

Contributions to the systematics of New World macro-moths V

Edited by

B. Christian Schmidt, J. Donald Lafontaine



Sofia–Moscow

2014

ZooKeys 421 (SPECIAL ISSUE)

CONTRIBUTIONS TO THE SYSTEMATICS OF NEW WORLD MACRO-MOTHS V

Edited by B. Christian Schmidt, J. Donald Lafontaine

First published 2014

ISBN 978-954-642-737-3 (paperback)

Pensoft Publishers

12 Prof. Georgi Zlatarski Street, 1700 Sofia, Bulgaria

Fax: +359-2-870-42-82

info@pensoft.net

www.pensoft.net

Printed in Bulgaria, June 2014

Contents

- I Contributions to the systematics of New World macro-moths V**
B. Christian Schmidt, J. Donald Lafontaine
- 3 The *Phyllodonta latrata* (Guenée) species group in Costa Rica (Geometridae, Ennominae)**
J. Bolling Sullivan
- 21 The *Disphragis notabilis* (Schaus) species-group in Costa Rica (Lepidoptera, Notodontidae)**
J. Bolling Sullivan, Michael G. Pogue
- 39 Four new species of *Symmerista* Hübner, 1816 (Notodontidae, Nystaleinae) from Costa Rica**
Isidro A. Chacón, Daniel H. Janzen, Winnie Hallwachs
- 65 The type-material of Arctiinae (Lepidoptera, Erebidae) described by Burmeister and Berg in the collection of the Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Buenos Aires, Argentina)**
Hernán M. Beccacece, Benoit Vincent, Fernando R. Navarro
- 91 Taxonomy and biogeography of the Nearctic *Raphia* Hübner (Lepidoptera, Noctuidae, Raphiinae)**
B. Christian Schmidt, Gary G. Anweiler
- 115 Polyphyly of Lichen-cryptic Dagger Moths: synonymy of *Agriopodes* Hampson and description of a new basal acronictine genus, *Chloronycta*, gen. n. (Lepidoptera, Noctuidae)**
B. Christian Schmidt, David L. Wagner, Brigitte V. Zacharczenko, Reza Zahiri, Gary G. Anweiler
- 139 A revision of the genus *Protorthodes* McDunnough with descriptions of a new genus and four new species (Lepidoptera, Noctuidae, Noctuinae, Eriopygini)**
J. Donald Lafontaine, J. Bruce Walsh, Clifford D. Ferris
- 181 A new apameine genus and species from the southern Appalachian Mountains, USA (Lepidoptera, Noctuidae, Noctuinae)**
Eric L. Quinter, J. Bolling Sullivan

Contributions to the systematics of New World macro-moths V

B. Christian Schmidt¹, J. Donald Lafontaine²

1 Canadian Food Inspection Agency, Canadian National Collection of Insects, Arachnids and Nematodes, K.W. Neatby Bldg., 960 Carling Ave., Ottawa, ON, Canada K1A 0C6 **2** Canadian National Collection of Insects, Arachnids, and Nematodes, Biodiversity Program, Agriculture and Agri-Food Canada, KW Neatby Bldg., C.E.F., Ottawa, Ontario, Canada K1A 0C6

Corresponding author: B. Christian Schmidt (Chris.Schmidt@inspection.gc.ca)

J. Donald Lafontaine (Don.Lafontaine@agr.gc.ca)

Received 6 June 2014 | Accepted 6 June 2014 | Published 27 June 2014

Citation: Schmidt BC, Lafontaine JD (2014) Contributions to the systematics of New World macro-moths V. In: Schmidt BC, Lafontaine JD (Eds) Contributions to the systematics of New World macro-moths V. ZooKeys 421: 1–2. doi: 10.3897/zookeys.421.8050

With the fifth installment of the “Contributions to the systematics of New World macro-moths” series, initiated in 2009 (Schmidt and Lafontaine 2009), systematics of taxa in the Geometridae, Notodontidae, Erebidae and Noctuidae are addressed. Geographic coverage is approximately equal between the Nearctic and Neotropic realms.

Despite the relatively advanced taxonomic knowledge of the North American macro-moth fauna, surprising discoveries continue – one new genus and species of Noctuidae is described from eastern North America (*Cherookeea* Quinter & Sullivan, gen. n.; *Cherookeea attakullakulla* Sullivan & Quinter, sp. n.), and two genera and four species, also Noctuidae, from western North America (*Chloronycta* Schmidt & Anweiler, gen. n., *Nudorthodes* Lafontaine, Walsh & Ferris, gen. n., *Nudorthodes molino* Lafontaine, Walsh & Ferris, sp. n., *Protorthodes ustulata* Lafontaine, Walsh & Ferris, sp. n., *Protorthodes texicana* Lafontaine, sp. n., *Protorthodes mexicana* Lafontaine, sp. n.). Four new generic combinations are proposed: *Chloronycta tybo* (Barnes), *Acronicta fallax* (Herrich-Schäffer), comb. n., *Nudorthodes texana* (Smith, 1900), comb. n., and *Nudorthodes variabilis* (Barnes & McDunnough, 1912), comb. n. Six previously recognized species are revised in status to subspecies: *Raphia frater abrupta* Grote, stat. n., *Raphia frater coloradensis* Putnam-Cramer, stat. rev., *Raphia frater piazzi* Hill,

stat. n., and *Raphia frater elbea* Smith, stat. n. Ongoing updates and corrections to the North American Noctuoidea checklist (Lafontaine and Schmidt 2011, 2013) will be published in the upcoming volume VI of “Contributions”.

Eight new species are described from the Neotropics, all from Costa Rica: *Phyllodonta esperanza* Sullivan, sp. n., *Phyllodonta intermediata* Sullivan, sp. n., *Phyllodonta alajuela* Sullivan, sp. n. (Geometridae); *Symmerista luisdiegogomezi* Chacón, sp. n., *Symmerista aura* Chacón, sp. n., *Symmerista inbioi* Chacón, sp. n., *Symmerista minaei* Chacón, sp. n. and *Disphragis bifurcata* Sullivan & Pogue, sp. n. (Notodontidae). The status of *Disphragis hemicera* (Schaus, 1910), stat. rev. is raised to species and *Elymiotis tlotzin* (Schaus, 1892), comb. n. is transferred from *Symmerista*. The type material of Neotropical Arctiinae (Erebidae) described by C. G. Burmesiter and C. Berg is reviewed, resulting in the following changes: *Opharus picturata* (Burmeister, 1878), comb. n. (= *Opharus brunnea* Gaede, 1923: 7, syn. n.); *Hypocrisias fuscipennis* (Burmeister, 1878) (= *Phaegoptera jonesi* Schaus, 1894, syn. n.); *Leucanopsis infucata* (Berg, 1882), stat. rev.; *Paracles argentina* (Berg, 1877), sp. rev.; *Paracles uruguayensis* (Berg, 1886), sp. rev. A lectotype is designated for *Halesidota picturata* Burmeister, 1878, *Halesidota cancellata* Burmeister, 1878 *Halesidota cancellata* Burmeister, 1878.

Seventeen authors contributed eight manuscripts for this volume, and the continued interest and support of these contributors makes this series (Schmidt and Lafontaine 2009, 2010, 2011, 2013) possible. Authors interested in contributing to future editions of “Contributions ...” are encouraged to contact us.

References

- Lafontaine JD, Schmidt BC (2011) Additions and corrections to the check list of the Noctuoidea (Insecta, Lepidoptera) of North America north of Mexico. In: Schmidt BC, Lafontaine JD (Eds) Contributions to the systematics of New World macro-moths III. ZooKeys 149: 145–161. doi: 10.3897/zookeys.149.1805
- Lafontaine JD, Schmidt BC (2013) Additions and corrections to the check list of the Noctuoidea (Insecta, Lepidoptera) of North America north of Mexico. In: Schmidt BC, Lafontaine JD (Eds) Contributions to the systematics of New World macro-moths IV. ZooKeys 264: 227–236. doi: 10.3897/zookeys.264.4443
- Schmidt BC, Lafontaine JD (2009) Contributions to the systematics of New World macro-moths. ZooKeys 9: 1–134. doi: 10.3897/zookeys.9.183
- Schmidt BC, Lafontaine JD (2010) Contributions to the systematics of New World macro-moths II. ZooKeys 39: 1–272. doi: 10.3897/zookeys.39.422
- Schmidt BC, Lafontaine JD (2011) Contributions to the systematics of New World macro-moths III. ZooKeys 149: 1–161. doi: 10.3897/zookeys.149.2383
- Schmidt BC, Lafontaine JD (2013) Contributions to the systematics of New World macro-moths IV. ZooKeys 264: 1–238. doi: 10.3897/zookeys.264.4687

The *Phyllodonta latrata* (Guenée) species group in Costa Rica (Geometridae, Ennominae)

J. Bolling Sullivan¹

¹ 200 Craven St., Beaufort, North Carolina 28516 USA

Corresponding author: J. Bolling Sullivan (sullivan14@earthlink.net)

Academic editor: C. Schmidt | Received 25 March 2014 | Accepted 15 May 2014 | Published 27 June 2014

<http://zoobank.org/156EFD4-E7E6-475B-A66D-74B8D5AB67BB>

Citation: Sullivan JB (2014) The *Phyllodonta latrata* (Guenée) species group in Costa Rica (Geometridae, Ennominae). In: Schmidt BC, Lafontaine JD (Eds) Contributions to the systematics of New World macro-moths V. ZooKeys 421: 3–19. doi: 10.3897/zookeys.421.7590

Abstract

Historically, the name *Phyllodonta latrata* (Guenée) has been applied to what is a complex of three undescribed species in Costa Rica. They are very similar in maculation, but can be differentiated by genitalic characters and barcodes. *P. alajuela* Sullivan, **sp. n.** occurs at lower altitudes in the northwestern part of Costa Rica whereas *P. intermediata* Sullivan, **sp. n.** and *P. esperanza* Sullivan, **sp. n.** are found at partially overlapping altitudes in the central mountain ranges.

Keywords

Geometridae, Ennominae, *Phyllodonta*, Costa Rica

Introduction

The genus *Phyllodonta* Warren currently consists of approximately 26 species of medium-sized geometrid moths that occur from the southern United States to Argentina (Pitkin 2002). Currently, eight species are thought to occur in Costa Rica (Pitkin et al. 1996). Unpublished mtDNA barcode data indicate that many of these species are complexes of similar-looking species often with non-overlapping geographic ranges. *Phyllodonta latrata* (Guenée) was described from Brazil and Colombia; in the British Museum the specimen from Nova Friburgo (state of Rio de Janeiro, Brazil) is labeled

as the type. It is unlikely that specimens from Colombia are conspecific. In Costa Rica, specimens that are very similar to *P. latrata* occur from about 500–3000 m, but mtDNA barcode sequences of distinct clusters suggest a complex of species. Four additional species from Peru and Ecuador have been subject to barcode analysis but no haplotype clusters overlap those from Costa Rica. There are no specimens of *P. latrata* from Brazil that have been barcoded nor have the types of *P. latrata* nor *P. succedens* (Walker) (TL: Quito, Ecuador and Bogota, Colombia) been dissected. Currently, *P. succedens* is placed as a synonym of *P. latrata* in the British Museum collections, although Pitkin (2002) regarded it as a valid species with *P. nolckeniana* (Snellen) (TL: Bogota, Colombia) as a synonym.

Materials and methods

Photographic methods used herein are described in Sullivan and Adams (2009). Procedures for dissecting and preparing genitalia follow that of Lafontaine (2004). DNA sequencing of the barcode fragment of the COI gene was carried out at the Canadian Center for DNA Barcoding in Guelph, Ontario. Barcode sequences were compared by nearest neighbor analyses as implemented on the Barcode of Life Data systems website (Ratnasingham and Hebert 2007).

Repository abbreviations

BMNH Natural History Museum, London, UK

INBio Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica

JBS J. Bolling Sullivan, Beaufort, North Carolina, USA

USNM National Museum of Natural History, Washington, District of Columbia, USA

Systematics

I have photographed and examined the types of 26 of the 31 names applied to this genus. *Phyllodonta latrata* (Gn.), *P. succedens* (Wlk.) and *P. nolckeniana* (Snellen) are distinguished by their rich brown color and will be referred to as the *P. latrata* complex. The antemedial and postmedial lines are usually distinct and are wavy or undulating. On the underside, these lines are distinct and the characteristic whitish blotch (Pitkin 2002) at the outer anal margin of the forewing is present with a blackish blotch proximal to it. The characteristic juxtal sac and socii (Pitkin 2002), unique to the genus, are present. *P. catephracta* Prout is somewhat similarly colored, but has a distinct, wide submarginal line on the forewing not present in the *latrata* group. *P. peccataria* (Barnes & McDunnough) and *P. sarukhani* Beutelspacher are similar in general color but the wing markings and genitalia are very different (Ferris and Walsh 2006). I have exam-

ined the genitalia of nine other taxa in the genus and the compact shape of the socii and maculation seem to distinguish the *latrata* group. Given that barcodes of the *latrata* group specimens from Ecuador and Peru do not match those of any of the Costa Rican species, and given that species of Southeastern Brazil rarely occur in Costa Rica, all of the species in Costa Rica are treated as new.

***Phyllodonta esperanza* Sullivan, sp. n.**

<http://zoobank.org/E9315F5A-D858-473C-8680-54323A1A371C>

Figs 1–5, 16

Type material. Holotype male: Costa Rica, Tapanti Parque (9.456°N; 83.417°W), Cartago Province, 1275 m, 7–9 July 2008, J. Bolling Sullivan (DNA voucher #11-CRBS-381) (INBio). **Paratypes:** 5♂, 4♀: 1♂, same data as holotype (DNA voucher #11-CRBS-288); 1♂, same data as holotype but 12–17 February 2005 (07-CRBS-1206), (dissection #JBS-3305); 1♂, Costa Rica, Parque National Volcan Poas (10.103°N; 84.342°W), Alajuela Province, 2500 m, 7–8 August 2007, J. Bolling Sullivan (07-CRBS-359), (dissection #JBS-2006); 2♀, same data (07-CRBS-357), (JBS-2007); 3♂, Costa Rica, Villa Mills (9.334°N; 83.423°W), Cartago Province, 2845 m, J. Bolling Sullivan (10-CRBS-764, 767, 1531), 2♀, same data (10-CRBS-765, 766). BMNH, INBio, JBS, USNM.

Etymology. The species is named for the biological station La Esperanza in the Talamanca Mountains, Cartago, Costa Rica, where many of the specimens were taken.

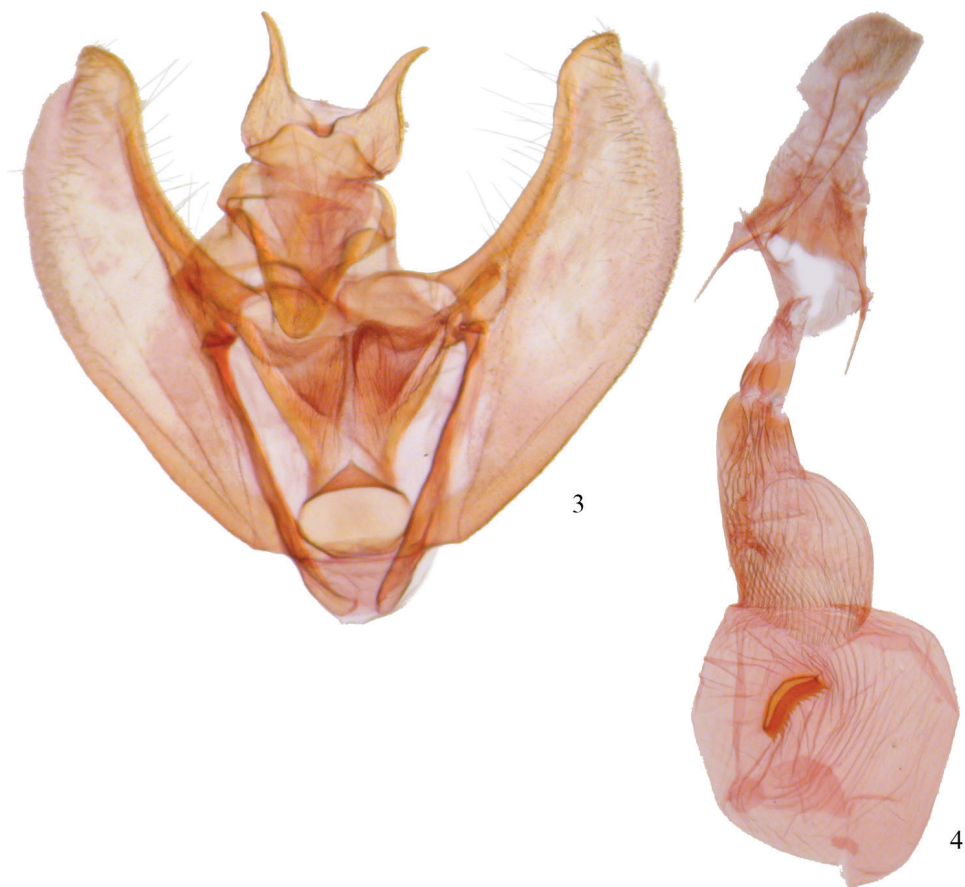
Diagnosis. Maculation does not seem to be diagnostic for distinguishing this species. It is best characterized by barcode data and the genitalia. It has the highest altitude distribution but does overlap that of *P. intermediata* below 2300 m. In the male, the base of the socius is usually swollen (straight in the other two species); the vesica is unarmed with pouches emanating from the left side (right side in *intermediata*, armed in *alajuela*). In the female, the collar on the ductus bursae is narrow and the signum on the corpus bursae is crescent shaped, often with a medial kink and with the anterior and posterior sides narrowly separated. In the other two species the collar is wider and the signa are more oval shaped, never kinked.

Description. Male. (Fig. 1) *Head*—labial palps warm brown, slightly porrect. First segment upcurved, second segment similar in length and tufted slightly over third segment, which is 1/3 as long and angled ventrally. Haustellum developed. Eyes hemispherical, large, ocellus present. Frons brown, slightly pointed with scaling directed anteriorly. Scape cream proximally, brown laterally and distally. Cream color extends along dorsal edge of antenna to tip. Antennal segments oblong with minute setae at base of each segment. Interantennal area warm brown, lighter onto collar. *Thorax and Abdomen*—Vertex brown, fine scaling extending onto thorax, most scales expanding to three pointed tip, a few black-tipped. Tegulae brown, abdomen with closely appressed scaling, gray brown dorsally, warm brown ventrally. Legs finely scaled, warm brown, tibia on first two legs with 3 evenly spaced white spots dorsally, proximal smallest,



Figures 1, 2. *Phyllodonta esperanza*. **1** male holotype (11-CRBS-381) **2** female (07-CRBS-359).

distal largest, tarsal spines prominent (0-2-4). *Wings*—forewings warm brown with prominent antemedial and postmedial lines that undulate, in both cases forming two outward bulges. Antemedial bulges separated by prominent cleft. Both lines black edged with lighter grayish scales proximally. Black scaling distal to reniform at costa and forming a diffuse line paralleling antemedial line. Reniform spot small, black and forming center of a gray circle. Forewings long, outer margin truncated at costa with a distinct notch medially, forewing length 23.0 mm (20–26 mm, n=18). Hindwing with prominent postmedial line, margin with submedial notch. Underside of wings warm brown, forewing with postmedial line prominent, medial line visible, anteme-



Figures 3, 4. *Phyllodonta esperanza*. **3** male valve (JBS-1248) **4** female genitalia (JBS-2007).

dial line absent. White blotch subterminal at notch, larger black blotch proximal to it. Small discal spot present. Hindwing underside with prominent postmedial line, prominent discal spot, small yellow line of scales distal to postmedial line on both wings. Cream streak from wing base widening to anal angle. *Male Genitalia* (Figs 3, 5) (20 dissections) –uncus unsclerotized, short with terminal setae. Socius triangular shaped at base and curving distally toward tip. Well-defined tegumen with triangular gnathos, rounded at tip with small setae. Juxta narrow basally, forming a pocket and widening toward transitilla lobes that widen medially. Costa well sclerotized, tapering to tip of valva. Valva broad with two ridges bearing setae. Subcostal ridge tapers slightly and meets a broader submarginal ridge that broadens to half width at valve tip. Saccus V-shaped and rounded slightly at basal point. Aedeagus partially sclerotized distally, a band of striations at tip. Ductus inserts sub-basally. Vesica sac-like, curving ventrally; two outpockets medially, most prominent one bifurcated and curving to left with smaller lobe to right. No cornuti or sclerotized areas. Vesica slightly longer than



Figures 5, 6. Aedeagi. **5** *Phyllodonta esperanza* **6** *Phyllodonta intermediata*.

aedeagus. **Female.** (Fig. 2) –similar to male but larger, gray-brown ground color, cross lines usually more prominent, forewing length 26.1 mm (25–27 mm, n=7) . Gray circle around reniform more distinct. Undersides similar to male but gray brown. *Female Genitalia* (Figs 4, 16) (8 dissections) –Anal papillae with setae, distally truncated in shape with anterior apophyses shorter than posterior apophyses. Anal plate not sclerotized, forming a broad funnel. Ductus bursae moderately short with sclerotized collar at posterior end. Collar ends form obvious abutment. Accessory bursae striated, widening significantly prior to midpoint and striations continuing onto corpus bursae. Corpus bursae 2× as wide as ductus bursae, mostly unstriated with crescent-shaped signum. Signum varies but usually an elongate crescent often kinked medially and with several rows of broad basal spines on anterior side of crescent.

Barcodes. Twenty nine specimens have been barcoded and exhibit twelve haplotypes that differ from each other by a maximum of 0.8%. They differ from those of *P. intermediata* by a minimum of 4.6% and from *P. alajuela* by a minimum of 4.8%. The most common haplotype (10-CRBS-762) is:

```
AACATTATATTTTATTTTGGGATTGAGCTGGAATAGTAGGAACATCTT
TAAGTTTATTAATTCGAGCTGAATTAGGAAATCCTGGATCTCTAATTG
GAGATGATCAAATTTATAATACTATTGTAAGTCTCATGCTTTT
ATTATAATTTTCTTTATAGTAATACCTATTATAATCGGAGGATTTG
GAAATTGATTAGTTCCTTTAATATTAGGAGCTCCTGATATGGCTTTC
CCTCGAATAAATAATATAAGATTTTGATTACTTCCACCTTCTATTA
CATTATTAATTTCTAGAAGAATTGTGGAAAATGGAGCTGGGACAG
```

GATGAACTGTTTATCCTCCTTTATCTTCTAATATTGCTCACGGTGG
 TAGTTCTGTTGACCTTGCTATTTTTTCATTACATTTAGCTGGTATTTTCAT
 CAATTTTAGGGGCTATTAATTTTATTACTACAATTATTAATATACGAT
 TAAATAATTTATCTTTTGATCAAATACCTTTATTTGTATGAGCAGTAG
 GAATTACTGCATTTTTATTATTATTATCATTACCTGTTTTAGCTGGAGC
 TATTACTATATTATTAACAGATCGAAATTTAAATACATCTTTTTTTGATC
 CTGCTGGAGGAGGAGATCCAATTTTATACCAACATTTATTT

Distribution. Known from above 1200 m in the Talamancas as well as the Central Volcanic and Tilaran ranges in Costa Rica. In flight throughout the year.

Remarks. Nothing is known about the biology of this species. Its range probably extends into the other mountain ranges in Costa Rican and perhaps in northern Panama.

***Phyllodonta intermediata* Sullivan, sp. n.**

<http://zoobank.org/FEE6C9E5-A097-4088-983C-D0573F1F0E1C>

Figs 6–10, 17

Holotype male. Costa Rica, tunnel road, Tapanti Parque (9.43°N; 83.46°W) Cartago Province, 1475 m, 7–8 July 2008, J. Bolling Sullivan (10-CRBS-283) (INBio), **Paratypes.** 5♂, 1♀, 2♂, 1♀, same data as holotype (11-CRBS-2726, 10-CRBS-285 (JBS-2817), 10-CRBS-282 (JBS-5409)); 2♂, Costa Rica, Tapanti Parque (9.46°N; 83.42°W), Cartago Province, 1275 m, 7–9 July 2008, J. Bolling Sullivan, (11-CRBS-286 (JBS-5416); 1♂, Costa Rica, Vera Blanca, La Paz Waterfall Garden (10.12°N; 84.10°W), Alajuela Province, J. Bolling Sullivan (07-CRBS-1202), (JBS-3306) (INBio, JBS, USNM).

Etymology. The species is named for the intermediate altitudes between 1200 and 1580 m where most of the specimens were taken. Two specimens were taken above 1600 m.

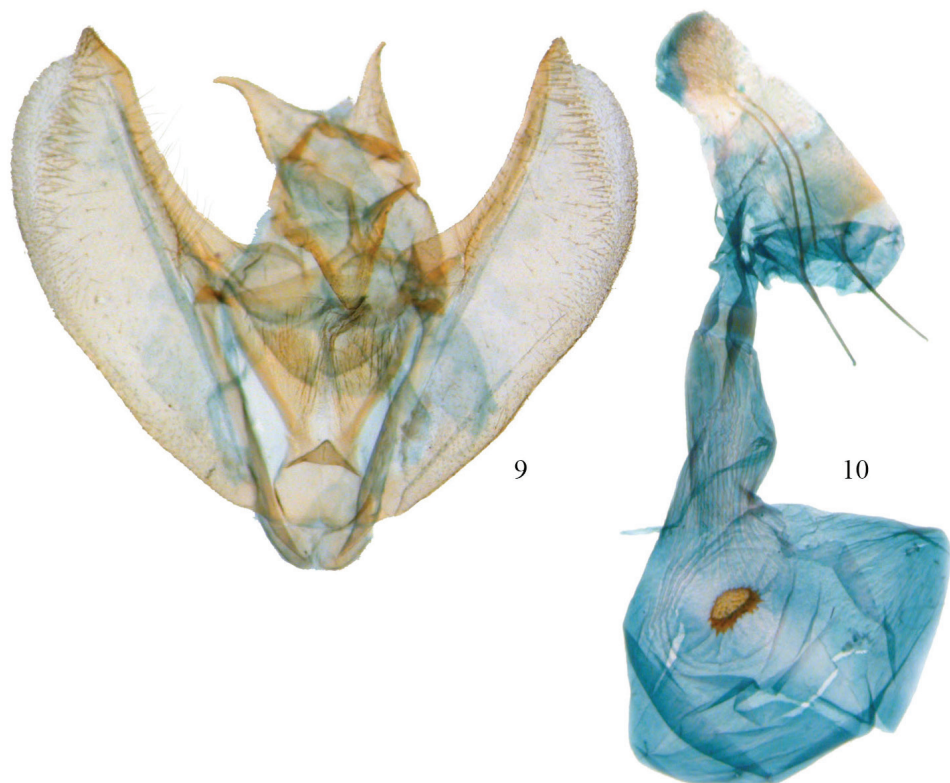
Diagnosis. Maculation is not diagnostic for identifying this species. It is best characterized by barcode data and the genitalia. In the male, the distal side of the socius is usually straight (swollen in *esperanza*), the vesica is unarmed and pouches emanate from the right side (in *alajuela* the vesica is armed, in *esperanza* the pouches emanate from the left side). In the female, the collar on the ductus bursae is narrow (broad in *esperanza*) and the signum on the corpus bursae is peanut-shaped with moderate spacing between the anterior and posterior sides (crescent shaped and narrowly spaced sides in *esperanza*, oval shaped in *alajuela*).

