe fenestrella* are listed in Table 1. Character states in parentheses indicate polymorphism. The matrix includes characters for species identification and is used to determine the systematic position of *Thisbe fenestrella*.
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: Ac, acdeaicus; Coe, coecum penis; Jx, juxta (= pedicel sensu Harvey, 1987); Ped, pedunculum; Sca, subcapitulum; 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 Tg7: 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. Posteromedia! on male Stn8: well scleritized (0); weakly scleritized (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 scleritized posteromedia! on male Stn8: extending to reach anterior edge of Stn8 (0); anterior edge of Stn8 well scleritized (1). Character 52 in Penz and DeVries (1999).

7. Un: entire (0); split (1). Character 54 in Penz and DeVries (1999).

8. Posteromedia! on 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. Sca: uniformly narrow (0); uniformly broad (1); broadly posteriorly and narrowed anteriorly (2); broad anteriorly and narrowed posteriorly (3). Character 65 in Penz and DeVries (1999).

16. In lateral view, Sca: 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 Sca: 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 scleritized 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: ½ or more the length of bulbous ejaculatorius (0); ½ 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.

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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 bursae; Dc.bu, ductus bursae; Gs, gnathos (= brachia sensu Muschamp in Ogata et al., 1957; falcí sensu Bethune-Baker, 1910); Jx, juxta (= pedicel sensu Harvey, 1987); L1, foreleg; Ob, ostium bursae; Ped, pedunculum; Sa, saccus; Sig, signum; Scs, subscaphium; Sm, sternite (numbers may follow abbreviation; e.g., Sm7, 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 of R4 (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 fourth-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 Sm7: 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.


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.


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. Sm8: 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). If 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.


23*. In ventral view, posterior end of Scs: 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. 62 (*U. lycoris*) 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); devoid 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*.

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