Description. Male. (Fig. 7) *Head*—labial palps warm brown, slightly porrect. First segment upcurved, second segment similar in length and tufted slightly over third segment, which is 1/3 as long and angled ventrally. Tongue developed. Eyes hemispherical, large, ocellus present. Frons brown, slightly pointed with scaling directed anteriorly. Scape cream proximally, brown laterally and distally. Cream color extends along dorsal edge of antennae to tip. Antennal segments oblong with minute setae at base of each segment. Interantennal area warm brown, lighter onto collar. *Thorax and Abdomen*—Vertex brown, fine scaling extending onto thorax, most scales expanding to three pointed tip, a



Figures 7, 8. *Phyllodonta intermediata*. **7** male holotype (10-CRBS-283) **8** female (10-CRBS-282).

few with black tips. Tegulae brown, abdomen with closely appressed scaling, gray brown dorsally, warm brown ventrally. Legs finely scaled, warm brown, tibia on first two legs with 3 evenly spaced white spots dorsally, proximal smallest, distal largest, tarsal spines prominent (0-2-4). *Wings*—forewings warm brown with prominent antemedial and postmedial lines that undulate, in both cases forming two outward bulges. Antemedial bulges separated by cleft. Both lines black edged with lighter grayish scales proximally. Black scaling distal to reniform at costa and forming a diffuse line paralleling antemedial line. Reniform spot small, black and forming center of a gray circle. Wings long, outer margin truncated at costa with a distinct notch medially, forewing length 23.1 mm (21–25 mm, n=10). Hindwing with prominent postmedial line, margin with submedial notch. Under-



Figures 9, 10. *Phyllodonta intermediata*. **9** male valve (JBS_3312) **10** female genitalia (JBS-5409).

side of wings warm brown, forewing with postmedial line prominent, medial line visible, antemedial line absent. White blotch subterminal at notch, larger black blotch proximal to it. Small discal spot present. Hindwing underside with prominent PM line, prominent discal spot, small yellow line of scales distal to PM line on both wings. Cream streak from wing base widening to anal angle. *Male Genitalia* (Figs 6, 9) (10 dissections) –uncus unsclerotized, short with terminal setae. Socius triangular shaped at base and curving distally toward tip. Outer margin often straight, but sometimes excurved basally. Well-defined tegumen with triangular gnathos, rounded at tip with small setae. Juxta narrow basally forming a pocket and widening toward transitilla lobes, which widen medially. Costa well sclerotized tapering to tip of valva. Valva broad with two ridges bearing setae. Subcostal ridge bears well-differentiated setae, tapers slightly and meets a broader submarginal ridge that broadens to half width at valve tip. Saccus vee-shaped and indented slightly at basal point. Aedeagus partially sclerotized distally, a band of striations at tip. Ductus inserts sub-basally. Vesica sac-like, curving ventrally; two outpockets medially, most prominent curving to right with smaller lobe to left. No cornuti or sclerotized areas. Vesica slightly longer than aedeagus. **Female.** (Fig. 8) – similar to male but larger, gray-brown ground color, cross lines usually more prominent, forewing length 24.3 mm (22.5–26.0, n=2).

Gray circle around reniform distinct. Undersides similar to male but gray brown. *Female Genitalia* (Figs 10, 17) (2 dissections) – Anal papillae with setae, distally truncated in shape with anterior apophyses shorter than posterior apophyses. Anal plate not sclerotized, forming a broad funnel. Ductus bursae short with sclerotized collar at posterior end; collar 2× as broad as in other two species. Accessory bursae striated, widening significantly at midpoint forming a hump and weak striations continuing onto broadly rounded, almost triangular corpus bursae. Corpus bursae 2× as wide as ductus bursae, mostly unstriated with crescent-like signum. Signum somewhat variable, often peanut shaped with large, broad spines anteriorly and short spines posteriorly. Very similar to the signum found in *P. esperanza* but always wider between anterior and posterior edges.

Barcodes. Seven specimens have been barcoded and exhibit two haplotypes that differ from each other by a maximum of 0.5%. They differ from those of *P. esperanza* by a minimum of 4.6% and from *P. alajuela* by a minimum of 6.3%. The most common haplotype (11-CRBS-286) is:

```
AACATTATATTTTATTTTGGGAATTGAGCTAGAATAGTGGGAACGTCTT
TAAGTTTATTAATTCGAGCAGAATTAGGGAATCCTGGGTCTTTAATTG
GAGATGATCAAATTTATAATACTATTGTAAGTGCACATGCTTTTAT
TATAATTTTCTTTATAGTAATACCTATTATAATTGGGGGATTTGGAAATT
GATTAATTCCTTTAATACTAGGGGCTCCTGATATAGCTTTCCCTC
GAATAAATAATATAAGATTTTGGTTACTTCCACCTTCCATTACATT
ATTAATTTTGTAGAAGAATTGTAGAAAATGGAGCTGGAACAGGATGAA
CAGTTTACCCACCTTTATCTTCTAATATTGCTCATGGGGGTAGTTCT
GTTGATCTTGCTATTTTTCATTACATTTAGCTGGTATTTTCATCAATTT
TAGGAGCTATTAATTTTCATCACCACAATTATTAATATACGATTAAATAATT
TATCTTTTGATCAAATACCTTTATTTGTATGAGCGGTAGGAATTACTG
CATTTTATTATTATTATCATTACCTGTTTTAGCTGGAGCTATTACTATAT
TATTAACCGATCGAAATTTAAATACATCTTTTTTTGACCCTGCTGGTG
GAGGAGATCCAATTTTATACCAACATTTATTT
```

Distribution. Known from between 1275 to 2280 m in the Talamancas, the Central Volcanic range, and the Tilaran range in Costa Rica. The moths are probably in flight throughout the year.

Remarks. Nothing is known about the biology of this species. Its range may extend into the other mountain ranges in Costa Rican and perhaps into northern Panama.

***Phyllodonta alajuela* Sullivan, sp. n.**

<http://zoobank.org/F193BB75-F3BF-42EC-9292-C10D65E15331>

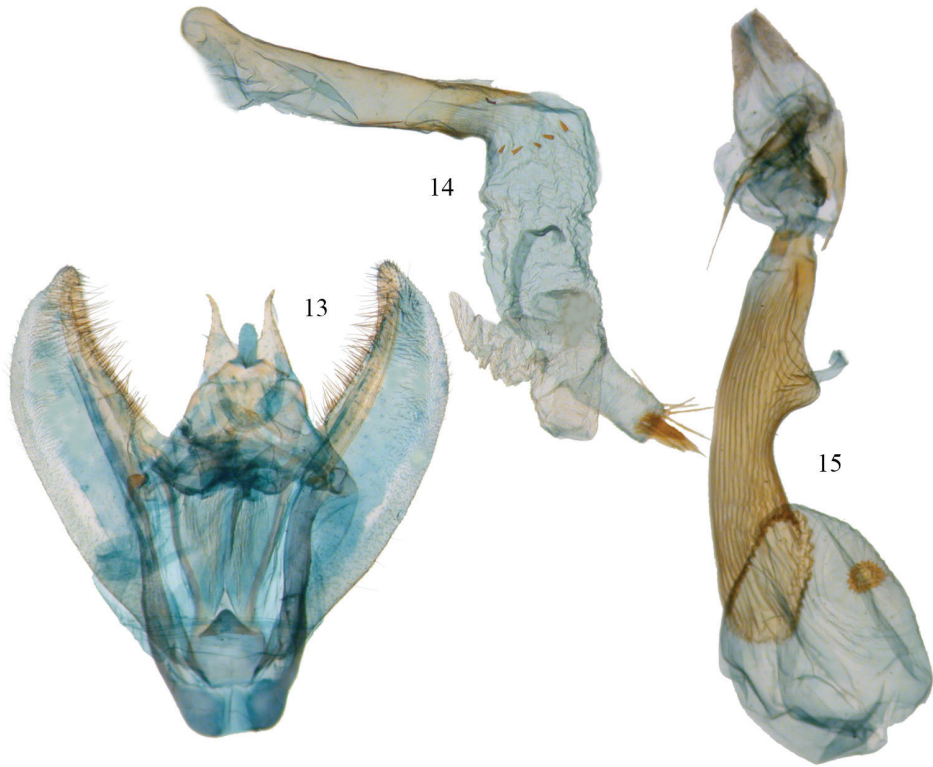
Figs 11–15, 18

Type material. Holotype male: Costa Rica, San Ramon Reserva Biol. Alberto M. Brenes Estacion Biol. (10.22°N; 85.62°W), Alajuela Province, 850 m, 7–11 February



Figures 11, 12. *Phyllodonta alajuella*. 11 male holotype (07-CRBS-365) 12 female (07-CRBS-366).

2005, J. Bolling Sullivan (07-CRBS-365, JBS-3303) (INBio). Paratypes: 4♂, 1♀: 2♂, same data as holotype (JBS-5401, 5407), 1♂, 1♀, Costa Rica, Upata. Estacion San Gerardo (10.89°N; 85.38°W), Alajuela Province, 550 m, 17–21 July 2006, J. Bolling Sullivan (JBS-5410, 07-CRBS-366,1205 (barcoded twice), JBS-3314). 1♂, Costa Rica, Upata Bijagua, Alberque Heliconias (10.43°N; 85.01°W), 800 m, Alajuela Province, J. Bolling Sullivan (JBS-3310).



Figures 13–15. *Phyllodonta alajuela*. **13** male valve (JBS-5400) **14** aedeagus (JBS-3303) **15** female genitalia (JBS-3314).

Etymology. The species is named for the province where the holotype and paratypes were taken. It has also been taken in Guanacaste province.

Diagnosis. Maculation does not seem to distinguish this species. It is best characterized by barcode data and the genitalia. To date it has been found below 1200 m and with no other member of the *P. latrata* complex. In the male, the distal sides of the socii are usually straight and the vesica is armed with cornuti at the end of the most prominent pouch (distal side of socii swollen in *esperanza*, both *esperanza* and *intermediata* have unarmed vesicas). The female has a broadened collar on the ductus bursae (narrow in *esperanza*) and the signum on the corpus bursae is almost round with equal-sized spines around it (crescent shaped in *esperanza*, peanut shaped in *intermediata*).

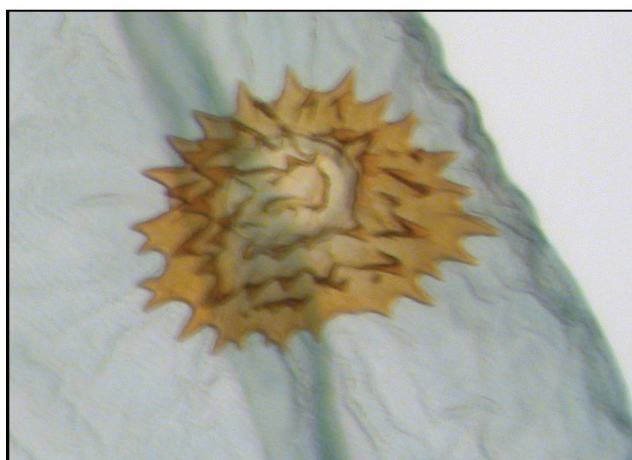
Description. Male. (Fig. 11) *Head*—labial palps warm brown, slightly porrect. First segment upcurved, second segment similar in length and tufted slightly over third segment, which is 1/3 as long and angled ventrally. Tongue developed. Eyes hemispherical, large, ocellus present. Frons brown, slightly pointed with scaling directed anteriorly. Scape cream proximally, brown laterally and distally. Cream color extends along dorsal edge of antennae to tip. Antennal segments oblong with minute setae at base of each segment. Interantennal area warm brown, lighter onto collar. *Thorax and Abdomen*—Vertex brown,



16



17



18

Figures 16–18. Comparison of signa. **16** *P. esperanza* (JBS-3315) **17** *P. intermediata* (JBS-5409) **18** *P. alajuela* (JBS-3314).

fine scaling extending onto thorax, most scales expanding to three pointed tip, a few black tipped. Tegulae brown, abdomen with closely appressed scaling, gray brown dorsally, warm brown ventrally. Legs finely scaled, warm brown, tibia on first two legs with 3 evenly spaced white spots dorsally, proximal smallest, distal largest, tarsal spines prominent (0-2-4). *Wings*—forewings warm brown with prominent antemedial and postmedial lines that undulate, in both cases forming two outward bulges. Antemedial bulges separated by cleft. Both lines black edged with lighter grayish scales proximally. Black scaling distal to reniform at costa and forming a diffuse line paralleling antemedial line. Reniform spot small, black, and forming center of a gray circle. Wings long, outer margin truncated at costa with a distinct notch medially, forewing length 24.1 mm (23.5–25.0 mm, n=6). Hindwing with prominent postmedial line, margin with submedial notch. Underside of wings warm brown, forewing with postmedial line prominent, medial line visible, antemedial line absent. White blotch subterminal at notch, larger black blotch proximal to it. Small discal spot present. Hindwing underside with prominent PM line, prominent discal spot, small yellow line of scales distal to PM line on both wings. Cream streak from wing base widening to anal angle. *Male Genitalia* (Figs 13–14) (6 dissections) —uncus unsclerotized, over half length of socii with terminal setae. Socius triangular shaped not swollen at base and curving distally toward tip. Well-defined tegumen with triangular gnathos, rounded at tip with small setae. Juxta narrow basally forming a pocket and widening toward transistilla lobes, which widen medially. Costa well sclerotized tapering to tip of valva. Valva broad with two ridges bearing setae. Subcostal ridge well developed with prominent setae, tapering slightly and meeting a broader submarginal ridge that broadens to half width at valve tip. Saccus vee-shaped and usually indented slightly at basal point. Aedeagus partially sclerotized distally, a band of striations at tip. Ductus inserts sub-basally. Vesica tubular with two outpockets distally, most prominent from left side and terminating with a patch of 10 or more moderately long cornuti. A row of small cornuti at base of vesica and variable in appearance, sometimes absent. Vesica slightly longer than aedeagus. **Female.** (Fig. 12) — similar to male but larger, gray-brown ground color, cross lines usually more prominent, forewing length 27 mm, n=1. Gray circle around reniform more distinct. Undersides similar to male but more gray brown. *Female Genitalia* (Figs 15, 18) (1 dissection) — Anal papillae with setae, distally truncated in shape with anterior apophyses shorter than posterior apophyses. Anal plate not sclerotized, forming a broad funnel. Ductus bursae short with narrow sclerotized collar at posterior end; collar ends form obvious abutment. Accessory bursae striated, widening significantly to form nipple at midpoint and weakly defined striations continuing onto bursae. Corpus bursae almost round. Signum circular with two or three rows of short spines radiating from fovea.

Barcodes. Twenty eight specimens have been barcoded and exhibit 9 haplotypes that differ from each other by a maximum of 1%. They differ from those of *P. esperanza* by a minimum of 4.8% and from *P. intermediata* by a minimum of 6.3%. The most common haplotype (09-SRNP-36297) is:

AACATTTATATTTTATTTTGGAAATTTGAGCTGGAATAGTAGGTACATCTT
TAAGTTTATTAATTCGAGCGGAATTAGGAAACCCTGGGTCTTTAATTG

GAGATGATCAAATTTATAATACTATTGTAAGTCTCATGCTTTTAT
TATAATTTTTTTTATGGTAATACCTATTATAATTGGGGGATTGGGAATT
GATTAGTTCCTTTAATATTGGGGGCCCCAGATATAGCTTTCCCAC
GAATAAATAATATAAGATTTTGATTACTTCCGCCTTCTATTACACTTT
TAATTTCTAGAAGAATTGTAGAAAATGGAGCCGGAAGTGGATGAAGT
GTCTACCCTCCTTTATCTTCTAATATTGCCACGGTGGTAGTTCT
GTTGATCTTGCTATTTTTTCATTACATTAGCTGGTATTCATCAATTT
TAGGGGCTATTAATTTTATTACAACAATTATTAATATACGATTAAATAACT
TATCTTTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATCACTG
CATTTTTATTATTATTATCATTACCTGTTTTAGCTGGAGCTATTACTAT
ATTATTAAGTATCGAAATTTAAATACATCTTTTTTTTGACCCTGCTGGAG
GAGGAGACCCAATTTTATATCAACATTTATTC

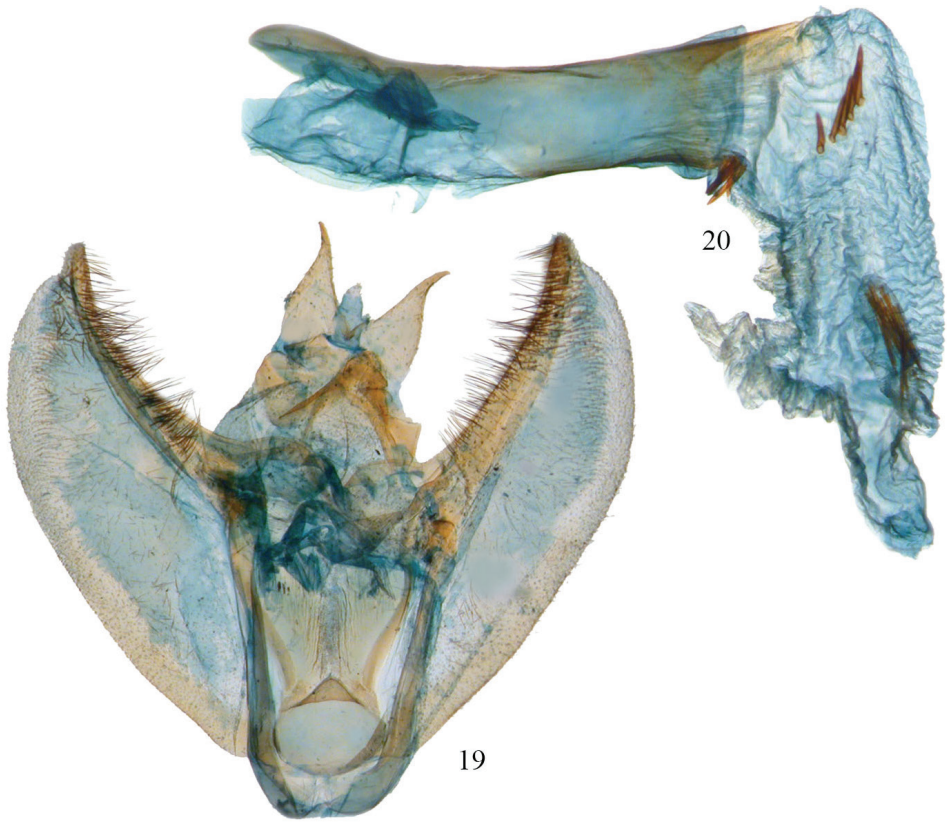
Distribution. Known from 500 to 1150 m in the provinces of Alajuela and Guanacaste. Moths are probably in flight throughout the year.

Remarks. Janzen and Hallwachs (2014) have reared this species 62 times. The larvae fed primarily (59 records) on *Witheringia solanacea* L. Hér. in the Solanaceae. One record may represent a second species on *Brugmansia × candida* (Solanaceae). The present range of *P. alajuela* seems to be limited to the Northwestern provinces of Costa Rica and may extend into Nicaragua. Southward and eastward its range is unknown. Specimens of the *latrata* complex from Anchicaya and Calima Dam in Valle Province of Colombia (four dissections) have similar male genitalia, but the basal spines on the vesica are larger; no specimens of it have been barcoded. Species of non-migratory moths common to Colombia and Costa Rica are often distributed in the western lowlands of both countries.

Discussion

As currently applied, the *Phyllodonta latrata* (Gn.) complex is represented in Costa Rica by three new species that can be differentiated by barcodes and genitalic features. *Phyllodonta alajuela* occurs at lower altitudes whereas *P. intermediata* and *P. esperanza* overlap at intermediate altitudes; but are often separate at the altitude extremes of their ranges. At the conclusion of this study, two male specimens in the *P. latrata* complex from the states of Bahia and Rio De Janeiro in Brazil were borrowed from the USNM and dissected. Both dissections showed characters not seen in any other members of the complex (Figs 19-20) and differed from each other as well.

The complex nature of species grouped under the name *Phyllodonta latrata* is not uncommon among mid and high elevation moth species in the neotropics (Sullivan 2011). Constant change in weather over long periods of time, and the rise and fall of mountains in the region, have provided optimal conditions for speciation. The use of barcoding provides a valuable tool for measuring species delineation and it is only when barcoding has segregated individuals of the apparent complexes that one can



Figures 19, 20. *Phyllodonta latrata* complex from Bahia State, Brazil (Camacan, 600 m, 2-III-1994, V. O. Becker) (USNM-50814). **19** male valve **20** aedeagus.

find reliable structural characters to sort the species. It is very difficult to sort normal interspecific variation in maculation and genitalic characters from intraspecific variation when species are closely related. If speciation is recent or ongoing, such characters may not be discernable but in the case of the *P. latrata* complex in Costa Rica such characters are apparent. The arrangement of the pouches emanating from the vesicas of the males and the shapes of the signa in the females are key structures (with their changes perhaps related) and are supported by other less obvious characters and geographic separation.

Barcodes and genitalic analyses also support the differentiation of other populations of the *P. latrata* complex in South America. Specimens from lowland western Colombia may be conspecific with *P. alajuela* but proof is lacking. Two male specimens taken above 2500 m in the central Andean range (Alto Rio Quindio) were dissected and differed from each other and all species from Costa Rica. Two specimens from coastal Brazil also were unique. Additional specimens barcoded from Ecuador and Peru are distinct. Thus, it is likely that the type locality for *P. latrata* (Brazil) and

high altitude locations throughout the Andes will provide a surprising number of additional species in the complex.

Acknowledgements

I would like to thank Jocelyn Gill, Don Lafontaine, and Chris Schmidt at the Canadian National Collection. Jocelyn for help with the illustrations, Don and Chris for suggestions regarding the manuscript. Paul Hebert of the University of Guelph, Guelph, Canada allowed the use of unpublished barcode data. Dan Janzen and Winnie Hallwachs shared unpublished barcode and life history data. Gunnar Brehm graciously shared his barcode data. Bernardo Espinosa at INBio enthusiastically helped me collect many of the specimens used in this study.

References

- Ferris CD, Walsh B (2006) Two *Phyllodonta* species from southern Arizona (Geometridae). *News of the Lepidopterists' Society* 48: 23–25.
- Janzen DH, Hallwachs W (2014) Caterpillars, pupae, butterflies & moths of ACG, Guanacaste, Costa Rica. <http://Janzen.sas.upenn.edu/caterpillars/database.lasso> [accessed 15 January 2014]
- Lafontaine JD (2004) Noctuoidea, Noctuidae (part), Noctuinae (part – Agrotini). In: Hodges RW (Ed) *The Moths of America North of Mexico* fasc. 27.1. The Wedge Entomological Research Foundation, Washington, 385 pp.
- Pitkin L (2002) Neotropical ennomine moths: a review of the genera (Lepidoptera: Geometridae). *Zoological Journal of the Linnean Society* 135: 121–401. doi: 10.1046/j.1096-3642.2002.01200.x
- Pitkin L, Mora RA, Scoble MJ (1996) A checklist to the Ennominae (Geometridae) of Costa Rica: taxonomy for a national biodiversity inventory. *Gayana Zoológica* 60: 21–155.
- Ratnasingham S, Hebert PD (2007) Bold: The barcode of life data system. *Molecular Ecology Notes* 7: 355–364. doi: 10.1111/j.1471-8286.2007.01678.x
- Sullivan JB (2011) Two new species of the *Hagnagora anicata* complex (Geometridae, Larentiinae) from Costa Rica. *ZooKeys* 149: 17–29. doi: 10.3897/zookeys.149.2345
- Sullivan JB, Adams JK (2009) A new species of *Morrisonia* (Noctuidae) from southeastern North America. *Journal of the Lepidopterists' Society* 63: 21–26.

The *Disphragis notabilis* (Schaus) species-group in Costa Rica (Lepidoptera, Notodontidae)

J. Bolling Sullivan¹, Michael G. Pogue²

1 200 Craven Street, Beaufort, North Carolina 28516 **2** Systematic Entomology Laboratory, PSI, Agricultural Research Service, U. S. Department of Agriculture, c/o Smithsonian Institution, P.O. Box 37012, NMNH, MRC-168, Washington, DC 20013-7012, USA.

Corresponding author: J. Bolling Sullivan (sullivan14@earthlink.net)

Academic editor: C. Schmidt | Received 20 February 2014 | Accepted 15 May 2014 | Published 27 June 2014

<http://zoobank.org/4B87F05B-1916-404E-B3E1-ECF514708A88>

Citation: Sullivan JB, Pogue MG (2014) The *Disphragis notabilis* (Schaus) species-group in Costa Rica (Lepidoptera, Notodontidae). In: Schmidt BC, Lafontaine JD (Eds) Contributions to the systematics of New World macro-moths V. ZooKeys 421: 21–38. doi: 10.3897/zookeys.421.7351

Abstract

The four described taxa in the *Disphragis notabilis* (Schaus) species-group are reviewed, including the types and their dissected genitalia. *Disphragis hemicera* (Schaus), **stat. rev.**, is elevated to species rank, *D. normula* (Dognin) is retained as a synonym of *D. notabilis*, *D. sobolis* Miller is confirmed as distinct from *D. hemicera*, and *D. bifurcata* **sp. n.**, is newly described. Both *D. hemicera* and *D. bifurcata* occur in Costa Rica. The known ranges of the other species are outlined. Defining characters of each species are presented and a key to species is provided. Unusual variation in the genitalia is noted.

Keywords

Taxonomy, genitalic variation

Introduction

The name *Disphragis notabilis* (Schaus), described from French Guiana, has been applied to prominent moths throughout Central and South America. Miller described *D. sobolis* from Ecuador and indicated that genitalic characters reveal yet another member of the complex in Ecuador (Miller and Thiaucourt 2011). Collections of so-called *D. notabilis* from Costa Rica are heterogeneous in maculation and dissections and barcodes reveal two distinct species. *Disphragis notabilis* has two junior synonyms, *D. hemicera* (Schaus) from Costa Rica and *D. normula* (Dognin) from Peru, so it is necessary to examine all named taxa in order to classify the species found in Costa Rica.

Materials and methods

Photographic methods used herein are described in Sullivan and Adams (2009). Procedures for dissecting and preparing genitalia follow those of Lafontaine (2004) and Pogue and Sullivan (2003). Genitalia are shown as dissected and stained, and flattened or not flattened. DNA sequencing of the barcode fragment of the COI gene was carried out at the Canadian Center for DNA barcoding in Guelph, Ontario. Barcode sequences were compared by nearest neighbor analyses as implemented on the Barcode of Life Data systems website (Ratnasingham and Hebert 2007). Genitalia dissection numbers are given in the format JBS-xxxx, DNA voucher numbers in the format xx-CRBS-xxxx and xx-MISC-xxx.

Repository abbreviations

BMNH Natural History Museum, London, UK

INBio Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica

JBS J. Bolling Sullivan collection, Beaufort, North Carolina, USA

USNM National Museum of Natural History, Washington, District of Columbia, USA

Key to species based on male genitalia

- 1 Socii short, 1/6 length of valva and upcurved below a short, almost hood-like uncus.....2
- Socii long, ½ length of valva, below triangular “dunce cap” uncus.....3
- 2 Phallus with two plates of flattened spines at base of sclerotized portion *D. hemicera*
- Phallus with a parallel extension at base of sclerotized portion *D. sobolis*
- 3 Socii large, bifurcated at tip *D. bifurcata*
- Socii smaller, tapering to single point with ventral spines..... *D. notabilis*

Systematics

The female type specimen of *Heterocampa notabilis* Schaus was named from French Guiana. Both *H. hemicera* Schaus (male) from Costa Rica and *H. normula* Dognin (male) from Peru are listed as synonyms of *Disphragis notabilis* by Gaede (1934). Miller described *D. sobolis* from the mountains of eastern Ecuador and noted that it was easily separated from specimens of *D. notabilis* by its darker color and more mottled appearance (Miller and Thiaucourt 2011). They also illustrate the genitalia of a male of *D. notabilis* from French Guiana and the male genitalia of *D. sobolis*.

Disphragis bifurcata Sullivan & Pogue, sp. n.

<http://zoobank.org/0944967F-1CB1-48C6-9702-0B8FA0D8E9B9>

Figs 1, 10, 14, 18, 22

Type material. Holotype male: Costa Rica, Reserva Hitoy Cerere (9.404°N 83.015°W), Limon Province, 354', 1–4 July 2008, J. Bolling Sullivan. INBio. **Paratypes:** 11♂, 3♀: 4♂, same data as holotype (JBS-2094, JBS-3053); 1♀, 22 March 2003, Monty Wood (JBS-3030); 1♂, Costa Rica, Est. Biol. La Selva (10.26°N, 84.01°W), Heredia Province, 50–150 m, 21–30 June 2003, Monty Volovsic (JBS-3040), 2♂, 29 Aug.–2 Sept. 2003, J. Bolling Sullivan (JBS-3038); 2♂, Costa Rica, Upata Estacion San Gerardo (10.89°N, 85.38°W), Alajuela Province, 550 m, 17–21 July 2006, J. Bolling Sullivan, B. Espinosa (JBS-3035); 1♂, Costa Rica, Puriscal Chires, Mastatal (N9.411; W-84.220), San Jose Province, 400 m, 16–18 Oct. 2011, J. Bolling Sullivan; 1♂, Costa Rica, Verugua Rainforest Campamento (9.553°N, 83.112°W), Limon Province, 400–500 m, 12–16 March 2010, J. Bolling Sullivan (11-CRBS-2066), (JBS-5427); 1♀, Costa Rica, Tuis, 2500', June, W. Schaus 1910-110. (BM-); 1♀, Costa Rica, Cashi, 8–10 1912 (Lankester), Rothschild Bequest, B. M. 1939-1. (BM-). (USNM, BMNH, JBS, INBio)

Etymology. The name *bifurcata* refers to the bifurcate tip of the socii, which is diagnostic.

Diagnosis. Maculation characters can usually be used to separate *D. bifurcata* and *D. notabilis* from the other two members of the complex. Forewing color is a warm brown, not mottled or brownish gray as in *D. sobolis* and *D. hemicera*. Additionally, the male antennal pectinations are shorter in *D. bifurcata* and *D. notabilis*. Males of *D. bifurcata* are easily distinguished by the large upturned and bifurcated socii in the male genitalia. In males of *D. notabilis* the socii usually have a single point at the apex, with many spines arising from the ventral edge. Females must be identified by maculation and geography; *D. bifurcata* occurs in Central America and central and western Colombia.

Description. Male. (Figs1, 10) *Head*—labial palps upturned, mahogany brown on basal segment, medial segment with cream scaling along distal margin, particularly near the terminus, and apical segment mostly cream scaled with scattered brown scales. De-



Figures 1–4. *Disphragis notabilis* complex holotypes. **1** *Disphragis bifurcata*, male holotype **2** *Disphragis hemicera*, male holotype **3** *Disphragis normula*, male holotype **4** *Disphragis notabilis*, female holotype.

nuded medial segment $2.4\times$ length of apical segment. Eye round, large, surrounded tightly with scaling. Front scaling mostly cream with scattered brown scales. Vertex with additional brown scales among white scaling. Scape with cream and brown scaling, cream extending onto antennal shaft for about 10–14 segments. Antenna bipectinate basally for 30 segments, then with minute basal seta on segments to tip (68 segments). Longest rami 0.44 mm. Thorax a blend of fine brown and cream scales giving a tan appearance. Metathorax bearing a central white spot with row of darker brown scales anteriorly. Abdomen with appressed brown scaling. Forewing (17.5 mm N = 10) elongate, rounded apically and with broad tan subcostal streak from base of wing to apex. Streak encloses chocolate reniform spot and has several slightly darker brown lines crossing obliquely from costa. Basal dash below streak paralleling costa. White streak below basal dash; warm brown patch distal to white streak bordered by white; wavy antemedial (AM) and postmedial (PM) lines. Chocolate shading from middle of forewing below costal streak and forming a wedge to margin (below costal streak to anal angle). Weak gray crescent on lower half of margin. Hind wing fuscous with darker margin and veins, weak darker brown anal markings almost a spot at anal angle. Underside of forewing fuscous, anal margin and cell yellowish. Basal $3/4$ of hind wing yellowish, margin brown and well differentiated. Legs a mixture of brown and white scales, appearing almost yellowish, with white scales forming rings at distal end of tarsal segments. Tibial spines 0–2–4. *Male genitalia* (Figs 14, 18) (8 dissections). Uncus an extended triangle, apex rounded with setae arranged almost in marginal rows. Tegumen broad, longer than vinculum. Socii extending from base of uncus as two large upcurved arms, scythe-like, apex bifurcate. Occasionally tip may be subdivided farther with arrowhead-like plates

embedded near apex (visible at higher magnification). However, plates do not form ventral spine-like projections as in *D. notabilis*. Gnathos absent, anal tube membranous. Valva elongated with costal half sclerotized, anal half membranous and enveloping deciduous scent hairs. Valva apex rounded, sclerotized costal half of valva with broad anal projection distally and sharper but rounded and more heavily sclerotized projection basally. Vinculum broad, short, rounded to saccus. Phallus long, narrow with subbasal keel, proximal half unsclerotized, ductus entering medially. Distal half of phallus sclerotized, enlarged basally at junction with membranous half, and with small teeth-like spines ventrally and laterally on basal half. Vesica emerges dorsally from aedeagus, forming a membranous tube that turns to parallel aedeagus and then to left with no major diverticula. A lightly sclerotized sliver-like cornutus often visible and often with small peg-like cornuti where vesica turns left. Eighth tergite broadly rounded, slightly sclerotized and crenulated medially at distal end. Eighth sternite lightly sclerotized, broadly rounded with well-defined, broad notch medially. Small sac-like flap in middle of sclerite, anterior end of sclerite with two broad, rounded projections with medial V-shaped notch. Ctenophores absent. **Female.** (Fig. 10). Female similar to male only larger (Forewing 21.3 mm, $n = 3$) and with fasciculate antennae. *Female genitalia* (Fig. 22) (3 dissections). Papillae anales bluntly rounded, slightly setose. Extension of 9th tergite forming dorsal flap. Anterior apophysis short, 25% as long as posterior apophysis. Genital plate small, elongate, consisting of a bifurcated middle phalanx with lateral “wings” from base. Ductus bursae slightly shorter than corpus bursae, narrow and tending to twist, unsclerotized. Corpus bursae egg shaped, with large signum on dorsal surface. Signum shield-like, about half as long as corpus bursae. Signum egg shaped with stippled lateral flanges anterior to midpoint. Proximal margin lightly sclerotized and faintly stippled.

DNA barcode sequence. Five barcoded specimens exhibit two haplotypes that differ from each other by a maximum of 0.15%. They differ from *D. hemicera* by a minimum of 5.61%, from *D. notabilis* by a minimum of 1.26%, and from *D. sobolis* by a minimum of 5.78%. The most common haplotype (11-CRBS-2066) is:

```
AACCTTATATTTTCATTTTTTGGAATTTGAGCAGGAATAGTAGGAAC
CTCTTTAAGTCTTCTAATTCGTGCTGAATTAGGAACCCCGG
GACTTTAATTGGAGATGATCAAATTTATAATACTATTGTAACAGCT
CATGCTTTTCATTATAATTTTTTTTATAGTAATACCTATTATAATTGGAG
GATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCCCCAGACAT
AGCTTTCCCACGAATAAATAATAAGTTTTTTGATTATTACCTCCTTCTT
TAATACTTTTAATTTTCGAGAAGTATTGTAGAAAATGGAGCAGGAACAG
GATGAACAGTTTACCCACCACTGTCATCTAATATTGCTCATAGAGGAA
GCTCTGTTGATTTAGCCATTTTTTCCCTTCACTTAGCTGGTATTTTCAT
CAATTTTAGGGGCTATTAATTTTATCACAACAATTATTAATATACGAT
TAAATAATATATCTTTTGATCAAATACCTTTATTTGTGTGAGCTGTAG
GAATTACTGCTTTTTTTACTTTTACTTTCTCTCCCAGTTCTAGCTG
GAGCTATTACTATACTTTTAACTGATCGTAATTTAAATACATCTTTTTTT
GACCCTGCAGGGGGAGGAGATCCTATTTTATACCAACATTTATTT
```

Distribution. Known from Guatemala to Colombia (Anchicaya, Valle, and the Magdalena Valley), and probably extending south into northern Ecuador.

Remarks. This species occurs at lower altitudes and moderate elevations (1000 m) where it occurs with *D. hemicera*.

***Disphragis hemicera* (Schaus, 1910), stat. rev.**

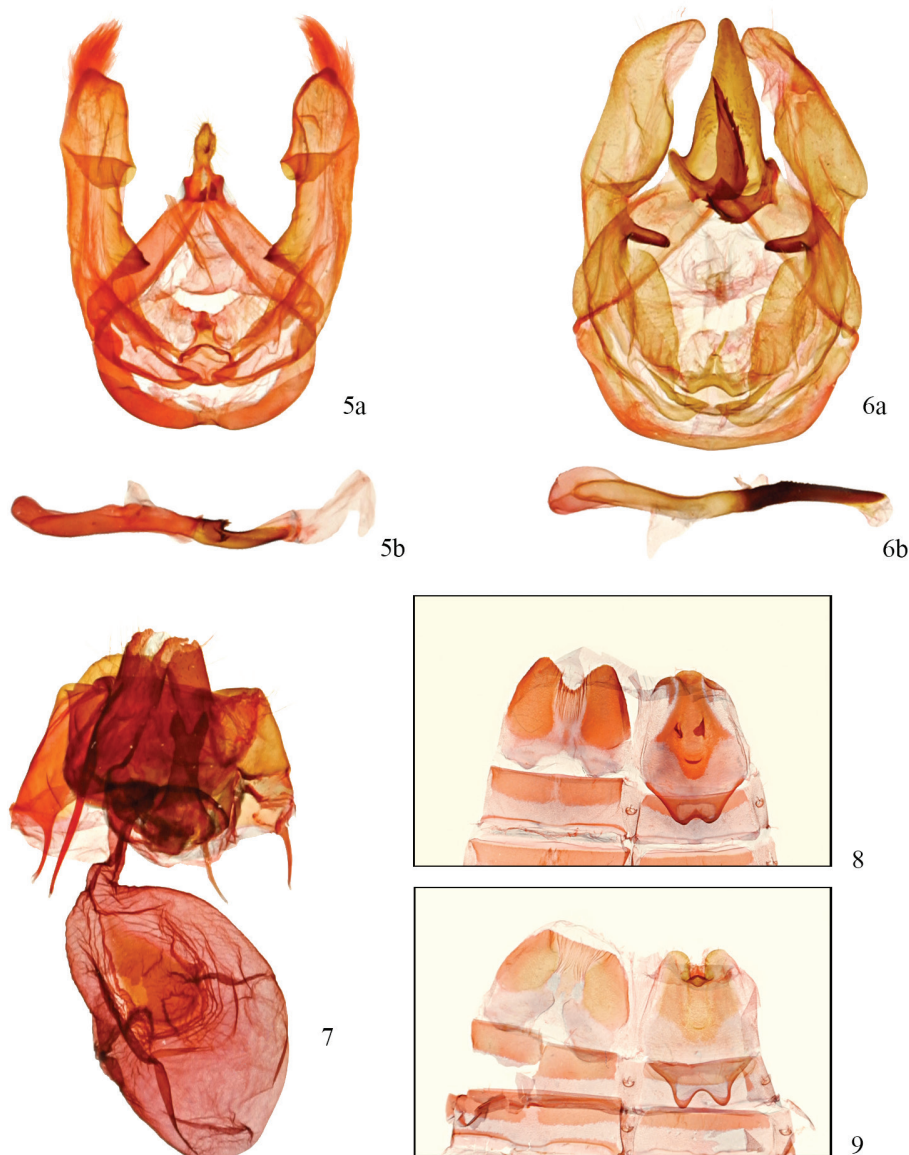
Figs 2, 5, 11, 15, 19, 23, 26–29

Heterocampa hemicera Schaus, 1910, Annals and Magazine of Natural History 6: 582.

Type locality. Costa Rica.

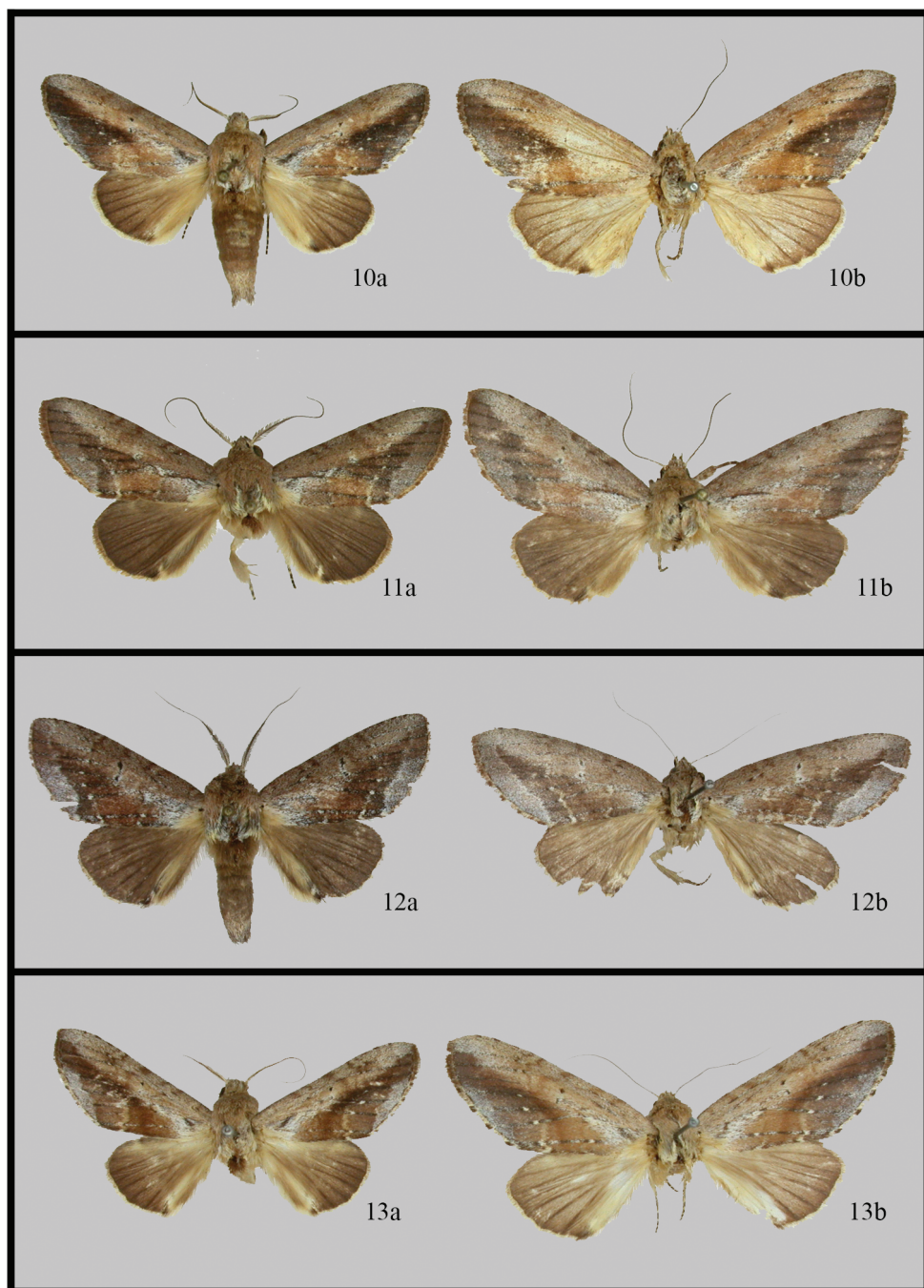
Diagnosis. Maculation will usually separate *D. hemicera* and *D. sobolis* from *D. notabilis* and *D. bifurcata*. Their appearance is mottled, grayish brown with a distinct dark band next to the PM line. Males may be distinguished by the shape of the phallus, which in *D. sobolis* has a distinct dorsal projection. Females can be separated by the shape of the genital plate, which in *D. sobolis* is bifurcate at the distal tip and in *D. hemicera* has a middle phalanx with lateral “wings” from the base. Geographic distribution also separates *D. hemicera* from *D. sobolis*, with *D. hemicera* in Central America and western Colombia, and *D. sobolis* along the western slopes of the Andes.

Description. Male. (Figs 2, 5) *Head*—labial palp upturned, mahogany brown on basal segment, medial segment with cream scaling along distal margin particularly near the terminus, and apical segment mostly cream scaled with scattered brown scales. Denuded medial segment is 3.2× length of apical segment that is shortened relative to *D. bifurcata*. Eye round, large, surrounded tightly with scaling. Front scaling mostly cream with scattered brown scales. Vertex with additional brown scales among cream scaling. Scape with cream and brown scaling, cream scaling extending onto antennal shaft for about 14–18 segments. Antenna bipectinated basally for 33 segments, then with minute basal seta on segments to apex (73 segments). Rami noticeably longer than in *D. bifurcata*, longest rami 0.53 mm. Thorax a blend of brown and cream scales giving a tan appearance. Metathorax with a central white spot with row of darker brown scales anteriorly. Abdomen with appressed brown scaling. Forewing (17.9 mm, n = 10) elongate, rounded apically and with broad light brown subcostal streak from base of wing to apex. Streak encloses chocolate reniform spot and has several slightly darker brown lines crossing obliquely from costa. Basal dash below streak perpendicular to thorax. White streak below dash; warm brown patch distal to white streak bordered by white; AM and PM lines wavy. Distinct brown line bisecting warm brown patch. Chocolate shading from middle of forewing below costal streak and forming a wedge to margin (below costal streak to anal angle). Gray crescent on lower half of margin with distinct brown band inward to PM line. Hind wing uniformly fuscous with brown anal markings forming something of a spot at anal margin. Light streak along anal edge. Underside of forewing fuscous with yellowish subapical crescent along costa. Basal half of hind wing yellowish, no well-differentiated margin. Legs a mixture of brown and white scales appearing somewhat yellowish with white scales forming rings at distal end of



Figures 5–9. *Disphragis notabilis* complex holotype genitalia. **5** *Disphragis hemicera*, male holotype (USNM-49851) **a** valve **b** phallus **6** *Disphragis normula*, male holotype (USNM-49852) **a** valve **b** phallus **7** *Disphragis notabilis*, female holotype (USNM-49853) **8** *Disphragis hemicera* male holotype (USNM-49851) tergites **9** *Disphragis normula* male holotype (USNM-49852) tergites.

tarsal joints. Tibial spines 0-2-4. *Male genitalia* (Figs 15, 19) (12 dissections). Uncus lightly sclerotized and rounded, turning 90 degrees ventrally and forming a rounded, setose pad. Socii small, upturned and pointed slightly, blade-like. Tegumen broad, triangular, similar in size to vinculum. Valve elongated rounded at apex and costal half sclerotized. Anal half



Figures 10–13. *Disphragis notabilis* complex adults. **10** *Disphragis bifurcata* **a** male (Costa Rica) **b** female (Costa Rica) **11** *Disphragis hemicera* **a** male (Costa Rica) **b** female (Costa Rica) **12** *Disphragis sobolis* **a** male (Ecuador) **b** female (Peru) **13** *Disphragis notabilis* **a** male (French Guiana) **b** female (Brazil).

of valve membranous and enclosing deciduous hair-like scent scales. Distal third of valve enlarged dorsally ending abruptly with shelf-like narrowing. Second narrowing of sclerotized subcostal area 1/3 distance from base, a rounded projection less shelf-like than distal projection, but more heavily sclerotized. Juxta shovel shaped with handle toward aedeagus. Vinculum rounded to saccus. Aedeagus long, narrow and with basal 2/3 membranous, subbasal keel present. Distal 1/3 sclerotized with two prominent toothed plates at junction with membranous portion. Vesica tube-like emerging dorsally then turning 90 degrees forward to plane of phallus. Distinct lateral diverticulum to left of midpoint. Cornuti absent. Ctenophore on pelt absent. Eighth tergite broadly rounded, slightly sclerotized and crenulated medially at distal end. Sternite lightly sclerotized with “happy face” consisting of two membranous flaps for “eyes” and a broad anterior one for “mouth.” Anterior edge tapered to blunt, indented terminus. **Female.** (Fig. 5). Female similar to male only larger (Forewing 21.0 mm, n = 5) and with fasciculate antennae. *Female genitalia* (Figs 23, 26–29) (10 dissections). Papillae anales bluntly rounded, slightly setose. Extension of 9th tergite forming dorsal flap in *D. bifurcata* greatly reduced to small crescent in *D. hemicera*. Anterior apophysis short, 25% as long as posterior apophysis. Genital plate small, slightly elongate, consisting of a middle phalanx with lateral “wings” from base. Phalanx usually shorter than in *D. bifurcata*. Tip of phalanx variable, usually blunt but can be indented or bifurcate. Ductus bursae slightly shorter than corpus bursae, narrow and tending to twist, membranous. Corpus bursae egg shaped with large signum on dorsal surface. Signum shield-like, about half as long as corpus bursae. Signum egg shaped with stippled lateral flanges below midpoint. Proximal margin lightly sclerotized and faintly stippled.

Barcodes. Fifty eight barcoded specimens exhibit seven haplotypes that differ from each other by a maximum of 0.30%. They differ from those of *D. bifurcata* by a minimum of 5.61%, from *D. notabilis* by a minimum of 5.65%, and from *D. sobolis* by a minimum of 6.13%. The most common haplotype (11-CRBS-2519) is:

```
AACTTTATATTTTATTTTGGAAATTGAGCAGGAATAGTAGGAACCTTCTT
TAAGTCTTTTAAATTCGTGCTGAATTAGGAACCCCGGGACTT
TAATTGGAGATGATCAAATTTATAATACTATCGTAACAGCTCATGCTTT
TATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTG
GAAATTGATTAGTCCCTTTAATACTAGGAGCACCAGATATAGCTTTC
CCACGAATAAATAATATAAGTTTTTGACTATTACCCCCTTCTT
TAATACTTCTAATTTCAAGAAGTATTGTAGAAAATGGAGCTGGTACAG
GATGAACAGTTTATCCCCCACTGTCATCAAATATTGCTCACGGAGGAA
GCTCTGTTGATTTAGCTATTTTTTCCCTTCATTTAGCGGGTATTTC
CTCAATTTTAGGGGCTATTAATTTTATTACAACAATTATTAATATACGAT
TAAATAATATATCTTTTGATCAAATACCTTTATTTGTATGAGCTGTAG
GAATTACTGCTTTTCTACTTTTACTTTTCACTCCCAGTATTAGCTGGAGC
TATTACTATACTTTTAACCGATCGTAATTTAAATACATCTTTTTTCGAC
CCTGCTGGGGGAGGAGATCCTATTTTATACCAACATTTATTT
```

Distribution. *Disphragis hemicera* occurs throughout Costa Rica at moderate altitudes. It is found south along the western coast of Colombia and may extend to the west coast of Ecuador. The northern limits are unknown but it probably occurs at least into Nicaragua.

Remarks. *Disphragis hemicera* is by far the most common member of the group in Costa Rica and appears to be absent below 500 m. At moderate altitudes both *D. hemicera* and *D. bifurcata* occur together.

***Disphragis notabilis* (Schaus, 1906)**

Figs 4, 7, 13, 17, 21, 25

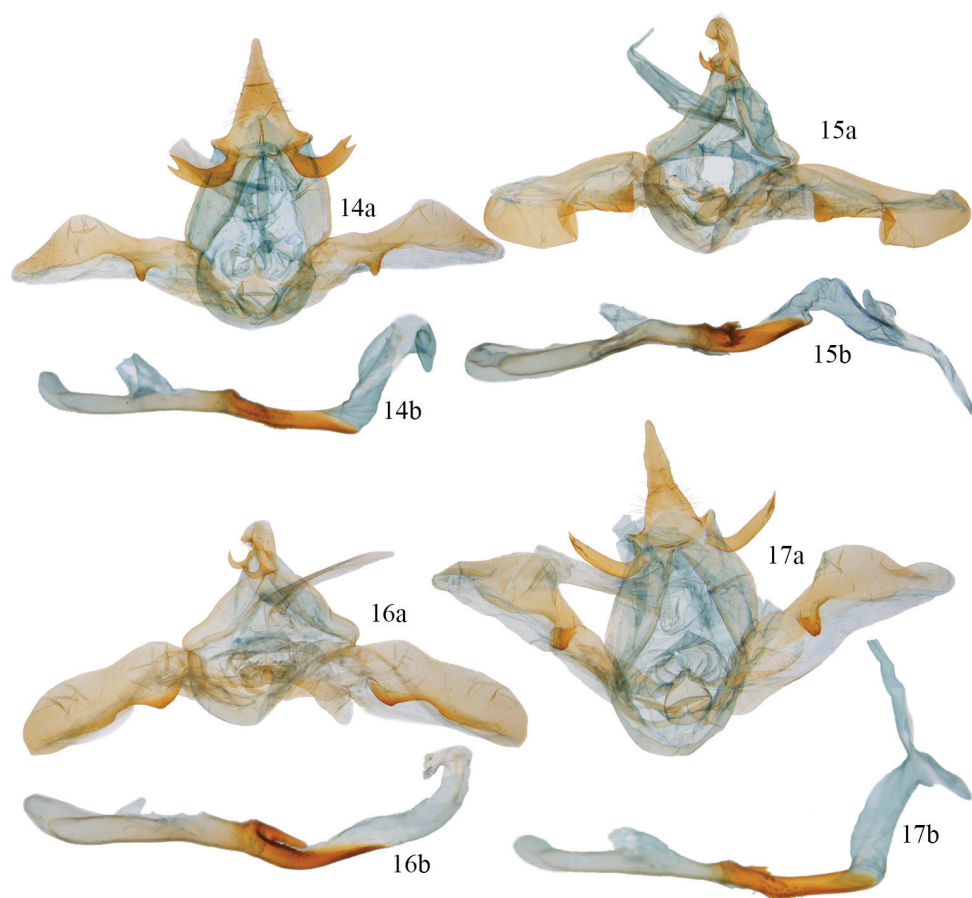
Heterocampa notabilis Schaus, 1906, Proceedings of the United States National Museum 29: 253.

Heterocampa normula Dognin, 1909, Annales de la Société entomologique de Belgique 53: 81. (Fig. 3)

Type locality. *notabilis*: French Guiana; *normula*: Peru

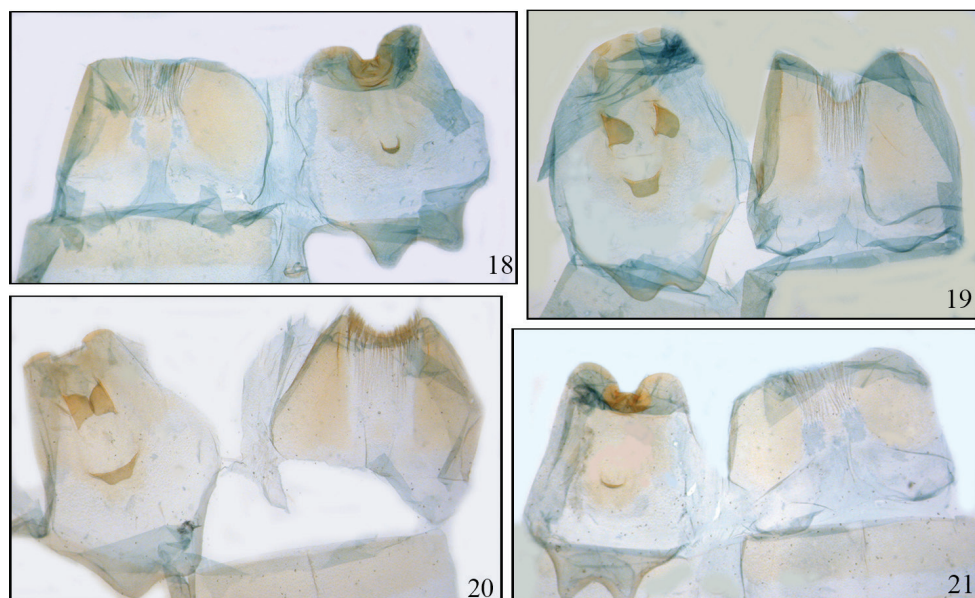
Diagnosis. Maculation characters can usually be used to separate *D. notabilis* and *D. bifurcata* from *D. hemicera* and *D. sobolis*. *D. notabilis* and *D. bifurcata* are warm brown, not mottled or brownish gray like *D. hemicera* and *D. sobolis*. The male antennal pectinations are shorter in *D. notabilis* than in *D. hemicera* and *D. sobolis*. Males of *D. notabilis* are easily distinguished by their moderately wide socii, which taper to a single point with many ventral spines. In males of *D. bifurcata* the socii are much broader and are bifurcate at the upturned apex. Females must be sorted by maculation and geography. *Disphragis notabilis* is Amazonian in distribution whereas *D. bifurcata* occurs from central and western Colombia north into Central America.

Description. Male. (Fig. 13) *Head*—palp upturned, mahogany brown on basal segment, medial segment with cream scaling along distal margin particularly near terminus; apical segment mostly cream with scattered brown scales. Denuded medial segment $4.1\times$ length of apical segment. Apical segment reduced in size relative to other species in complex. Eye round, large, surrounded tightly with scaling. Front scaling mostly cream with scattered brown scales. Vertex with additional brown scales among white scaling. Scape with cream and brown scaling, white scaling extending onto antennal shaft for about 10–14 segments. Antenna bipectinate basally for 29 segments then with minute basal setae on segments to apex (71 segments). Longest rami 0.34 mm, shortest of all species. Thorax a blend of brown and cream scales giving a tan appearance. Metathorax bearing a central white spot with row of darker brown scales anteriorly. Abdomen with appressed brown scaling. Forewing (17.0 mm, $n = 10$) elongate, rounded apically and with broad tan subcostal streak from base of wing to apex. Streak encloses chocolate reniform spot and has several slightly darker brown lines crossing obliquely from costa. Basal dash below streak perpendicular to thorax, abbreviated relative to that of *D. bifurcata*. White streak



Figures 14–16. *Disphragis notabilis* complex male valves and phalli. **14** *Disphragis bifurcata* (JBS-3035) **a** valve **b** phallus **15** *Disphragis hemicera* (JBS-3037) **a** valve **b** phallus **16** *Disphragis sobolis* (BMNH-NOTO1964) **a** valve **b** phallus **17** *Disphragis notabilis* (BMNH-NOTO1968) **a** valve **b** phallus.

below dash; warm brown patch distal to white streak bordered by white; AM and PM lines wavy. Chocolate shading from middle of wing below costal streak and forming a wedge to margin (below costal streak to above mid point of margin). Weak gray crescent on lower half of margin. Warm brown from patch expanded almost to margin and reducing size of chocolate wedge seen in *D. bifurcata*. Hind wing fuscous with darker margin, weak darker brown anal markings almost forming a spot. Underside of forewing fuscous, anal margin and cell yellowish. Basal 3/4 of hind wing yellowish, margin brown and moderately differentiated. Legs a mixture of brown and white scales appearing almost yellowish with white scales forming rings at distal end of tarsal joints. Tibial spines 0-2-4. *Male genitalia* (Figs 17, 21) (13 dissections). Uncus an extended triangle, rounded apex with setae arranged almost in marginal rows. Tegumen broad, longer than vinculum. Socii extending from base of uncus as two upcurved arms, scythe-like with small, spine-like



Figures 18–21. *Disphragis notabilis* complex male tergites. **18** *Disphragis bifurcata* (JBS-3035) **19** *Disphragis hemicera* (JBS-3037) **20** *Disphragis sobolis* (BMNH-NOTO1964) **21** *Disphragis notabilis* (BMNH-NOTO1968).

projections on ventral surface. Degree of spination variable from several to many extending down to angle of socius. Gnathos absent, anal tube unsclerotized. Valve elongated with costal half sclerotized, anal half membranous and enveloping deciduous scent hairs. Valve apex rounded, sclerotized costal half of valva with broad anal projection distally and sharper shelf-like projection basally. Vinculum broad, short and rounded to saccus. Aedeagus long, narrow with basal phallus, proximal 60% unsclerotized with ductus entering medially. Distal 40% of aedeagus sclerotized, enlarged basally at junction with membranous half, and with raised mound of spines ventrally about 1/3 distal from junction. Vesica emerges dorsally from aedeagus, an unsclerotized tube with a long dorsal diverticulum. Cornuti absent. Eighth tergite broadly rounded, slightly sclerotized and crenulated medially at distal end. Eighth sternite lightly sclerotized, broadly rounded with well-defined, broad notch medially, usually broader than in *D. bifurcata*. Small sac-like flap in middle of sclerite usually in form of narrow crescent, anterior end of sclerite with two broad, rounded projections with medial V-shaped notch. Ctenophores absent on pelt. **Female.** (Figs 4, 13). Female similar to male only larger (Forewing 20.9 mm, $n = 6$) and with fasciculate antennae. *Female genitalia* (Fig. 25) (5 dissections). Papillae anales bluntly rounded, slightly setose. Extension of 9th tergite forming dorsal flap. Anterior apophysis short, 25% as long as posterior apophysis. Genital plate small, elongate, consisting of a bifurcated middle phalanx with lateral “wings” from base. Phalanx somewhat longer than in *D. bifurcata*. Ductus bursae slightly shorter than corpus bursae, twice as wide as in *D. bifurcata* and tending to twist, unsclerotized.

Corpus bursae egg-shaped with large signum on dorsal side. Signum shield-like, about half as long as corpus bursae. Signum egg shaped with stipulated lateral flanges below midpoint. Proximal margin lightly sclerotized and faintly stippled.

Barcodes. Two barcoded specimens exhibit 2 haplotypes that differ from each other by 0.30%. They differ from those of *D. hemicera* by a minimum of 5.65%, from *D. bifurcata* by a minimum of 1.26%, and from *D. sobolis* by a minimum of 4.78%. One haplotype (11-MISC-302) is:

```
AACTTTATATTTTCATTTTTTGGGAATTTGAGCAGGAATAGTAGGAAC
CTCTTTAAGTCTTCTAATTCGTGCTGAATTAGGAACCCCGG
GACTTTAATTGGAGATGACCAAATTTATAATACTATCGTAACAGCT
CATGCTTTCATTATAATTTTTTTTATAGTAATACCTATTATAATTGGAG
GATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCCCCAGACAT
AGCTTTCCCACGAATAAATAATAAGTTTTTGATTATTACCTCCTTCTT
TAATACTTTTAATTTCAAGAAGTATTGTAGAAAATGGAGCAGGAACAG
GATGAACAGTTTACCCACCACCTGTCATCTAATATTGCCCATAGAGGAA
GCTCTGTTGATTTAGCCATTTTTTCCCTTCACTTAGCCGGTATTTTCAT
CAATTTTAGGGGCTATTAATTTTATCACAACAATTATTAATATACGAT
TAAATAATATATCTTTTGATCAAATACCTTTATTTGTATGAGCTGTAG
GAATTACTGCTTTTTTACTTTTACTTTTCTCTTCCAGTTCTAGCTGGAGC
TATTACTATACTTTTAACTGATCGTAATTTAAATACATCTTTTTTTTGACC
CTGCAGGGGGAGGAGATCCTATTTTATACCAACATTTATTT
```

Distribution. This species occurs throughout the Amazon basin from western Venezuela eastward and southward to at least Bolivia.

Remarks. *Disphragis notabilis* is by far the most common member of the group in South America, however, earlier references to this species should be confirmed in light of the additional species described here.

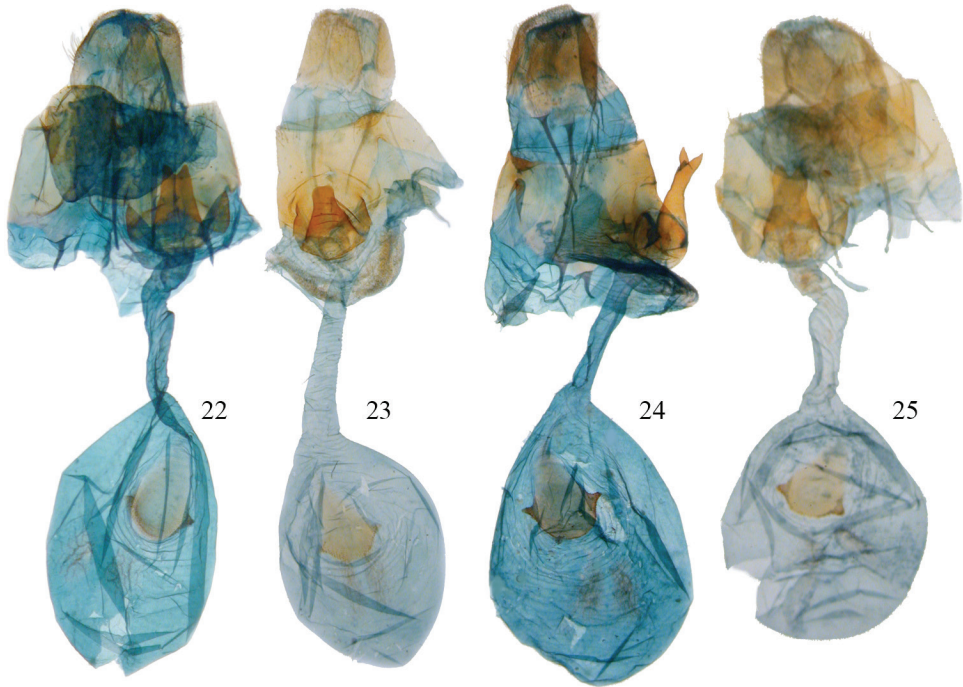
Disphragis sobolis Miller, 2011

Figs 12, 16, 20, 24

Disphragis sobolis Miller, 2011. In Miller and Thiaucourt 2011, Annals of the Entomological Society of America 104: 1058.

Type locality. Ecuador.

Description. Male. (Fig. 12) *Head*—labial palpus upturned, mahogany brown on basal segment, medial segment with cream scaling along distal margin, particularly near the terminus, and apical segment mostly cream scaled with scattered brown scales. Denuded medial segment 2.6× length of apical segment. Eye round, large, surrounded tightly with scaling. Front scaling mostly cream with scattered brown scales. Vertex with additional brown scales among cream scaling. Scape with cream and brown scaling, white



Figures 22–25. *Disphragis notabilis* complex female genitalia. **22** *Disphragis bifurcata* (BMNH-NOTO1984) **23** *Disphragis hemicera* (JBS-3049) **24** *Disphragis sobolis* (BMNH-NOTO1988) **25** *Disphragis notabilis* (BMNH-NOTO1972).

scaling extending onto antennal shaft for about 14–18 segments. Antenna bipectinated basally for 33 segments then with minute basal seta on segments to tip (68 segments). Rami noticeably longer than in *D. hemicera*, longest 0.59 mm. Thorax a blend of brown and cream scales giving a tan appearance. Metathorax bearing a central white spot with row of darker brown scales anteriorly. Abdomen with appressed brown scaling. Forewing (19.3 mm, n = 5) elongate, rounded apically and with broad light brown subcostal streak from base of wing to apex. Streak encloses chocolate reniform spot and has several slightly darker brown lines crossing obliquely from costa. Brown scaling throughout as well as several black streaks. Basal dash below streak perpendicular to thorax and greatly reduced in length. White streak below dash; warm brown patch distal to white streak bordered by white; AM and PM lines wavy. Distinct brown line bisecting warm brown patch. Chocolate shading from middle of forewing below costal streak and forming a wedge to margin (below costal streak to anal angle) more extensive than in *D. hemicera*. Prominent gray crescent on lower half of margin with distinct brown band inward to PM line. Hind wing uniformly fuscous with brown anal markings almost a spot. Light streak along anal edge. Underside of forewing fuscous with yellowish subapical crescent along costa. Basal half of hind wing yellowish, no well-differentiated margin. Legs a mixture of brown and white scales, appearing almost yellowish with white scales forming rings at distal end of tarsal joints. Tibial spines 0-2-4. *Male genitalia* (Figs 16, 20)

(5 dissections). Uncus lightly sclerotized and rounded, turning 90 degrees ventrally and forming a much smaller setose pad than in *D. hemicera*. Socii small but 2× larger than in *D. hemicera*, upturned and pointed slightly, blade-like. Tegumen broad, triangular similar in size to vinculum. Valve elongated, rounded at tip and costal half sclerotized. Anal half of valve membranous and enclosing deciduous hair-like scent scales. Distal third of valve considerably enlarged dorsally then gradually narrowing. Second narrowing of sclerotized subcostal area 1/3 distance from base, a rounded projection, more heavily sclerotized. Juxta shovel shaped with handle toward aedeagus. Vinculum rounded to saccus. Aedeagus long, narrow and with basal 2/3 membranous, aedeagus present. Distal 1/3 sclerotized with prominent basal process. Vesica tube-like emerging dorsally then turning 90° to plane of aedeagus. Distinct lateral diverticulum to left of midpoint. Cornuti absent. Crenophore absent on pelt. Eighth tergite broadly rounded, slightly sclerotized and crenulated medially at distal end. Eighth sternite lightly sclerotized with “happy face” consisting of two membranous flaps for “eyes” and a broad anterior one for “mouth.” Anterior edge tapers to blunt, indented terminus. **Female.** (Fig. 12) Female similar to male only larger and with fasciculate antennae. *Female genitalia* (Fig. 24) (3 dissections). Papillae anales bluntly rounded, slightly setose. Extension of 9th tergite forming dorsal flap in *D. bifurcata* and *D. notabilis* greatly reduced to small crescent in *D. sobolis*. Anterior apophysis short, 25% as long as posterior apophysis. Genital plate small, elongated, consisting of a middle phalanx with lateral “wings” from base. Phalanx longer than in other related species. Tip of phalanx forming a Y-shape. Ductus bursae slightly shorter than corpus bursae, narrow and tending to twist, unsclerotized. Corpus bursae egg shaped with large signum on dorsal surface. Signum shield-like, about half as long as corpus bursae. Signum egg shaped with stipulated lateral flanges below midpoint. Proximal margin lightly sclerotized and faintly stippled.

Barcodes. One specimen has been barcoded and differs from that of *D. hemicera* by a minimum of 6.13%, from *D. bifurcata* by a minimum of 5.78%, and from *D. notabilis* by a minimum of 4.78%. The haplotype (11-MISC-495) is:

```
AACTTTATATTTTATTTTGGGAATTTGAGCAGGAATAGTAGGAAC
CTCTTTAAGTCTCCTAATTCGTGCTGAATTAGGAACCCCGGGACTT
TAATTGGAGATGATCAAATTTATAATACTATTGTAACAGCTCATGCTTT
TATTATAATTTTTTTTATAGTAATACCCATTATAATTGGAGGATTTG
GTAATTGATTAGTTCCCTCTAATATTAGGAGCTCCAGATATAGCTTTCC
CACGAATAAATAATATAAGTTTTTGATTATTACCCCCCTCTCTAATACTTT
TAATTTCAAGAAGTATTGTAGAAAATGGAGCAGGAACAGGATGAA
CAGTTTACCCCCCACTGTCATCAAACATTGCTCATAGAGGAAGATCT
GTTGATTTAGCTATTTTTTCCCTTCACTTAGCAGGTATTTTCAT
CAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAT
TAAATAACATATCTTTTGATCAAATACCTTTATTTGTTTGAGCTGTAG
GAATTACTGCTTTTTTACTTTTACTCTCTCTTCCAGTATTAGCAGGAGC
TATTACTATATTATTAACCGATCGTAATTAAATACATCTTTTTTTGACCC
CGCTGGGGGAGGAGATCCTATTTTATATCAACATTTATTT
```

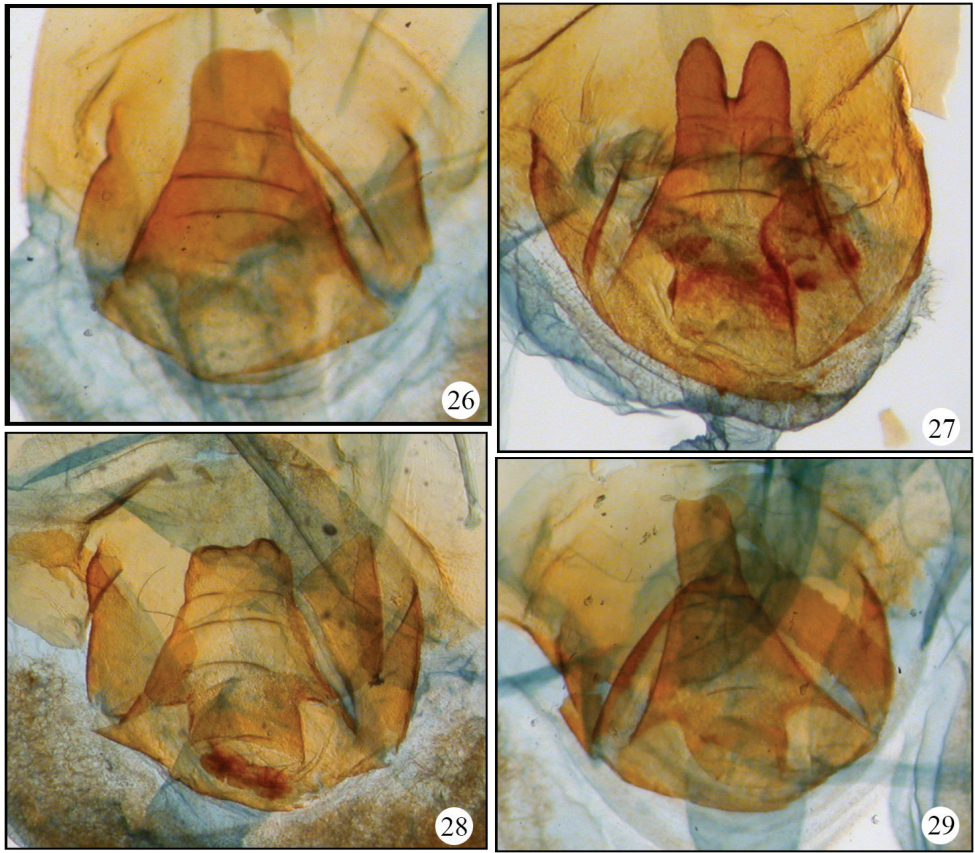



Figure 26–29. Variable genital plates of *Disphragis hemicera* from Costa Rica. **26** Costa Rica (JBS-3049) **27** Costa Rica (JBS-3041) **28** Costa Rica (JBS-3050) **29** Costa Rica (JBS-3046).

Distribution. This species appears to be limited to the eastern slopes of the Andes from Bolivia to Villavicencio, Colombia.

Remarks. *Disphragis sobolis* was recently described from Ecuador; the species appears to have a much greater geographical range and occurs to almost 3000 m. The lower altitude limits of its range are undefined, as is the southern boundary.

Discussion

The *Disphragis notabilis* complex is typical of many neotropical species. When studied in detail, they frequently are found to consist of a number of very similar species that do have structural differences, can be separated by barcoding, and occupy different altitudes or geographic ranges. The correct generic placement of this complex is not in *Disphragis* (as placed by Schintlmeister 2013), but its phylogenetic relationships remain unresolved. In general, we find most neotropical notodontid genera to be het-

erogeneous. The structures of the unci and socii in the *notabilis* complex are divergent and illustrate the difficulty in proper generic identification. Although all 4 species are very similar in maculation, they fall into two distinct groupings based on the shape of the uncus and socii. In the *notabilis* group, the uncus is large, triangular and elongate. In the *hemicera* group the uncus is short, robust and bent ventrally. Normally, differences of this magnitude would warrant separate genera but the slight differences in maculation and female genitalia are quite normal for closely related species. If such dramatic transitions are common among the notodontids, correctly associating species into monophyletic genera will continue to be difficult.

A second difficulty encountered in this study was the hyper-variation of the female genital plate in *D. hemicera* (Figs 26–29). This intraspecific variation (in individuals with identical barcodes) has also been seen in *Didugua* Druce (JBS, unpubl. data) and makes the delineation of species and their defining characters with female specimens extremely difficult. Fortunately, such extreme variation has not been observed in males.

The exact distribution of the four species of the *notabilis* complex found in Colombia (and probably Ecuador) remains to be elucidated but should highlight the individual habitat requirements of each species. Neither larvae nor foodplants are known. The geographical area where *D. bifurcata* and *D. notabilis* come into contact should be particularly interesting because the two species differ by 1.4% in their barcodes, a magnitude lower than between most congeneric species. However, there are a number of characters that separate the two species and characters do not seem to intergrade in individuals from central Colombia and western Venezuela.

Acknowledgements

We would like to thank Jocelyn Gill, Don Lafontaine, and Chris Schmidt at the Canadian National Collection. Jocelyn for help with the illustrations, Don and Chris for suggestions regarding the manuscript. Paul Hebert of the University of Guelph, Guelph, Canada allowed the use of unpublished barcode data. Dan Janzen and Winnie Hallwachs shared unpublished barcode and life history data. Paul Thiaucourt shared his genitalic preparations and extensive knowledge of notodontids. Bernardo Espinosa at INBio enthusiastically helped collect many of the specimens used in this study.

References

- Gaede M (1934) Lepidopterorum Catalogus, Vol. 59: Notodontidae. W. Junk, Berlin, 351 pp.
- Lafontaine JD (2004) Noctuoidea, Noctuidae (part), Noctuinae (part – Agrotini). In: Hodges RW (Ed) The Moths of America North of Mexico fasc. 27.1. The Wedge Entomological Research Foundation, Washington, 385 pp.
- Miller JM, Thiaucourt P (2011) Diversity of prominent moths (Lepidoptera: Noctuoidea: Notodontidae) in the cloud forests of northeastern Ecuador, with descriptions of 27 new

- species. *Annals of the Entomological Society of America* 104: 1033–1077. doi: 10.1603/AN10141
- Pogue MG, Sullivan JB (2003) Re-evaluation of the *Elaphria festivoides* (Guenée) species complex (Lepidoptera: Noctuidae). *Proceeding of the Entomological Society of Washington* 105: 331–347.
- Ratnasingham S, Hebert PD (2007) Bold: The barcode of life data system. *Molecular Ecology Notes* 7: 355–364. doi: 10.1111/j.1471-8286.2007.01678.x
- Schaus W (1928) New moths of the family Ceruridae (Notodontidae) in the United States National Museum. *Proceedings of the United States National Museum* 73: 1–90. doi: 10.5479/si.00963801.2740
- Schintlmeister A (2013) *World Catalogue of Insects*, Vol. 11, Notodontidae & Oenosandridae (Lepidoptera), 608 pp.
- Sullivan JB, Adams JK (2009) A new species of *Morrisonia* (Noctuidae) from southeastern North America. *Journal of the Lepidopterists' Society* 63: 21–26.

Four new species of *Symmerista* Hübner, 1816 (Notodontidae, Nystaleinae) from Costa Rica

Isidro A. Chacón¹, Daniel H. Janzen², Winnie Hallwachs²

1 Instituto Nacional de Biodiversidad (INBio), Apdo. 22-3100, Santo Domingo de, Heredia, Costa Rica

2 Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA

Corresponding author: Isidro A. Chacón (ichacon@inbio.ac.cr)

Academic editor: D. Lafontaine | Received 30 September 2013 | Accepted 24 January 2014 | Published 27 June 2014

<http://zoobank.org/748B0457-9F84-43E5-A165-C2CE1A36CE58>

Citation: Chacón IA, Janzen DH, Hallwachs W (2014) Four new species of *Symmerista* Hübner, 1816 (Notodontidae, Nystaleinae) from Costa Rica. In: Schmidt BC, Lafontaine JD (Eds) Contributions to the systematics of New World macro-moths V. ZooKeys 421: 39–63. doi: 10.3897/zookeys.421.6342

Abstract

The genus *Symmerista* Hübner (Notodontidae, Nystaleinae) is reviewed for Costa Rica, based on 49 wild-caught specimens. Four species are newly described: *Symmerista luisdiegogomezi* Chacón, *Symmerista inbioi* Chacón, *Symmerista minaei* Chacón and *Symmerista aura* Chacón. All are from the cloud forests of the Talamanca mountain range, southern Costa Rica. Photographs of the adults, male and female genitalia, and barcodes are also provided. The species *Symmerista tlotzin* Schaus (1892) is removed from *Symmerista* and assigned to the genus *Elymiotis* Walker as a new combination.

Keywords

Symmerista, *Elymiotis*, *Elasmia*, Nystaleinae, moths, DNA barcodes, Neotropical, cloud forest, INBio, MINAE, Costa Rica

Introduction

The family Notodontidae includes about 3500 described species worldwide (Weller 1992). Approximately 896 species in 127 genera have been recorded in Costa Rica

(Chacón et al. 2013). The subfamily Nystaleinae contains approximately 300 species and is restricted almost entirely to the Neotropics (Miller 1991), with a few species extending as far north as Canada (Forbes 1948). In Costa Rica, 191 Nystaleinae species are known to occur.

Hübner (1821) established the genus *Symmerista*, which until now has contained 12 described species (Franclemont 1946; Thiaucourt 2007; Thiaucourt and Monzón 2013). Species of *Symmerista* occur from Panama as far north as southeastern Canada. We have discovered four species of this genus in Costa Rica, found in the Talamanca Cordillera (Talamanca mountain range), from the cloud forests at altitudes between 1000 and 2600 meters.

Our studies of *Symmerista tlotzin* (Schaus, 1892) male genitalia morphology and barcodes (Janzen et al. 2009) suggest that it was improperly placed in that genus; here we assign *Symmerista tlotzin* to the genus *Elymiotis* Walker, 1857, as a new combination.

Material and methods

Forty-nine specimens of *Symmerista* from the collection of the Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica were examined, sexed and identified. Of those, 12 were DNA barcoded and dissected. All holotypes and paratypes are deposited in the collections at INBio. Fifty-six specimens of reared and wild-caught *Elymiotis tlotzin*, previously known as *Symmerista tlotzin*, were also examined.

Repository abbreviations

INBio Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica
USNM National Museum of Natural History, Smithsonian Institution, Washington DC, USA

Key to morphological terminology

| | |
|------------|-----------------|
| AD | Adterminal line |
| CB | Corpus bursae |
| DB | Ductus bursae |
| FW | Forewing |
| HW | Hindwing |
| M | Medial line |
| PM | Postmedial line |
| ST8 | Sternum 8 |
| T8 | Tergum 8 |
| WL | Wing length |

Systematics

Symmerista Hübner

Symmerista Hübner, 1821. Verz. bekannt. Schmett. : 248.

Type-species. *Noctua albicosta* Hübner, 1809, Samml. eur. Schmett. 4: pl. 93, fig. 440. By subsequent designation by Kirby, 1892, Syn. Cat. Lepid. Het. Het. 1: 572.

Type specimens. Type(s), [North America]: Mistakenly included by Hübner as a European species; *Noctua albicosta* occurs in Canada and the US.

Notes. Nye (1975) stated: *Symmerista* was originally proposed in the Noctuidae.

Watson et al. (1980) stated: *N. albicosta* is a form of *Phalaena albifrons* Smith, 1797, in Smith & Abbot, Nat. Hist. rarer lepid. Insects Georgia 2: 159, pl. 80.

Diagnosis. Adults – Medium-sized notodontid moth, FW = 16–22 mm, females larger than males; male antenna pectinate nearly to apex, terminal 10–12 annulations simple or antenna bipectinate, six terminal flagellomeres without rami; antennae of female simple; labial palpus porrect; haustellum reduced to two small lobes, completely hidden by labial palpi; ocelli absent; eye smooth, round; thorax generally dark brown with beige tegula; all scales of thorax long and forked; scales of patagium and prothorax beige and cream colored. FW with the costa straight, apex marked, the outer margin evenly rounded; accessory cell present, narrow; R_{2+5} , stalked, R_5 arising beyond R_2 , M_1 from apex of accessory cell or nearly so. **Male genitalia** – ST8 with a wide, deep emargination; valva membranous, finely pubescent, costulae absent; tegumen narrowed dorsally; uncus concave, the socii subquadrate and lobed or long, wide, pubescent at bases, narrow and flattened at apices; vinculum slightly sclerotized; manica membranous, fused to juxta; ventral process of phallus long and forked, its tip well beyond the tip of the medial, dorsal process; vesica bulbous with a scobinate patch.

Female genitalia – Papillae anales membranous, covered with short, scattered setae; posterior apophyses long and slender; DB sclerotized for approximately two-thirds of its length; CB rounded; anterior vaginal plate asymmetrical, slightly swollen and inflated in middle.

The genus *Symmerista* is characterized by: haustellum reduced to two small lobes, completely hidden by labial palpi; valva membranous; costulae absent; uncus concave; manica membranous, fused to juxta and ductus bursae sclerotized for approximately two-thirds of its length. *Symmerista* differs of the genera *Elasmia* and *Elymiotis* by the following characteristics: *Elasmia* has a well-developed haustellum, sacculus pleated and saccular scent organ present, manica sclerotized, deciduous cornuti, costulae present, costal margin sclerotized, ST8 with long and curvy lateral sclerotized projections like forceps, midplate with tiny pleats and membranous; uncus elongate, setose, with two dorsal protuberances and two tiny spines at the apex. *Elymiotis* has the haustellum well developed, sacculus pleated, deciduous cornuti, costal margin sclerotized, St8 posterior margin irregularly sclerotized and convex with tiny lateral projections, uncus thin and long with apex acute and setose. All of these characteristics are absent in *Symmerista*.

***Symmerista luisdiegogomezi* Chacón, sp. n.**

<http://zoobank.org/81A8E740-7368-45A7-9BBE-6113BBC43D3E>

Figs 1–9

Material examined. 16 specimens (14 males, 2 females)

Type material. **Holotype** male: INB0003536238 (dissected, COI barcoded), Costa Rica, Prov. Cartago, P.N. Tapanti, Macizo de La Muerte, Est. La Esperanza 9.69129-83.87683, 2600 m, September 2002, R. Delgado (INBio).

Paratypes: 13 males, 2 females. 2 males: INB0003756237, INB0003756364 Costa Rica, Prov. Limon, Parque Internacional La Amistad, Valle del Silencio, Alrededor del Refugio y el Sendero Circular, 9.110281-82.961934, 2450 m, 22–27 September 2003, D. Rubi, R. Gonzalez, R. Delgado (INBio). 4 males: INB0003316532, INB0003316533, INB0003316534, INB0003316535 Costa Rica, Prov. Cartago, El Guarco, Macizo de la Muerte, Sector La Esperanza, 9.686771-83.87775, 2600 m, June 2001, R. Delgado (INBio). Male: INB0003352709 Costa Rica, Prov. Cartago, Reserva Forestal Rio Macho. El Guarco, Macizo de la Muerte, Sector La Esperanza, 9.686771-83.87775, 2600 m, August 2001, R. Delgado (INBio). 2 males: INB0003387641 (dissected), INB0003387642, Costa Rica, Prov. Cartago, Reserva Forestal Rio Macho, El Guarco, Macizo de la Muerte, 9.686771-83.87775, 2600 m, October 2001, R. Delgado (INBio). 2 males: INB0003536234 (COI barcoded), INB0003536235 (COI Barcoded), INB0003536237 (COI barcoded), Costa Rica, Prov. Cartago, Parque Nacional Tapanti, Macizo de La Muerte, Est. La Esperanza, 9.69129-83.876832, 2600 m, September 2002, R. Delgado (INBio). 2 males: INB0003545221 (dissected, COI barcoded), INB0003545222 (COI barcoded) Costa Rica, Prov. Cartago, Parque Nacional Tapanti, Macizo de La Muerte, Est. La Esperanza, 9.69129-83.876832, 2600 m, October 2002, R. Delgado (INBio). Female: INB0003339209 (dissected, COI barcoded) Costa Rica, Prov. Cartago, El Guarco, Macizo de la Muerte, Est. La Esperanza. 9.686771-83.87775, 2600 m. July 2001. R. Delgado (INBio). Female: INB0003756274 Costa Rica, Prov. Limon, Parque Internacional La Amistad, Valle del Silencio, Alrededor Refugio y Sendero Circular, 9.110281-82.961934, 2450 m, 22–27 September 2003, D. Rubi, R. Gonzalez, R. Delgado (INBio).

Etymology. This species is named in honor of the late Professor Luis Diego Gómez Pignataro of San Jose, Costa Rica, for his outstanding contribution to our knowledge of Costa Rican biodiversity, his support of the Museo Nacional de Costa Rica, and for inspiring me to become a naturalist and taxonomist.

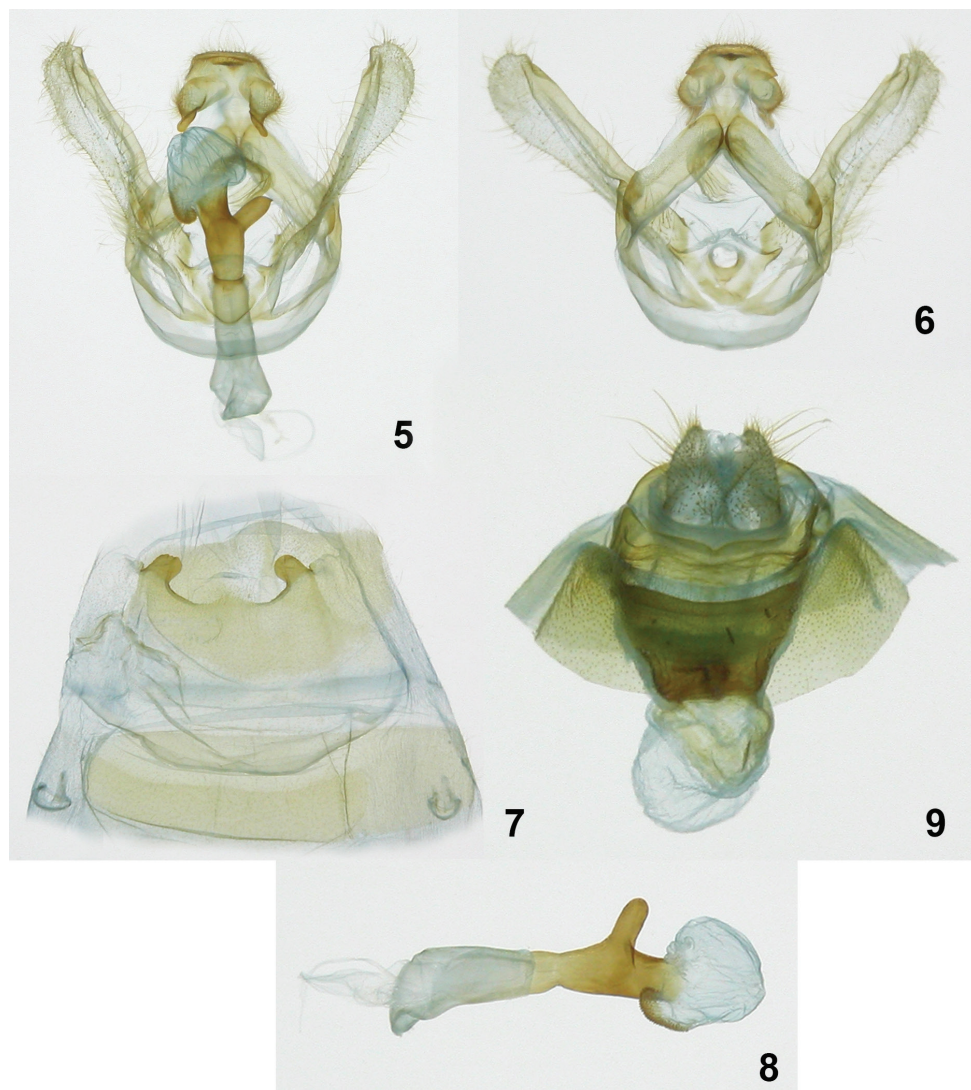
Diagnosis. Dorsal FW ground color dark brown with costal margin black; an irregular, long thin cream-colored mark from the reniform spot to the apex; fringe dark brown with beige scales where veins touch termen; dorsal HW dark brown. **Male genitalia:** St8 posterior margin concave with a pair of short postero-lateral projections, projections robust and heavily sclerotized with blunt apices; valva membranous, finely pubescent, sacculus smooth, its margin uniform, costa straight with a distal protuberance near apex; valva with two triangular spine-like processes, one at base, the other at juxta near anellus; uncus slightly concave, somewhat helmet shaped, dorsal surface



Figures 1–4. *Symmerista luisdiegogomezi* **1, 2** Holotype male dorsal and ventral INB0003536238 **3, 4** Paratype female dorsal and ventral INB0003339209.

rough, pubescent, ventral surface smooth with sparse pubescence; socii long, wide, pubescent at bases, narrow and flattened at apices, shape as in the figure; length of the phallus 3.1 mm, proximal part of phallus tube wide at the base, narrow in the middle, distal part of phallus tube robust, sclerotized, with a tubular lateral projection and rounded apex; proximal part of the vesica with a ventral scobinate patch, distal part of the vesica bulbous. **Female genitalia:** posterior apophyses longer and more slender than anterior apophyses; CB rounded and membranous, lacking a signum; DB wide and sclerotized; posterior margin of postvaginal plate sclerotized and emarginate.

Description. Male (Figs 1, 2, 5–8). **Head** – Antenna bipectinate, dark brown, six terminal flagellomeres without rami, antennal shaft dark brown dorsally and beige ventrally; scape bearing a long tuft of beige scales; haustellum reduced to two small lobes; eye smooth, round, black; frons mostly dark brown and black with brown-yellow scales; labial palpus porrect, dark brown ventrally, light brown dorsally; vertex brown yellow; patagium light brown. **Thorax and abdomen** – Tegula dark brown at base, a mix of cream and dark brown scales distally; mesoscutellum dark brown; thoracic pleuron from creamy white to dark brown; dorsal area of metathorax with black hair-like scales; legs mostly dark brown with cream-colored scales between segments; abdominal dorsum dirty beige, venter beige. **Wings** – Dorsal FW ground color dark brown, with reniform spot black; basal band light brown; M sinuous, light brown; postmedial band light brown; an irregular, thin cream-colored bar from reniform spot to apex; AD black; fringe dark brown with beige scales where veins touch termen;



Figures 5–9. *Symmerista luisdiegogomezi* **5, 6** Holotype male genitalia INB0003536238 **7** Male St8 **8** Phallus **9** Paratype female genitalia INB0003339209.

a light beige area between subterminal line and postmedial band of M_3 extending to tornus; dorsal HW dark brown; fringe dark brown with beige scales where veins touch termen (Figs 1, 2) (WL 17.20–19.21 mm). **Genitalia** (Figs 5–8) – T8 wider than long, with two windows, anterior margin slightly concave, posterior margin sclerotized; St8 wide at base, narrowing posteriorly, posterior margin concave with tiny sclerotized teeth on edge, with a pair of short lateral projections, these sclerotized with blunt apices (Fig. 7); valva membranous, finely pubescent, costulae absent, sacculus smooth, its margin uniform, costa straight with a distal protuberance near apex;

valva with two triangular spine-like processes, one at base, other at juxta near anellus; tegumen narrowed dorsally; uncus slightly concave, somewhat helmet shaped, dorsal surface rough, pubescent, ventral surface smooth with sparse pubescence; socii long, wide, pubescent at bases, narrow and flattened at apices, shape as in the figure; juxta ovoid; vinculum lightly sclerotized (Fig. 5); length of phallus 3.1 mm, proximal part of phallus tube wide at base, narrow in middle, distal part of phallus tube robust, sclerotized, with a tubular lateral projection and rounded apex; proximal part of vesica with a ventral scobinate patch, distal part of the vesica bulbous (Fig. 8).

Female (Figs 3, 4, 9) Similar to the male: **Head** – Antenna filiform, antennal shaft dark brown with cream scales, scape bearing a long tuft of cream scales; frons and vertex dark brown; haustellum vestigial; labial palpus dark brown. **Thorax and abdomen** – Mostly dark brown, tegula beige; dorsal area of metathorax with black hair-like scales; abdominal dorsum light brown, venter beige. **Wings** – Dorsal FW ground color dark brown; antemedial band beige, lined on both sides by sinuous dark brown lines; irregular white thin bar from apex to reniform spot; reniform spot black; postmedial band beige, subterminal line black; a light beige area between subterminal line and postmedial band of M_3 extending to tornus; fringe dark brown with beige scales located where veins touch termen. Dorsal HW dirty beige; postmedial line light brown; discal spot black; fringe dark brown with beige scales located where veins touch termen (Figs 3, 4) (WL 20.22–21.51 mm). **Genitalia** (Fig. 9) – Papillae anales slightly ovoid, setose; posterior apophyses longer and more slender than anterior apophyses; DB wide and sclerotized; CB rounded and membranous, lacking a signum; posterior margin of postvaginal plate sclerotized and emarginate.

Distribution and habitat. *Symmerista luisdiegogomezi* has been collected only between 2450 and 2600 m in the highland cloud forests dominated by *Quercus* trees in the foothills west of the Cordillera de Talamanca (Talamanca Mountain Range), southern Costa Rica (Fig. 49).

Remarks. DNA barcode of male holotype INB0003536238.

MHMX012-08 | INB0003536238 | *Symmerista luisdiegogomezi* | COI-5P

ACATTATATTTTCATTTTTGGAATTTGAGCAGGTATAGTTGGAACCTT
CATTAAAGCCTATTAATTCGAGCTGAATTAGGAAATCCAGGATCCCTTA
TTGGGGATGATCAAATTTATAATACAATTGTTACAGCCCATGCCTTTA
TTATAATTTTTTTTATAGTAATACCTATTATAATTGGGGGATTTGGTA
ATTGATTAATTCCCCTTATATTAGGGGGCCCCAGACATAGCATTCCCA
CGTATAAATAATATAAGTTTTTGACTTTTACCCCCCTCCTTAACCCCTT
TTAATTTCAAGAAGAATTGTAGAAAATGGGGCAGGAACTGGATGAACA
GTGTACCCCCCACTATCATCCAATATTGCTCATAGTGGAAGTTCTGTA
GATTTAGCTATTTTTTCCCTTCATTTAGCTGGAATTTTCATCAATTTTA
GGGGCCATTAATTTTATTACAACAATTATTAATATACGTCTCAATAATA
TATCCTTTGATCAAATACCTTTATTTGTTTGGGCTGTTGGGATTACA
GCATTTTTACTTTTACTTTCTTTACCTGTTTTAGCTGGAGCTATTACA
ATACTACTAACTGATCGAAATTTAAACACATCTTTTTTTGACCCTGCAG
GAGGGGGAGATCCAATTTTATATCAACATTTA

***Symmerista inbioi* Chacón, sp. n.**

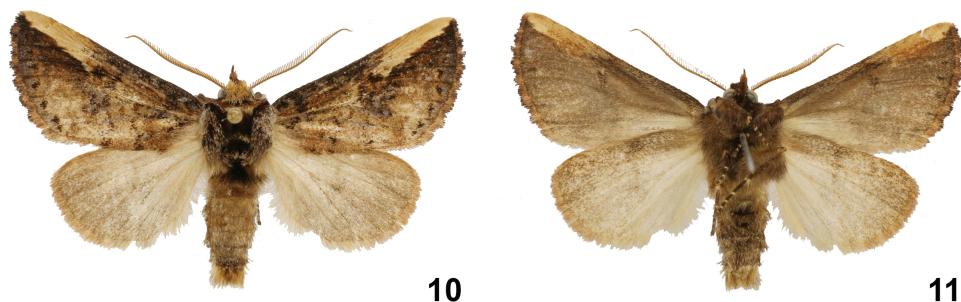
<http://zoobank.org/72BC7743-A984-4260-8CD8-CF7E47FDB9AA>

Figs 10–16

Material examined. 21 specimens (21 males).

Type material. Holotype male: INB0003487050 (dissected, COI barcoded), Costa Rica, Prov. Cartago, El Guarco, Reserva Forestal Rio Macho, Macizo de la Muerte, Sector La Esperanza 9.686771-83.87775, 2600 m, May 2002, R. Delgado (INBio).

Paratypes: Male: INB0003153991 Costa Rica, Prov. Cartago, El Guarco, San Isidro, Est. La Esperanza 9.687685-83.884582, 2450 m, March 2001, R. Delgado (INBio). 2 males: INB0003316531, INB0003316537 Costa Rica, Prov. Cartago, El Guarco, Macizo de la Muerte, Sector La Esperanza, 9.686771-83.87775, 2600 m, June 2001, R. Delgado (INBio). Male: INB0003320716 Costa Rica, Prov. Cartago, Parque Nacional Tapanti, El Guarco, San Isidro, Est. La Esperanza, 9.683922-83.876688, 2600 m, May 2001, R. Delgado (INBio). Male: INB0003334468 Costa Rica, Prov. Cartago, Parque Nacional Tapanti, Macizo de la Muerte, Est. La Esperanza, 9.686771-83.87775, 2600-2700 m, April 2001, R. Delgado (INBio). 3 males: INB0003339195, INB0003339197, INB0003339198 Costa Rica, Prov. Cartago, El Guarco, Parque Nacional Tapanti, Macizo de la Muerte, Est. La Esperanza 9.686771-83.87775, 2600 m, July 2001, R. Delgado (INBio). Male: INB0003387640 Costa Rica, Prov. Cartago, Reserva Forestal Rio Macho, El Guarco, Macizo de la Muerte, 9.686771-83.87775, 2600 m, October 2001, R. Delgado (INBio). Male: INB0003478225 (dissected, COI barcoded), Costa Rica, Prov. Cartago, Parque Nacional Tapanti, Macizo de La Muerte, Est. La Esperanza, 9.69397-83.854504, 2700 m, 13–14 May 2002, J. Montero (INBio). 2 males: INB0003536236 (dissected, COI barcoded), INB0003536239 (COI Barcoded) Costa Rica, Prov. Cartago, Parque Nacional Tapanti, Macizo de La Muerte, Est. La Esperanza, 9.69129-83.876832, 2600 m, September 2002, R. Delgado (INBio). Male: INB0003545219 (dissected, COI barcoded) Costa Rica, Prov. Cartago, Parque Nacional Tapanti, Macizo de La Muerte, Est. La Esperanza, 9.69129-83.876832, 2600 m, October 2002, R. Delgado (INBio). 3 males: INB0003756229, INB0003756321, INB0003756418 Costa Rica, Prov. Limon, Parque Internacional La Amistad, Valle del Silencio, Alrededor del Refugio y Sendero Circular, 9.110281-82.961934, 2450 m, 22–27 September 2003, D. Rubi, R. Gonzalez, R. Delgado (INBio). Male: INBIOCRI001359567 Costa Rica, Prov. Cartago, Quebrada Segunda, Parque Nacional Tapanti, 9.762583-83.788328, 1250 m, February 1993, G. Mora. Male: INBIOCRI002210601 Costa Rica, Prov. Cartago, La Represa, Tapanti, 9.695643-83.768399, 1800 m, July 1995, R. Delgado (INBio). Male: INBIOCRI002253344 Costa Rica, Prov. Cartago, Rio Grande de Orosi, desde Puente Rio Dos Amigos hasta la Represa, 9.695643-83.768399, 1400-1800 m, March 1995, R. Delgado (INBio). Male: INBIOCRI002423774 Costa Rica, Prov. Cartago, Rio Grande de Orosi, desde Puente Rio Dos Amigos hasta la Represa, 9.695643-83.768399, 1800 m, February 1995, R. Delgado (INBio). Male, INBIOCRI002427627 Costa Rica, Prov. Cartago, Rio Grande de Orosi, desde Puente Rio Dos Amigos hasta la Represa, 9.695643-83.768399, 1400-1800 m, 22 August–15 September 1995, R. Delgado (INBio).



Figures 10, 11. *Symmerista inbioi* Holotype male dorsal and ventral INB0003487050.

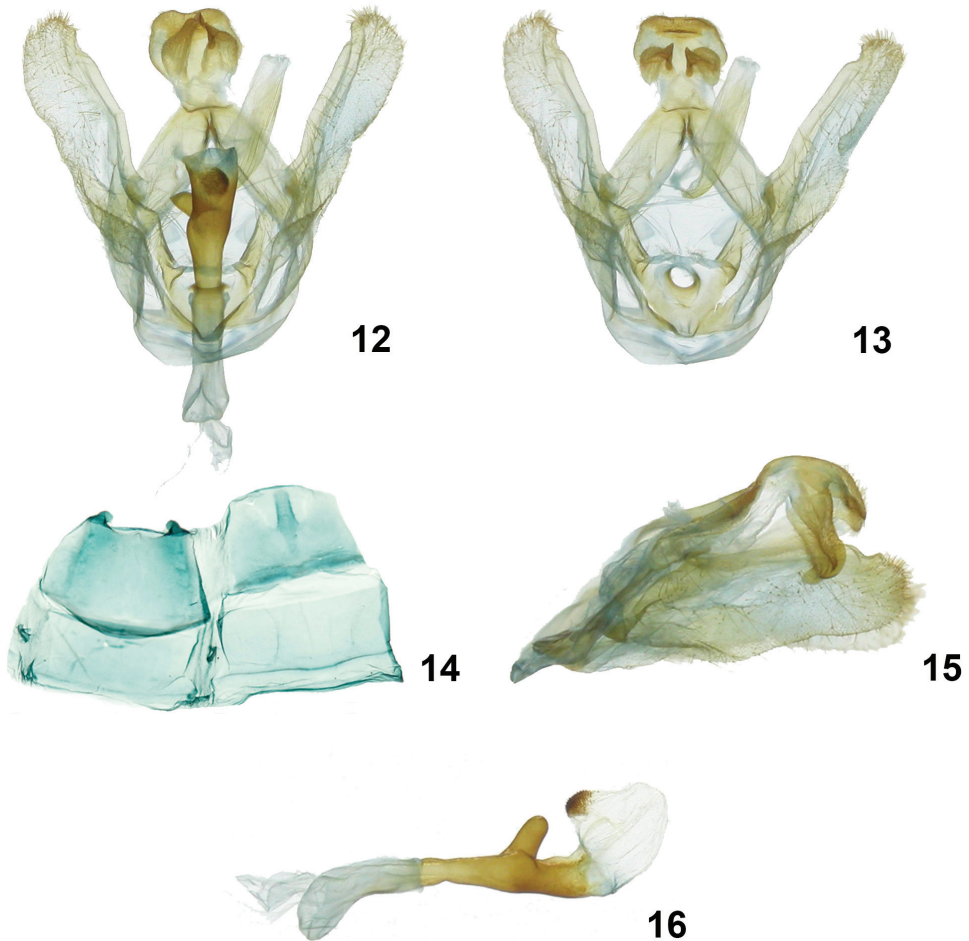
Etymology. This species is dedicated to the Instituto Nacional de Biodiversidad (IN-Bio) in recognition of its 25 years of support for developing an understanding of the biodiversity of Costa Rica and exporting that understanding to the nation and the world.

Diagnosis. *Symmerista inbioi* differs from *Symmerista luisdiegogomezi* on: dorsal FW ground color light brown; from the reniform spot to the apex there is an uniform long, thin, white cream-colored band; fringe reddish brown; dorsal HW dirty beige.

Male genitalia: St8 wide at base, anterior margin convex, posterior margin slightly irregular with a pair of very short projections, these sclerotized with blunt apices; valva membranous, saccular margin slightly jagged, costal margin smooth, with a distal protuberance near the apex; elongate finger-shaped process on the saccular margin at the internal base of the valve; uncus plate slightly concave, with papillae and setae on the dorsal and ventral edge; socii elongated, broad at base, narrow and flattened at the apex, with papillae and setae in the dorsal surface; length of the phallus 3.9 mm, proximal part of phallus curved at the base, slightly narrow in the middle, distal part of phallus tube sclerotized, narrow at the base, robust, irregular and wide at the end, with a tubular lateral projection with the distal nipple; proximal part of the vesica with a dorsal scobinate patch, distal part of the vesica bulbous. The genital armature of *Symmerista inbioi* is more robust and larger than *Symmerista luisdiegogomezi*.

Description. Male (Figs 10, 11, 12–16). **Head** – Antenna bipectinate nine terminal flagellomeres without rami, antennal shaft cream dorsally and light brown ventrally, scape bearing a long tuft of yellow-brown scales; haustellum vestigial; eye smooth, round, black; frons dark brown; labial palpus porrect, brown; patagium light brown near midline, dark brown laterally. **Thorax and abdomen** – Tegula dark brown at base, a mix of cream and dark brown scales distally; mesoscutellum black; thoracic pleuron dark brown; legs dark brown with cream-colored scales between segments; abdominal dorsum light brown, venter dark brown.

Wings – Dorsal FW ground color light brown; with reniform spot black; from reniform spot to apex with a uniform, long, thin, creamy-white band; costal margin black until R_1 ; AD black; purple scales between terminal line and the AD; fringe reddish brown; dorsal HW dirty beige, fringe light brown (Figs 10, 11) (WL 16.42–19.44 mm). **Male genitalia** (Figs 12–16) – T8 rectangular, wider than long,



Figures 12–16. *Symmerista inbioi* **12, 13** Holotype male genitalia INB0003487050 **14** Male St8 **15** Uncus **16** Phallus.

posterior margin slightly sclerotized and serrated; St8 wide at base, anterior margin convex, posterior margin slightly irregular with a pair of very short projections, these sclerotized with blunt apices (Fig. 14); valva membranous, costulate absent, saccular margin slightly jagged, costal margin smooth, with a distal protuberance near apex; elongate finger-shaped process on saccular margin at internal base of valve; tegumen narrow at point of intersection of both arms, margins heavily sclerotized (Figs 12, 13); uncus plate concave, with papillae and setae on dorsal and ventral edge; socii elongated, broad at base, narrow and flattened at apex, with papillae and setae in dorsal surface (Figs 12, 13, 15); juxta heart shaped (Fig. 13); vinculum membranous, slightly sclerotized (Fig. 12); length of phallus 3.9 mm, proximal part of phallus curved at base, slightly narrow in middle, distal part of phallus tube sclerotized, narrow at base, robust, irregular and wide at end, with a tubular lateral

projection with distal nipple; proximal part of vesica with a dorsal scobinate patch, distal part of vesica bulbous (Fig. 16).

Female: unknown

Distribution and habitat. *Symmerista inbioi* has been collected only at elevations between 1250 and 2700 m in highland cloud forests of the Cordillera de Talamanca (Talamanca Mountain Range) (Fig. 49).

Remarks. DNA barcode of holotype male INB0003487050

MHMXP003-08 | INB0003487050 | *Symmerista inbioi* | COI-5P:

AACATTATATTTTATTTTGGGATTTGAGCAGGTATAGTAG
GAACTTCTTTAAGTCTATTAATTTCGAGCTGAATTAGGAAACCCCG
GATCACTTATTGGGGATGATCAAATTTATAATACAATTGTTACAGCC
CATGCCTTTATTATAATTTTTTTTATGGTAATACCTATTATAATTGGGG
GATTTGGTAATTGATTAGTCCCTCTTATACTAGGAGCCCCAGATATAG
CATCCCCCGCATAAATAATATAAGTTTTTGACTTTTGCCCCCTTCTT
TAACCCTTTTAATTTCAAGAAGAATCGTAGAAAATGGAGCAGGAACTG
GATGGACAGTGTAACCCCCACTATCCGCCAACATTGCCCATAGTG
GAAGTTCTGTAGATTTAGCTATTTTTTCCCTTCATTTAGCTGGAATTC
CTCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGC
CTCAATAATATATCTTTTGATCAAATACCTTTATTTGTTTGAGCTGTTG
GAATTACAGCATTTTTACTTTTACTTTCTTTACCTGTTTTAGCGGGAGC
TATTACAATACTACTAACTGACCGTAATTTAAATACATCCTTTTTTGAC
CCTGCTGGGGGAGGAGATCCAATTTTATACCAACATTTATTT

***Symmerista minaei* Chacón, sp. n.**

<http://zoobank.org/71A2F18E-A8EC-4BF6-9991-ACEC39D20799>

Figs 17–25

Material examined. 4 specimens (1 male, 3 females)

Type material. Holotype female: INB0003339208 (dissected, COI barcoded), Costa Rica, Prov. Cartago, El Guarco, Macizo de la Muerte, Estacion La Esperanza, 9.68677–83.87775, 2600 m, July 2001, R. Delgado (INBio). **Paratypes:** Female: INB0003155283 (COI barcoded), Costa Rica, Prov. Limon, Bratsi, Valle del Silencio, 9.107197–82.961749, 2472 m, 11–12 October 2000, R. Delgado (INBio). Female: INB0003352700 (COI barcoded), Costa Rica, Prov. Cartago, Reserva Forestal Rio Macho, El Guarco, Macizo de la Muerte, Sector La Esperanza, 9.686771–83.87775, 2600 m, August 2001, R. Delgado (INBio).

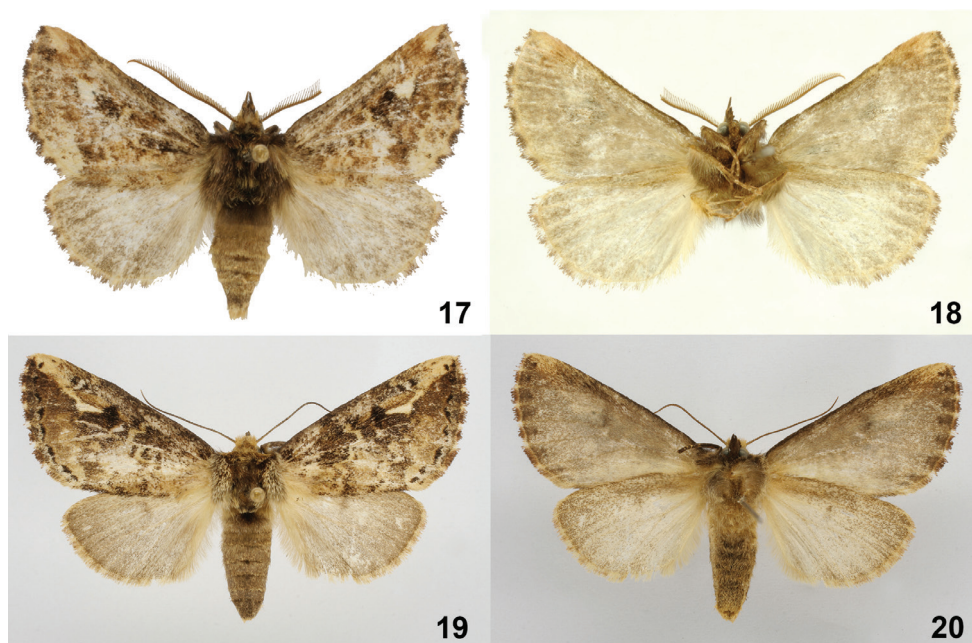
Other material examined: 1 Male, INB00033387642 (dissected) Costa Rica, Prov. Cartago, Reserva Forestal Rio Macho, El Guarco, Macizo de la Muerte, 9.68677–83.87775, 2600 m, October 2001. R. Delgado (INBio).

Etymology. This species is dedicated to the Ministerio del Ambiente y Energía (MINAE) of the government of Costa Rica in recognition of its 28 years of continuous and widespread support for the survival and conservation of the wild biodiversity of Costa Rica.

Diagnosis. *Symmerista minaei* differs from *Symmerista luisdiegogomezi* on: dorsal FW ground color beige and light brown, square mark creamy near the reniform spot; beige mark in the apex; fringe beige yellow; dorsal HW beige. **Male genitalia:** T8 anterior margin slightly concave, posterior margin finely serrated with a window in the center; St8 lateral margins wide at the base, narrow to posterior margin, anterior margin concave, slightly sclerotized with a short projection in the center, posterior margin with robust projections, highly sclerotized on each side, with blunt apices, a little dome in the middle of the posterior margin; length of the phallus 3.3 mm, proximal part of phallus tube wide at base, distal part of phallus tube robust, sclerotized, with a tubular lateral projection rounded apex with the distal nipple; proximal part of the vesica with a ventral scobinate patch, distal part of the vesica bulbous. **Female genitalia:** Anterior and posterior apophyses the same size, long and slender; DB sclerotized; CB rounded, membranous and pleated; posterior margin of postvaginal plate sclerotized, slightly irregular, inverted V-shape.

Description. Male (Figs 17, 18, 21–24). **Head** – Antenna bipectinate, dark brown, six terminal flagellomeres with very short rami, antennal shaft brown dorsally and light brown ventrally; scape bearing a long tuft of beige scales, sensilla beige; eye smooth, round, black; frons mostly dark brown and black with beige scales; labial palpus porrect, dark brown ventrally, light brown dorsally; vertex beige with black scales; patagium dark brown and light brown.

Thorax and abdomen – Tegula dark brown at base, a mix of dark brown and light brown scales distally; mesoscutellum beige and dark brown; thoracic pleuron from beige to dark brown; dorsal area of metathorax with black and dark brown hair-like scales; legs mostly dark brown with beige scales between segments; abdominal dorsum dirty beige, venter beige. **Wings** – dorsal FW ground color beige and light brown, with reniform spot black; basal band light brown; postmedial band light brown; a creamy-white square distal to reniform spot; AD black; fringe dark brown with beige scales where veins touch termen; beige mark in apex; dorsal HW beige; fringe beige-yellow (Figs 17, 18) (WL 17.20–19.21 mm). **Male genitalia** (Figs 21–24) – T8 wider than long, anterior margin slightly concave, posterior margin finely serrated with a window in center; St8 lateral margins wide at base, narrow to posterior margins, anterior margin convex, slightly sclerotized with a short projection in center, posterior margin concave with a pair of short projections, these sclerotized with blunt apices, a small setose dome in middle of posterior margin (Fig. 23); valva membranous, mildly pubescent, margin of sacculus slightly serrated, costa with straight margin with a distal protuberance close to apex; valva with a triangular spine-like process; tegumen narrowed dorsally; uncus plate slightly concave, somewhat helmet shaped, dorsal surface rough, pubescent, ventral surface smooth with sparse pubescence, socii long, wide, pubescent at bases, narrow and flattened at apex, form s-shaped; vinculum slightly sclerotized (Figs 21, 22); length of phallus 3.3 mm, proximal part of phallus tube wide at base, distal part of phallus tube robust, sclerotized, with a tubular lateral projection rounded apex with distal nipple; proximal part of vesica with a ventral scobinate patch,

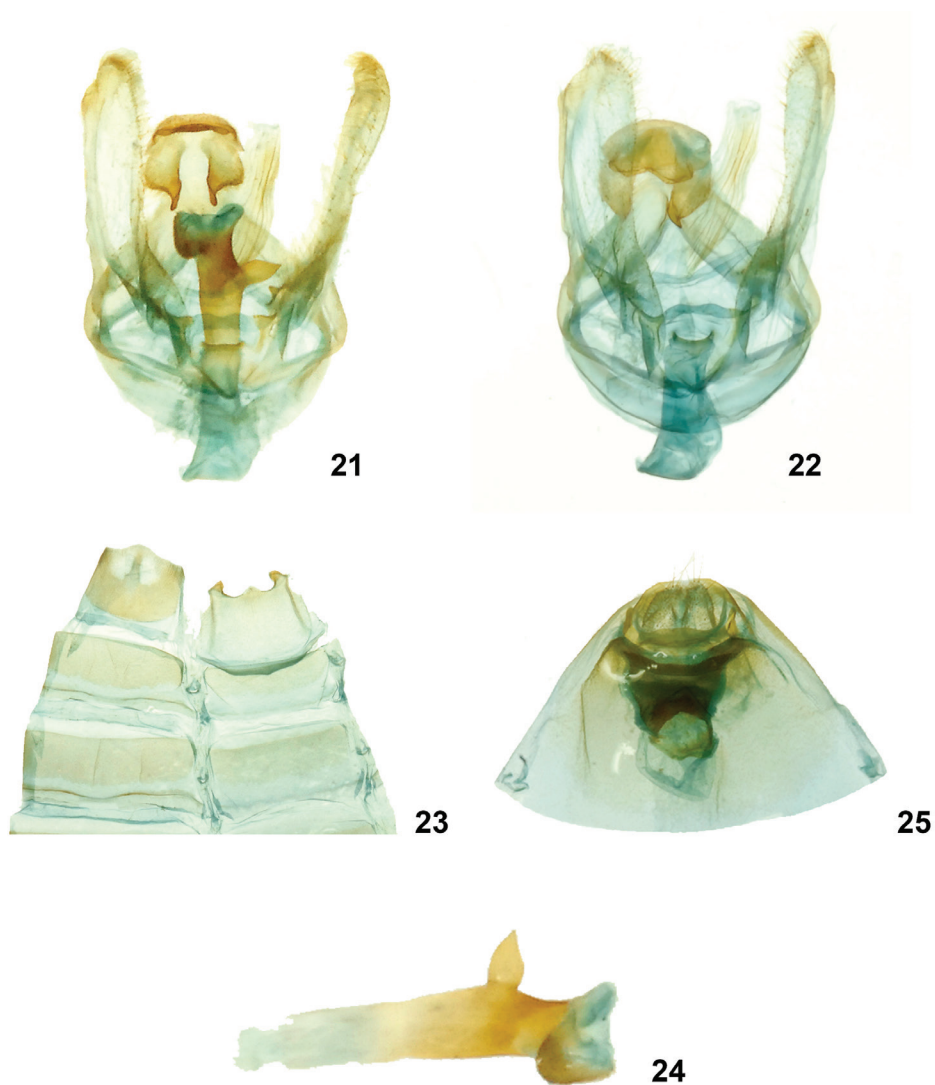


Figures 17–20. *Symmerista minaei* **17, 18** Paratype male dorsal and ventral INB0003387642 **19, 20** Holotype female dorsal and ventral INB0003339208.

distal part of vesica bulbous (Fig. 24). **Female** (Figs 19, 20, 25) **Head** – Antenna simple, shaft dark brown with cream-colored scales, scape with a tuft of cream-colored scales; eyes naked; frons dark brown, vertex dark brown with groups of beige scales at base and between antennal bases; haustellum vestigial, labial palpus dark brown.

Thorax and abdomen – Generally dark brown, tegula beige, scales of thorax long and forked. Patagium and prothorax with beige and cream scales; mesothorax with scales cream, dark brown and beige; metathorax with a group of black hair-like scales along posterior margin; abdomen light brownish gray, abdominal apex with a thick group of beige scales.

Wings – dorsally FW ground color dark brown; antemedial beige band lined at both sides by sinuous dirty dark brown lines; reniform spot black; an irregular thin white to beige line extends from the apex to the reniform spot; postmedial line beige, lined on each side with dark brown; adterminal line black; light beige area between adterminal line and postmedial band from M3 to tornus; fringe dark brown with beige scales where veins touch termen; dorsal HW dirty beige, fringe beige (Figs 19, 20) (WL 19.63–21.18 mm). **Female genitalia** (Fig. 25) – Papillae anales membranous with short, scattered setae with longer, inwardly-curved setae arising from base. Anterior and posterior apophyses of same size, long and slender; DB sclerotized; CB rounded, membranous and pleated; posterior margin of postvaginal plate sclerotized, slightly irregular, inverted V-shape.



Figures 21–25. *Symmerista minaei* INB0003387642 **21, 22** Paratype male genitalia **23** Male St8 **24** Phallus **25** Holotype female genitalia INB0003339208,

Distribution and habitat. *Symmerista minaei* has only been collected at elevations between 2400 and 2600 m in highland cloud forests of the Cordillera de Talamanca (Talamanca Mountain Range) (Fig. 49).

Remarks. DNA barcode paratype female INB0003155283.

MHMXP006-08 | INB0003155283 | *Symmerista minaei* | COI-5P:

AACATTATATTTCATTTTGGAAATTTGAGCAGGTATAGTTGGAAC
TTCATAAGCCTATTAATTCGAGCTGAATTAGGAAATCCCGGATCCCT
TATTGGAGATGATCAAATTTATAACACAATTGTTACAGCCCATGCCTT

TATTATAAATTTTTTTTATAGTAATACCTATTATAATTGGGGGATTTGG
 TAATTGATTAGTCCCCCTTATGCTAGGAGCCCCAGATATAGCATTCC
 CACGTATAAATAATATAAGTTTTTGACTTTTACCCCCCTCCTTAACCC
 TTTTAATTTCAAGAAGAATCGTCGAAAATGGGGCAGGAACCGGATGGA
 CAGTGTACCCCCCACTATCCTCCAATATTGCCACAGTGGAAGTTCTG
 TAGATTTAGCTATTTTTTCCCTACATTTAGCTGGAATTTTCATCAATTT
 TAGGGGCCATTAATTTTATCACAACAATTATTAATATACGTCTCAATAA
 CATATCTTTTGATCAAATACCCTTATTTGTTTGAGCTGTTGGAATTA
 CAGCATTTTTACTTTTACTTTCTTTACCTGTTCTAGGGAGCTATTACA
 ATACTACTAACGGATCGTAATTTAAATACATCTTTTTTTTGATCCTGCAG
 GAGGAGGAGATCCAATTTTATATCAACATTTATTT

***Symmerista aura* Chacón, sp. n.**

<http://zoobank.org/31DCFCFA-B792-406E-A667-CAAA17B5111F>

Figs 26–35

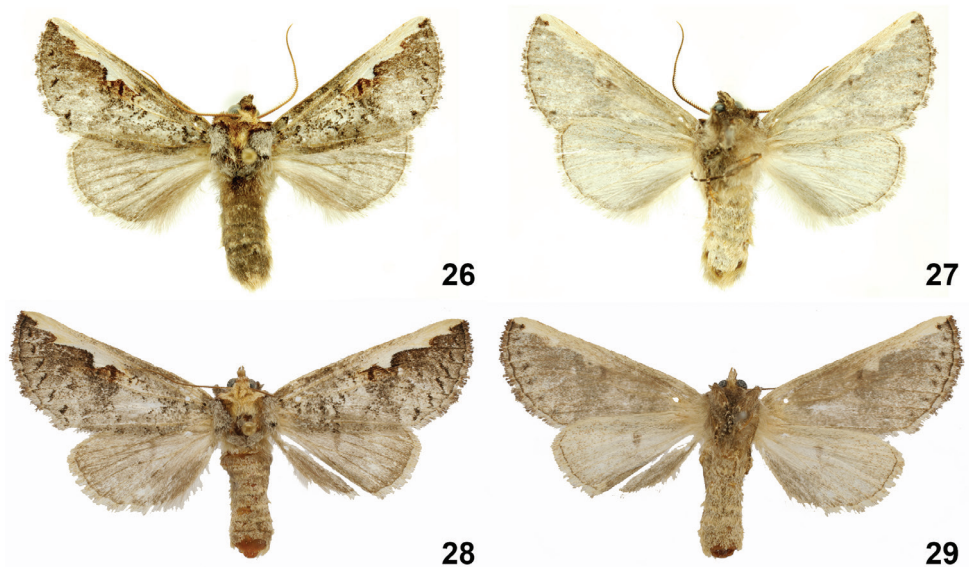
Material examined. 4 specimens (2 males, 2 females)

Type material. Holotype male: INB0003116415 (dissected, COI barcoded), Costa Rica, Prov. Cartago, Paraiso, P.N. Tapanti, Macizo de La Muerte, Estacion Quebrada Segunda, 9.762583-83.788328, 1300 m, November 2000, R. Delgado (INBio).

Paratypes: 1 males, 2 females. Male: INBIOCRI002442681 (COI barcoded), Costa Rica, Prov. Puntarenas, Buenos Aires, Potrero Grande, Estacion Altamira, 1 Km. S del Cerro Biolley, 9.032987-83.010887, 1450 m, 13–26 May 1996, R. Villalobos (INBio). Female: INBIOCRI002549508 (COI barcoded), Costa Rica, Prov. Puntarenas, Coto Brus, Sabalito, Send. El ripario a 3 Km NE. de Progreso, 8.917676-82.78469, 1300 m, 6–9 April 1997, A. Picado (INBio). Female: INBIOCRI002754030 Costa Rica, Prov. Cartago, Turrialba, Tayutic, Moravia de Chirripo Shipiri, 9.837781-83.453639, 1000 m, 10 May 1983, D. H. Janzen & W. Hallwachs (INBio).

Etymology. This species is dedicated to Isidro Chacón's daughter, Aura Chacón, for 25 years of understanding an absent father obsessed with his work.

Diagnosis. Dorsal FW ground color light gray; a white cream mark from the discal cell to the apex. **Male genitalia:** St8 anterior margin with a sclerotized triangular projection in the middle, posterior margin sclerotized, irregular, with a rectangular projection at the center bearing two highly sclerotic and sharply serrated structures; proximal part of phallus tube wide and short at the base, with a blade-like lateral projection, sharp at the distal apex; a small rounded projection and curve off the previous, distal part of phallus tube robust, sclerotized, with a small bulge on the ventral side; proximal part of the vesica with a ventral scobinate patch, distal part of the vesica bulbous. **Female genitalia:** papillae anales ovoid-triangular, setose; posterior apophyses longer and more slender than anterior apophyses; DB sclerotized; CB elongated, membranous and pleated, lacking a signum; margin distal of antevaginalis plate very sclerotized and lightly depressed at the center, concave to the sides, proximal margin convex.

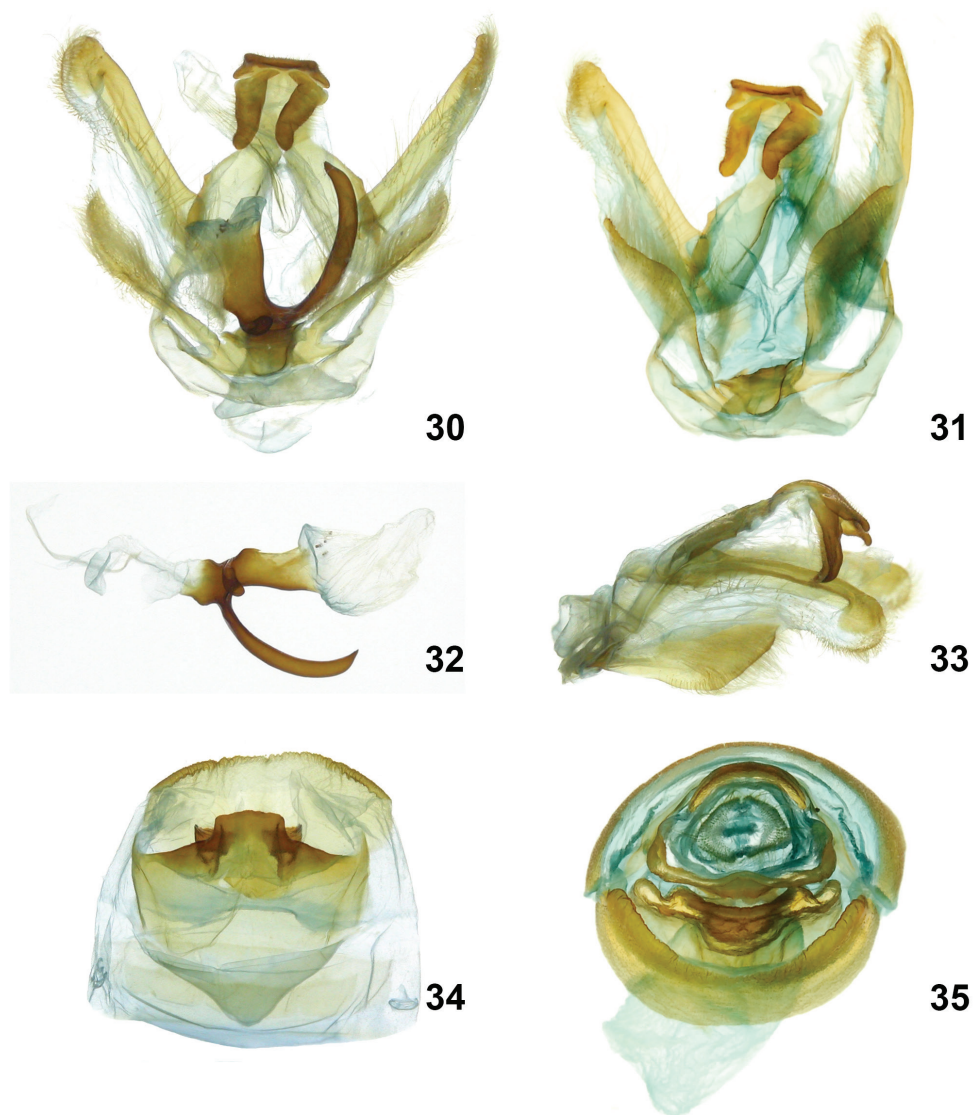


Figures 26–29. *Symmerista aura* **26, 27** Paratype male dorsal and ventral INBIOCRI002442681 **28, 29** Paratype female dorsal and ventral INBIOCRI002549508.

The female of *Symmerista aura* differs from female of *Symmerista meridionalis* Thiaucourt, 2007 in the shape of the antivaginalis plate; the CB elongated, membranous and pleated, lacking a signum; margin distal of antevaginalis plate very sclerotized and lightly depressed at the center, concave to the sides, proximal margin convex. This is the description of the female genitalia of *Symmerista meridionalis* published by Thiaucourt in 2007 which mentions the differences, “Female terminalia: distal edge of lamella postvaginalis slightly incurved; lamella antevaginalis rectangular, almost square; its distal margin strongly sclerotized; mouth of the ostium bursae oval, densely sclerotized under the margin; ductus bursae beyond the constriction under the ostium, forming a short funnel; bursa membranous inserted on the dorsal surface of the extremity of the duct; signum distinct.” The male of *Symmerista meridionalis* is unknown.

Description. Male (Figs 26, 27, 30–34) **Head** – antenna bipectinate, ventral shaft dark brown, dorsal light brown, scape bearing a tuft of beige scales; haustellum vestigial; eye smooth, round, black; front dark brown; labial palpus porrect, dark brown laterally, beige ventrally; patagium dark brown. **Thorax and abdomen** – tegula light gray; mesoscutum dark brown anteriorly, light brown and cream posteriorly; mesoscutellum black and gray; thoracic pleuron beige; legs dark brown on outer surfaces, beige on inner ones; abdominal dorsum dark brown, venter beige.

Wings – Dorsal FW ground color light gray; mark white cream from the discal cell to apex; costal margin beige until R1; subterminal line black; fringe light gray; dorsal HW light gray, fringe cream (Figs 26, 27) (WL 16.26–17.32 mm).



Figures 30–35. *Symmerista aura* INB0003116415 **30, 31** Holotype male genitalia **32** Phallus **33** Uncus **34** Male St8 **35** Paratype female genitalia INBIOCRI002549508.

Male genitalia (Figs 30–34) – T8 wider than long, posterior margin sclerotized and highly irregular; St8 anterior margin with a sclerotized triangular projection in middle, posterior margin sclerotized, irregular, with a rectangular projection at center bearing two highly sclerotic and sharply serrated structures (Fig. 34). Valvae membranous with saccular margin esclerotized, slightly irregular and setose; costal

margin smooth, apex rounded, sclerotized and setose; tegumen with margins very sclerotized, narrowed where both arms intersect; uncus slightly concave plate, with papillae and setae in dorsal and ventral edge, with socii elongate, wide at base, narrowed and flattened at apex with papillae and setae in dorsal part (Figs 30, 31, 33); juxta heart shaped; vinculum membranous slightly sclerotized (Fig. 31); proximal part of phallus tube wide and short in base, with a blade-like lateral projection, sharp at distal apex and a small rounded curved projection, distal part of phallus tube robust, sclerotized, with a small bulge on ventral side; proximal part of vesica with a ventral scobinate patch, distal part of vesica bulbous (Fig. 32).

Female (Figs 28, 29, 35) Similar to male: **Head** – Antenna filiform, antennal shaft light brown with cream scales, scape bearing a long tuft of cream scales; frons and vertex cream; haustellum vestigial; labial palpus mostly cream with black lateral scales. **Thorax and abdomen** – tegula light gray; mesoscutum dark brown anteriorly, light brown and cream posteriorly; mesoscutellum black and gray; thoracic pleuron beige; legs dark brown on outer surfaces, beige on inner ones; abdominal dorsum dark brown, venter beige. **Wings** – Dorsal FW ground color light gray; mark white cream from the discal cell to apex; costal margin beige until R1; subterminal line black; fringe light gray; dorsal HW light gray, fringe cream (Figs 28, 29) (WL 20.22–21.51 mm). **Female genitalia** (Fig. 35) – papillae anales ovoid triangular, setose; posterior apophyses longer and more slender than anterior apophyses; DB sclerotized; CB elongated, membranous and pleated, lacking signum; margin distal of antevaginalis plate very sclerotized and lightly depressed at center, concave to sides, proximal margin convex.

Distribution and habitat. In Costa Rica, *Symmerista aura* has been collected between 1000 to 1400 m on both slopes of the Cordillera de Talamanca (Talamanca Mountain Range) (Fig. 49).

Remarks. DNA barcode paratype male INB0003116415.

MHMXP017-08 | INB0003116415 | *Symmerista aura* | COI-5P:

```
ACATTATATTTTATTTTTTGGGGTTTGAGCTGGGATAGTTGGAAC
TTCCCTAAGTTTACTAATTCGAGCTGAATTGGGTAACCCCTGGATCTT
TAATTGGAGATGATCAAATTTATAATACAATTGTAACAGCCCATGCTT
TTATTATAATTTTTTTTATAGTTATACCCACCATAATCGGGGGATTTG
GTAATTGACTAGTTCCTCTTATATTAGGGGCACCGGATATAGCATTTTC
CACGTATAAATAACATAAGTTTTTGACTTCTACCCCTTCTTTAACCC
TTTTAATTTCAAGAAGAATTGTCGAAAATGGAGCTGGAACAGGATGAA
CAGTGTACCCCCCATTGTCATCTAATATTGCTCATGGTGGTAGTTCC
GTAGATTTAGCTATTTTTTCACTTCATTTAGTGGAATTTCTTCAATTT
TAGGGGCTATTAATTTTATTACAACAATCATTAATATACGTCTTAATA
ATATATCTTTTGACCAAATACCTTTATTTGTGTGAGCTGTAGGGATTA
CAGCATTTTTACTTTTACTTTCTTTACCTGTATTAGCTGGAGCTATTA
CAATATTATTAAGTATCGTAATCTAAACACATCTTTTTTTTGATCCC
GCTGGAGGAGGAGATCCTATTTTATAC
```

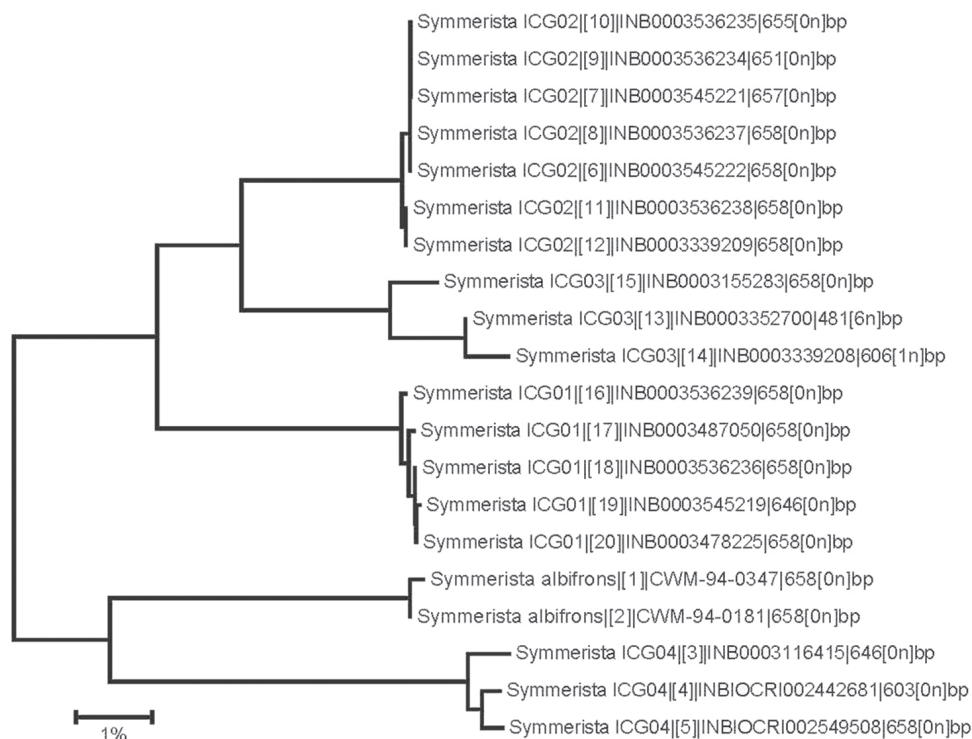


Figure 36. The *Symmerista* species from Costa Rica in a NJ barcoding tree. ICG01, *S. inbioi*; ICG02, *S. luisdiegogomezi*; ICG03, *S. minaei*; ICG04, *S. aura*.

Elymiotis tlotzin (Schaus, 1892), comb. n.

Figs 37–45

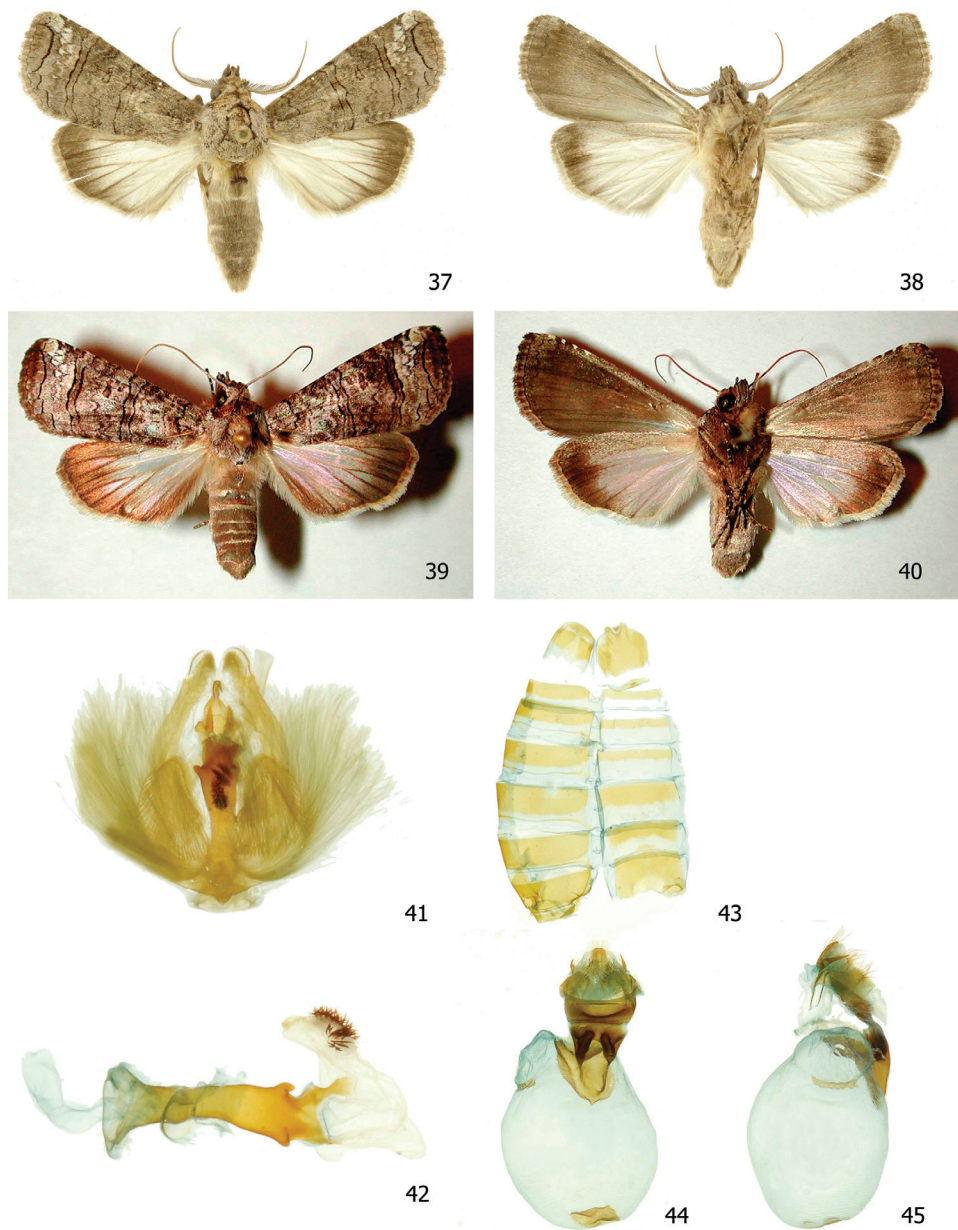
Material examined. 11 males 12 females.

Wild-caught adults: 2 Males: INBIOCRI000584965 Costa Rica, Prov. Guanacaste, Bagaces, Ref. Nac. Fauna Silv. R. L. Rodriguez, Estacion Palo Verde, 10.349119-85.352345, 10 m, May 1991, U. Chavarria (INBio). Male: INB0003072431 Costa Rica, Prov. Guanacaste, Bagaces, Pque. Nal. Palo Verde, Sector Palo Verde, 10.366668-85.383266, 0–50 m, 3 May 2000, H. Mendez (INBio). Male: INBIOCRI000386810 Costa Rica, Prov. Guanacaste, Liberia, P. N. Sta. Rosa, Playa Naranjo, 10.80275-85.666572, 0–10 m, May 1991, E. Alcazar (INBio). Male: INBIOCRI002426620 Costa Rica, Prov. Guanacaste, Liberia, Sector Las Pailas, 4.5 Km. SW del Volcan Rincon de la Vieja, 10.776784-85.351913, 800 m, 24 June 1995, K. Taylor (INBio). Male: INB0004065577 Costa Rica, Prov. Guanacaste, Liberia, Santa Rosa Nat. Pk., 10.83641-85.615491, 300 m, 4–6 December 1979, D. H. Janzen (INBio). Male: INB0003319696 Costa Rica, Prov. Guanacaste, Nicoya, P.N. Barra Honda, Sector

Barra Honda, 10.169826-85.379137, 50 m, 25–30 December 2000, H. Mendez (INBio). Female: INBIOCRI001184551 Costa Rica, Prov. Guanacaste, Bagaces, P. N. Palo Verde, Estacion Palo Verde, 10.349119-85.352345, 10 m, 20 June 1993, U. Chavarria (INBio). Female: INB0003300310 Costa Rica, Prov. Guanacaste, Hojancha, Z.P. Nosara, Hojancha, R.F. Monte Alto, 10.011248-85.402778, 400 a 500 m, 27 July – 3 August 2000, H. Mendez (INBio). Female: INBIOCRI000674401 Costa Rica, Prov. Guanacaste, Liberia, P.N.Sta. Rosa, Playa Naranjo, 10.802713 – 85.67479, 0–10 m, March 1991, E. Alcazar (INBio). Female: INB0003956448 Costa Rica, Prov. Guanacaste, Nicoya, San Antonio, Humedal Mata Redonda, 10.328094-85.42111, 8 m, 6 July 2005, B. Gamboa, J. Azofeifa, J. Gutierrez, M. Moraga, Y. Cardenas (INBio).

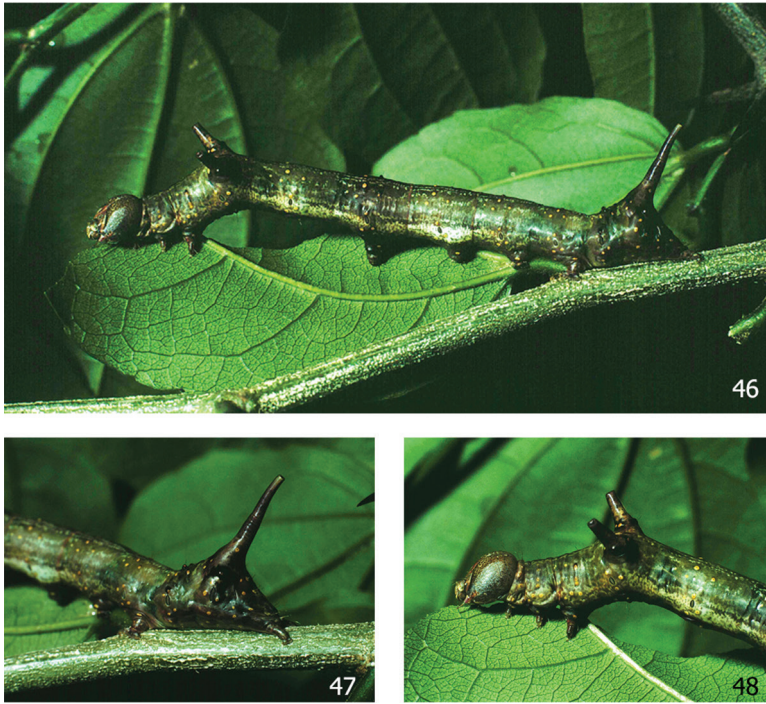
Reared from wild-caught caterpillars feeding on foliage of *Zizyphus guatemalensis* (Rhamnaceae): Male: 94-SRNP-2964 Costa Rica, Area Conservacion Guanacaste, Prov. Guanacaste, Sector Santa Rosa, Estero Naranjo, 10.80426-85.68285, 2 m, 9 June 1994, Gusaderos. Male: 98-SRNP-9137 (COI barcoded), Costa Rica, Area Conservacion Guanacaste, Prov. Guanacaste, Sector Santa Rosa, Area Administrativa, 10.83764-85.61871, 295 m, 14 August 1998, Manuel Pereira. Male: 01-SRNP-17295 (COI barcoded), Costa Rica, Area Conservacion Guanacaste, Prov. Guanacaste, Sector Santa Rosa, Sendero Carbonal, 10.77594-85.65799, 7 m, 2 November 2001, Gusaderos. Male: 06-SRNP-13290 (COI barcoded), Costa Rica, Area Conservacion Guanacaste, Prov. Guanacaste, Sector Santa Rosa, Estero Naranjo, 10.80426-85.68285, 2 m, 31 May 2006, Eilyn Camacho.

Female: 92-SRNP-736 Costa Rica, Area Conservacion Guanacaste, Prov. Guanacaste, Sector Santa Rosa, Vado Nisperal, 10.80212-85.65372, 10 m, 20 May 1992, Gusaderos. Female: 96-SRNP-1331 (COI barcoded), Costa Rica, Area Conservacion Guanacaste, Prov. Guanacaste, Sector Santa Rosa, Sendero Palo Seco, 10.79342-85.6666, 5 m, 31 May 1996, Gusaderos. Female: 96-SRNP-1332 Costa Rica, Area Conservacion Guanacaste, Prov. Guanacaste, Sector Santa Rosa, Sendero Palo Seco, 10.79342-85.6666, 5 m, 2 June 1996, Gusaderos. Female: 98-SRNP-9134 (COI barcoded), Costa Rica, Area Conservacion Guanacaste, Prov. Guanacaste, Sector Santa Rosa, Area Administrativa (adult at light), 10.83764-85.61871, 295 m, 2 August 1998, Guillermo Pereira. Female: 98-SRNP-9137 Costa Rica, Area Conservacion Guanacaste, Prov. Guanacaste, Sector Santa Rosa, Area Administrativa (adult at light), 10.83764-85.61871, 295 m, 14 August 1998, Guillermo Pereira. Female: 01-SRNP-17336 (COI barcoded), Costa Rica, Area Conservacion Guanacaste, Prov. Guanacaste, Sector Santa Rosa, Sendero Carbonal, 10.77594-85.65799, 7 m, 28 October 2001, Gusaderos. Female: 01-SRNP-17336 Costa Rica, Area Conservacion Guanacaste, Prov. Guanacaste, Sector Santa Rosa, Sendero Carbonal, 10.77594-85.65799, 7 m, 28 October 2001, Gusaderos. Female: 07-SRNP-112736 (COI barcoded), Costa Rica, Area Conservacion Guanacaste, Prov. Guanacaste, Sector Santa Rosa, Sendero los Patos (adult at light), 10.82097-85.63323, 251 m, 8 December 2007, H. Cambronero & S. Rios. Female: 11-SRNP-12732 (COI Barcoded), Costa Rica, Area Conservacion Guanacaste, Prov. Guanacaste, Sector Santa Rosa, Area Administrativa (adult at light), 10.83764-85.61871, 295 m, 1 June 2011, Daniel H. Janzen



Figures 37–45. *Elymiotis tlotzin* **37, 38** Male dorsal and ventral INBIOCRI002426620 **39, 40** Female dorsal and ventral 96-SRNP-1332 **41** Male genitalia INBIOCRI002426620 **42** Phallus **43** Male St8 **44, 45** Female genitalia INBIOCRI006744401.

Diagnosis. Adults – (Figs 37–40) Medium-sized notodontid moths, FW = 15.42–19.28 mm, females larger than males; male antenna narrowly bipectinate, gradually narrowing to apex, which is simple; antennae of female simple; labial palpus porrect, com-



Figures 46–48. Ultimate instar of *Elymiotis tlotzin* 90-SRNP-1223 on its food plant (Rhamnaceae: *Zizyphus guatemalensis*).

posed by three segments; haustellum is well developed, ocelli absent; eyes smooth, round. Thorax mostly gray, tegula gray, all scales of the thorax are long and forked; patagium and prothorax with beige and light brown scales. FW costa straight, outer margin almost straight; accessory cell present. **Male genitalia** – (Figs 41–43) valvae elongated, sclerotized and mildly setose; sacculus pleats highly developed; uncus thin and long, with apex acute and setose, each socius wide at the base with two thin projections, acute and setose; saccus acute (Figs 41); phallus robust, wide at the base with two single subterminal lateral bumps, vesica long but shorter than phallus, wide at the base, long and thin distally, caltrop cornuti (Fig. 42); T8 rectangular shorter than St8, lateral margins straight, anterior margin simple and membranous, posterior margin slightly concave; St8 wide at anterior margin, posterior margin with a single median depression and two sclerotized small projections (Fig. 43). **Female genitalia** (Figs 44, 45) – The papillae anales small, roughly ovoid with elongated dorsal setae; lateral process of postvaginal plate with apices acute and sclerotized; posterior apophyses short and thin; lamella postvaginalis rectangular, sclerotized; ostium sclerotized, wide, funnel shape; DB short; CB wide and long, ovoid with surface membranous slightly rough; signum brick shape with a rough surface.

Thiaucourt (2007) “The species was described in the genus *Edema*, cited by DRUCE (1898) in this genus, the species should be now in another genus.” KIRBY (1892) lists *Edema* (Walker, 1855) as a junior synonym of *Symmerista* Hubner, [1821].

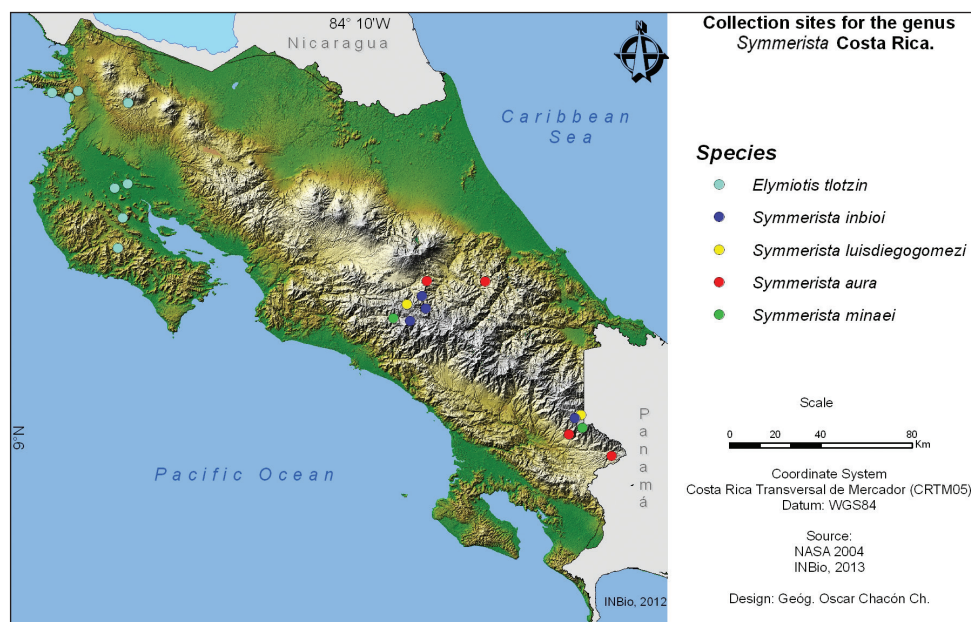


Figure 49. Map of Costa Rican collection sites for the four species of Notodontidae discussed here.

The adult lacks the apical white stripe, the male genitalia framework places the genus in the Nystaleini, but it differs from that of *Symmerista* (Plate II, Fig. 10). Male genitalia: uncus with acute and long apex; socci in brackets; valve costa without apical membranous area, pleats highly developed; exopenis with two single subterminal lateral bumps; beam cornuti extensions, obsolete; distal edge St 8 with a single median depression, two sclerotized thickenings near the distal edge of T8.

We propose that *Symmerista tlotzin* should be allocated to the genus *Elymiotis* Walker, 1857 for the following characteristics of the male genitalia: valvae elongated, sclerotized and setose; sacculus pleats highly developed; uncus thin and long, with apex acute and setose; socius wide at the base with two thin projections, acute and setose and caltrop cornuti.

Natural history (Figs 46, 47, 48). 33 rearing records from Sector Santa Rosa, ACG.

Food plants. Rhamnaceae, *Zizyphus guatemalensis* Hemsl. (n=33).

Parasitoids. Eulophidae: *Euplectrus* (n=1).

Distribution and habitat. Adult *Elymiotis tlotzin* have been collected in the dry forest ecosystem of Peninsula de Nicoya, and in the dry forests of Sector Santa Rosa and Sector Pailas of ACG, at elevations of 0 to 800 m. (Fig. 49).

Remarks. DNA barcode female 11-SRNP-12732.

MHMYM2073-11 | 11-SRNP-12732 | *Elymiotis tlotzin* | COI-5P:

AACATTATATTTTATTTTGGGAATTTGAGCAGGAATAGTAG
GAACTTCTTTAAGTTTATTAATTCGAGCTGAATTAGGAAATCCAG
GATCTTTAATTGGTGATGATCAAATTTATAATACTATTGTAACAGCT

CATGCTTTTATTATAATTTTTTTTTTATAGTAATGCCTATTATAATTG
 GAGGATTTGGAAATTGACTAGTTCCATTAATATTAGGAGCCCCAGA
 TATAGCTTTCCCCCGAATAAATAATATAAGATTTTGACTACTTCCAC
 CCTCACTAACTTTATTGATTTCAAGAAGTATTGTAGAAAATGGAGCAG
 GAACTGGATGAACAGTTTATCCCCCCTTTTCATCTAA0TATTGCACAT
 AGAGGAAGATCTGTAGATTTAGCAATTTTTTTCACTTCATTTAGCTG
 GTATTTTCATCGATTTTAGGAGCTATTAATTTTTATTACAACGATTAT
 TAATATACGACTTAATAACATAACTTTTGATCAAATACCTTTATTT
 GTTTGAGCAGTAGGAATTACAGCTTTTTTTATTATTATTATCTTTAC
 CTGTTTTAGCCGGAGCGATTACTATATTATTAACAGACCGTAATTTAA
 ATACTTCATTTTTTCGACCCTGCTGGTGGAGGAGATCCAATTCTTTAT
 CAACATTTATTT

Acknowledgments

We gratefully acknowledge the team of ACG parataxonomists (Janzen et al 2009) who found and reared the caterpillars used in this study, and the team of biodiversity managers who keep the ACG forests that host these moths alive. The study has been supported by U.S. National Science Foundation grants BSR 9024770 and DEB 9306296, 9400829, 9705072, 0072730, 0515699, and grants from the Wege Foundation, International Conservation Fund of Canada, Jessie B. Cox Charitable Trust, Blue Moon Fund, Guanacaste Dry Forest Conservation Fund, Area de Conservación Guanacaste, Permian Global, and University of Pennsylvania. This study has been supported by the Government of Canada through Genome Canada and the Ontario Genomics Institute. We want to give special thanks to; Jim Miller for all his help on the revision and editing of the manuscript and the anonymous reviewers; to Juan Mata for the genitalia photographs; Carlos Mena for the plate construction and the former INBio parataxonomists that collected the adults in the Talamanca Cordillera.

References

- Chacón IA, Janzen DH, Hallwachs W, Sullivan JB, Hajibabaei M (2013) Cryptic species within cryptic moths: new species of *Dunama* Schaus (Notodontidae, Nystaleinae) in Costa Rica. In: Schmidt BC, Lafontaine JD (Eds) Contributions to the systematics of New World macro-moths IV. ZooKeys 264: 11–45. doi: 10.3897/zookeys.264.4440
- Forbes WTM (1948) Lepidoptera of New York and neighboring states. Part 2. Notodontidae. Cornell Agricultural Experiment Station Memoirs 274: 203–237.
- Franclemont JG (1946) A Revision of the Species of *Symmerista* Hübner known to occur North of the Mexican border (Lepidoptera, Notodontidae). The Canadian Entomologist 78: 96–103. doi: 10.4039/Ent7896-5
- Gaede M (1934) Notodontidae. Lepidopterorum catalogus. Junk, Gravenhage, 351 pp.

- Janzen DH, Hallwachs W, Blandin P, Burns JM, Cadiou J, Chacon I, Dapkey T, Deans AR, Epstein ME, Espinoza B, Franclemont JG, Haber WA, Hajibabaei M, Hall JPW, Hebert PDN, Gauld ID, Harvey DJ, Hausmann A, Kitching I, Lafontaine D, Landry J, Lemaire C, Miller JY, Miller JS, Miller L, Miller SE, Montero J, Munroe E, Rab Green S, Ratnasingham S, Rawlins JE, Robbins RK, Rodriguez JJ, Rougerie R, Sharkey MJ, Smith MA, Solis MA, Sullivan JB, Thiaucourt P, Wahl DB, Weller SJ, Whitfield JB, Willmott KR, Wood DM, Woodley NE, Wilson JJ (2009) Integration of DNA barcoding into an ongoing inventory of complex tropical biodiversity. *Molecular Ecology Resources* 9 (Suppl. 1): 1–26. doi: 10.1111/j.1755-0998.2009.02628.x
- Miller JS (1991) Cladistics and classification of the Notodontidae (Lepidoptera: Noctuoidea) based on larval and adult morphology. *Bulletin of the American Museum of Natural History* 204: 1–230.
- Thiaucourt P (2007) *Symmerista* Hübner [1821] Description D'Espèces Nouvelles Mesoaméricaines (Lepidoptera: Notodontidae). *Lambillionea* 107: 531–538.
- Thiaucourt P, Monzón J (2013) *Symmerista brucesuttoni* nouvelle espèce du Guatemala (Lepidoptera, Notodontidae). *Bull. Soc. ent. Mulhouse* 69(1): 13–14.
- Weller SJ (1992) Survey of Adult Morphology in Nystaleinae and Related Neotropical Subfamilies (Noctuoidea: Notodontidae). *Journal of Research on the Lepidoptera* 31(3–4): 233–277.

The type-material of Arctiinae (Lepidoptera, Erebidae) described by Burmeister and Berg in the collection of the Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Buenos Aires, Argentina)

Hernán M. Beccacece¹, Benoit Vincent², Fernando R. Navarro³

1 Centro de Investigaciones Entomológicas de Córdoba, Instituto de Investigaciones Biológicas y Tecnológicas - CONICET, Av. Vélez Sársfield 1611, 5016, Córdoba, Argentina **2** 1 rue Roger Rameau, F – 93110 Rosny sous Bois. Correspondant au Muséum national d'Histoire naturelle, département Systématique et Evolution, CP 50 (Entomologie), F – 75231 Paris cedex 05 **3** Instituto Superior de Entomología “Dr. Abraham Willink” (UNT) - CONICET, Miguel Lillo 205, 4000, San Miguel de Tucumán, Tucumán, Argentina

Corresponding author: Hernán M. Beccacece (beccacecehernan@gmail.com; giclargentinis@gmail.com)

Academic editor: C. Schmidt | Received 21 November 2013 | Accepted 15 April 2014 | Published 27 June 2014

<http://zoobank.org/44B3D0A5-F01F-42AA-861F-AEAFAB173BE3>

Citation: Beccacece HM, Vincent B, Navarro FR (2014) The type-material of Arctiinae (Lepidoptera, Erebidae) described by Burmeister and Berg in the collection of the Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Buenos Aires, Argentina). In: Schmidt BC, Lafontaine JD (Eds) Contributions to the systematics of New World macro-moths V. ZooKeys 421: 65–89. doi: 10.3897/zookeys.421.6666

Abstract

Carlos G. Burmeister and Carlos Berg were among the most important and influential naturalists and zoologists in Argentina and South America and described 241 species and 34 genera of Lepidoptera. The Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN) housed some of the Lepidoptera type specimens of these authors. In this study we present a catalogue with complete information and photographs of 11 Burmeister type specimens and 10 Berg type specimens of Phaegopterina, Arctiina and Pericopina (Lepidoptera, Erebidae, Arctiinae, Arctiini) housed in the MACN. Lectotypes or holotypes were designated where primary type specimens could be recognized; in some cases we were not able to recognize types. The catalogue also proposes nomenclatural changes and new synonymies: *Opharus picturata* (Burmeister, 1878), **comb. n.**; *Opharus brunnea* Gaede, 1923: 7, **syn. n.**; *Hypocrisis jonesi* (Schaus, 1894), **syn. n.**; *Leucanopsis infucata* (Berg, 1882), **stat. rev.**; *Paracles argentina* (Berg, 1877), **sp. rev.**; *Paracles uruguayensis* (Berg, 1886), **sp. rev.**

Keywords

MACN, type specimens, Lepidoptera, Erebidae, Arctiinae, Neotropics

Introduction

Karl Hermann Konrad Burmeister or Carlos Germán Conrado Burmeister (15.I.1807–02.V.1892) and Friedrich Wilhelm Karl Berg or Carlos Berg (02.IV.1843–19.I.1902) (Fig. 1) were among the most important and influential zoologists in Argentina and were directors of the Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN).

Burmeister was born in Stralsund (Prussia, current-day Germany) and followed his studies there until 1825. He obtained his doctorate in medicine in 1829 at the University of Halle (Germany). He taught as a professor of zoology beginning in 1837. Thanks to the support of his protector Alexander von Humboldt, he made a voyage of exploration in Brazil from September 1850 to March 1852. Then he had a mission in Argentina and Uruguay from 1856 to 1860. He resigned his professorship in zoology in 1861 to become director of the MACN. With just a museum of curiosities, he contributed to make it a significant scientific institution. A fall from a ladder and broken glass of a showcase exhibit in the museum caused him serious injuries in February 8, 1892. He recommended Carlos Berg to the Government of the Republic of Argentina as his successor as Director of the MACN. Carlos Burmeister died due to his injuries May 2, 1892. Among his many publications (about 270 articles), he published his manual of entomology in 5 volumes (1832–1855) and “*Description physique de la République Argentine: d’après des observations personnelles et étrangères*” in 4 volumes (1876–1886). For the order Lepidoptera, between 1854 and 1880, he described and named over 13 genera and 119 species.

Around 1872, Professor Burmeister searched for entomologists to fill the newly created position of inspector at the MACN. He contacted in particular his German colleagues, who recommended Carlos Berg. Berg was born in Tukums (Russia, current-day Latvia). Fascinated by natural history since his childhood, he started in the trade and worked as a librarian. In 1870, he became curator of the museum of Riga (Latvia). For medical reasons, he had to leave Riga and reside in warmer climates. Around 1872, he assumed his post at MACN in June 1873 and became professor of Natural History at the National College of Buenos Aires in March 1876. In 1890, he was responsible for organizing the National Museum of Montevideo, Uruguay. In April 1892, on the recommendations of Burmeister, who was side-lined by his injury, Berg was named Director of the MACN. During the 10 years of his leadership, he reorganized all collections by making many adjustments in identifications and labelling. Much of the material studied by Berg came from his expeditions to Patagonia (1874), Cordoba and Catamarca (1875), Corrientes and Misiones (1876–1877), San Luis, Mendoza and Chile (1878–1879) as well as many trips around Buenos Aires and Uruguay. He published on entomology, other zoological groups, paleontology and botany (about 200 articles). One of the most important Lepidoptera publication was “*Lepidopteros patagónicos observados en el viaje de 1874*” (1875), also translated into German simultaneously in the Bulletin de la Societe Imperiale des Naturalistes de Moscou. Berg described and named over 21 genera and 122 species of Lepidoptera between 1875 and 1901.

Further detail about Burmeister’s and Berg’s lives can be obtained respectively in Berg (1895a, b) and Gallardo (1902).



Figure 1. Portraits of Carlos Burmeister (approximately 1885) (Left) and Carlos Berg (undated) (Right) taken from Berg (1895b) and Gallardo (1902), respectively.

Methods and materials

The types of the nominal taxa described by Burmeister and Berg and preserved in MACN have been recognized as types with the exception of some taxa that could not be identified. A number of Arctiina, Phaegopterina and Pericopina types described by Burmeister and Berg, presumed to be in MACN, are still missing and are probably lost.

Burmeister types. Each taxon represented in the Burmeister collection carries a square white label with a black frame on which the genus and/or species is underlined. Some labels have his last name abbreviated as “Burm.” or in full “Burmeister,” the country abbreviated as “R. A.” or “Rep. Arg.” [Republic of Argentina] and sometimes the city or town is stated and the initials “Nob.” [Nobis] (Fig. 2). These labels were pinned to the bottom of the box with one or two short pins at its upper and lower edge, or at the middle. The specimens were placed below this label. In some cases, the white square label was pinned to the first specimen.

Labels. A great disadvantage of the Burmeister collection is that the specimens are not labelled as types, so we had to find additional evidence to associate these specimens with the original type series.

Arrangement. The type material of Burmeister’s species are placed as follows: six species in the Burmeister collection, four species in the Berg collection and one species in both collections.

Berg types. Each taxon represented in the Berg collection carries a square white label with a black frame with the genus and another with the same form with the



Figure 2. Square labels handwritten by Burmeister. These are the main labels preceding the specimen series.



Figure 3. Square labels handwritten by Berg. These are the main labels preceding the specimen series.

species (Figure 3). These labels, like Burmeister's, were pinned to the bottom of the box with one pin at the middle of the upper and lower edge. The specimens were placed below these labels. A white label with "Berg" handwritten in pencil with the genus, the species' name, or the binominal name, is pinned to the type specimen (Figure 4).

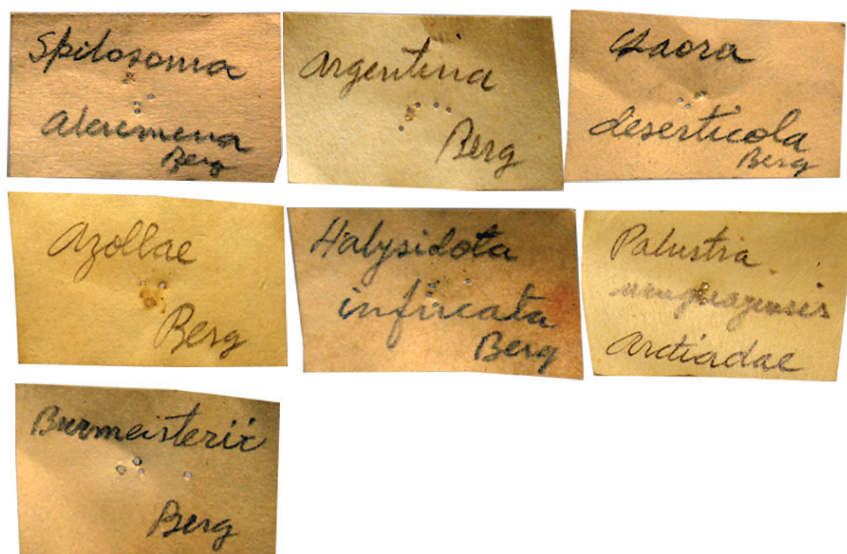


Figure 4. Labels handwritten by Berg in pencil. These labels are pinned on type specimens.

Labels. The type specimen has a label that identifies them as such; only two species are unlabelled.

Arrangement. The type material of Berg's species are placed as follows: six species in the Berg collection, one in the Burmeister collection and three species in both collections.

Burmeister's entomological collection was held in Martin-Luther-Universität, Wissenschaftsbereich Zoologie, Halle (MLUH) until he resigned his position as professor of zoology and travelled to Argentina in 1861. Since then, his collection has been kept in MACN. Burmeister described neotropical Arctiinae since 1878. Therefore, all Burmeister type specimens should be in MACN as well as those described by Berg. Berg's entomological collection is placed entirely in this institution.

When no indication of the number of specimens examined was given by Berg or Burmeister in the original description, we treated the specimens as syntypes even if only a single specimen was found. For nomenclature stability, and in order to establish the identity of several species-group names, we assign lectotypes.

Acronyms

MACN Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina.

ZMHB Zoologisches Museum, Humboldt Universität, Berlin, Germany.

USNM National Museum of Natural History, formerly United States National Museum, Washington DC, United States of America.

Results

There are some square labels handwritten by Burmeister that include the last name of Karl Berg as, for instance, the description of *Antarctia multifarior* (Burmeister, 1878) (Fig. 5). Moreover, on the square label handwritten by Burmeister of *Halesidota* (sic) *picturata* (Burmeister, 1878) the abbreviation of both authors' last names appears as "Bg." [Berg] and "Burm." [Burmeister]. In the original description, the genus and specific names are followed by Berg (as in the author's description) but there are no other previous publications, so the specific name is assigned by Burmeister. The same problem occurs with *Ecpantheria anomala* (Burmeister, 1883); on the label handwritten by Burmeister, the abbreviation "Kk." [Kinkelin] appears as well as the original description (Fig. 5). Possibly, he placed the name in honor of the collector. In his publication, Burmeister indicated the author and year of the original description below the genus and specific name only if he included a redescription.

Catalogue of type specimens. All species of the subtribes Phaegopterina, Arctiina and Pericopina (Arctiinae) described by Burmeister and Berg found in MACN are listed below in the systematic order of the catalogue of the neotropical Arctiinae (Watson and Goodger 1986). For each taxon, the following entries are given:

Original combination. The taxon appears in the text of the original description.

Current identity. The currently accepted classification of the taxon before this article.

Material. The status of the specimen type (syntype or holotype), the sex, and the number of type specimen as stated in the original description. The potential interpretations of the original description are in brackets as well as additional information.

Type locality. Since there were syntypes from more than one locality, it is important to state clearly what the lectotype locality is, based on information in the original description and on the type labels.

MACN. The number of type specimens, sex (if recognizable), type status and condition of the specimens found in MACN; the text of the labels is in italics and between quotation marks. The interpretations of the text of some labels are between brackets; additional information is between parentheses.

Remarks. Discussions on specimen type or other specimens and on the proposed recombination are provided.

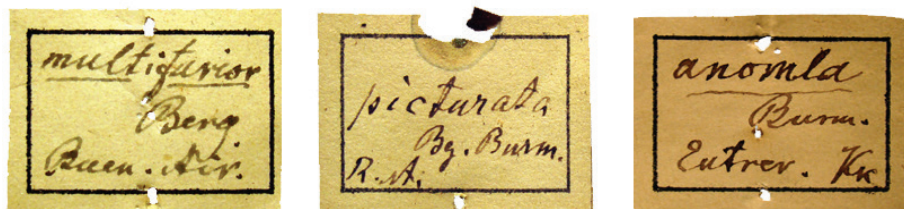


Figure 5. Labels handwritten by Burmeister with other authors' names. These are the main labels preceding the specimen series.

Arctiinae, Arctiini, Phaegopterina

Halesidota picturata Burmeister, 1878: 442

Fig. 6

Current identity. *Phaegoptera picturata* (Burmeister, 1878).

Material. Described based on two female syntypes. A female from Las Conchas (Buenos Aires, Argentina) collected by M. Ruscheweyh; a female reared by Berg from a caterpillar found in “Bande Orientale de l’Uruguay” [Republic of Uruguay].

Type locality. “Bande Orientale de l’Uruguay” [Republic of Uruguay].

MACN. A female syntype housed in the Berg collection with a white label with the inscription “Typus,” a green label with the inscription “Banda Oriental” and another red label with the inscription “Lectotype ♀ *Halesidota picturata* Burmeister assigned by Beccacece, Vincent & Navarro.” We hereby designate it as lectotype [MACN]. It is in moderate to poor condition; the abdomen and distal half of the left antenna are missing (Fig. 6).

Remarks. The other female specimen from Las Conchas was not found in the MACN. A male specimen labelled “Cumtypo/comparat.” and “Banda Oriental” is associated with the female lectotype. It possibly corresponds to the same taxon, but it was incorrectly labelled cotype as it was not mentioned in the original description. The female lectotype presents the same habitus as *Opharus brunnea* Gaede, 1923. This taxon was described from a female holotype from the State of Rio Grande do Sul (Brazil), housed in the ZMHB. The proximity of type localities, associated with a similar habitus, particularly in the ornamentation of the forewings, justifies the synonymy of the two taxa. However, the placement of the taxon *picturata* in the genus *Opharus* Walker, 1855 seems more consistent than its current placement in the genus *Phaegoptera* Herrich-Schäffer, [1853]. We therefore propose the following new combination and synonymy.

Opharus picturata (Burmeister, 1878), **comb. n.** = *Opharus brunnea* Gaede, 1923: 7, **syn. n.**

Halesidota cancellata Burmeister, 1878: 445

Fig. 7

Current identity. *Tessellota cancellata* (Burmeister, 1878).

Material. Described from an unspecified number of syntypes from Buénos-Ayres [Buenos Aires].

Type locality. Buénos-Ayres [Buenos Aires].

MACN. A female syntype housed in the Berg collection with a green label with the inscription “Buenos Aires” and a red label with the inscription “Lectotype ♀

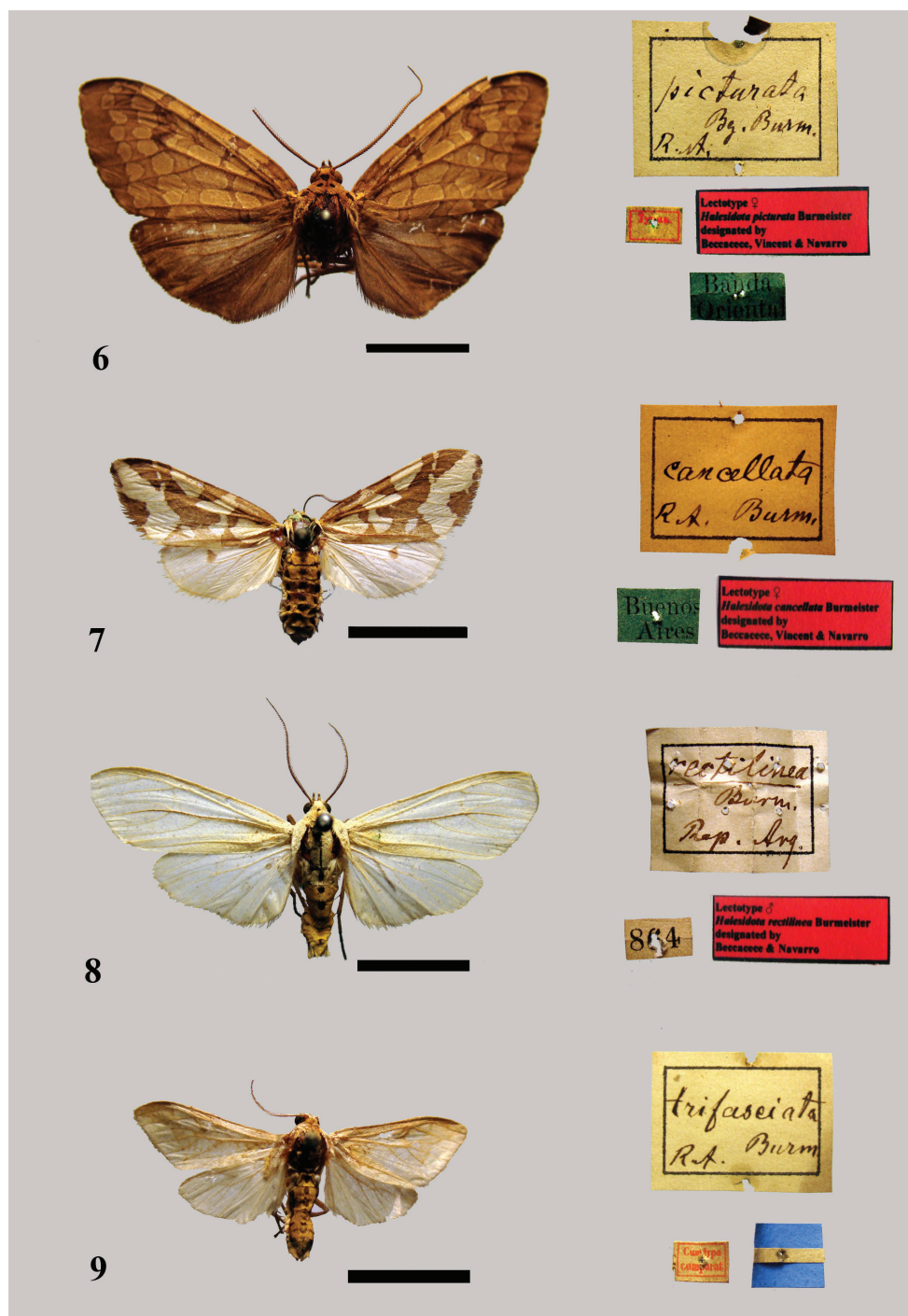


Figure 6–9. 6 Lectotype female *Halesidota picturata* Burmeister 7 Lectotype female *Halesidota cancellata* Burmeister 8 Lectotype male *Halesidota rectilinea* Burmeister 9 Possible holotype specimen of *Halesidota trifasciata* Burmeister.

Halesidota cancellata Burmeister designated by Beccacece, Vincent & Navarro.” We hereby designate it as lectotype [MACN]. It is in quite good overall condition, although it is missing the left antenna (Fig. 7). There are two paralectotypes: a male: “Buenos Arres” [Buenos Aires], which is in moderate to good condition; a male: “Buenos Aires” in moderate to poor condition with no antennae, the apices of both forewings are missing and the right hindwing is ripped.

Remarks. There is no distinctive label indicating that these specimens are syntypes. However, the origin of these specimens located in Buenos Aires and their inclusion in the Berg collection, below a square label with Burmeister’s handwriting, leads us to believe that these specimens are syntypes that were studied by Burmeister. Indeed, it seems that Berg and Burmeister frequently exchanged specimens (Roig, pers. comm.). In addition, wing spans indicated in the original description (1–1.2 inches) correspond to the specimens that we consider syntypes.

Halesidota rectilinea Burmeister, 1878: 445

Fig. 8

Current identity. *Biturix rectilinea* (Burmeister, 1878).

Material. Described from an unspecified number of specimens from the interior of the Republic [of Argentina].

Type locality. Interior of the Republic [of Argentina].

MACN. A male syntype included in the Burmeister collection with a square label “*rectilinea* Burm[eister] Rep[ublic] Arg[entina]” (handwritten by Burmeister), a white label with the inscription “864” and a red label with the inscription “Lectotype ♂ *Halesidota rectilinea* designated by Beccacece & Navarro” (Beccacece & Navarro, in press) [MACN]. It is in quite good conditions (Fig. 8).

Remarks. The label with “864” printed on it is the catalogue number in the database of the MACN.

Halesidota trifasciata Burmeister, 1878: 446

Fig. 9

Current combination. *Tessellota trifasciata trifasciata* (Burmeister, 1878).

Material. Described from a single male from Buénos-Ayres [Buenos Aires].

Type locality. Buénos-Ayres [Buenos Aires].

MACN. In the Berg collection there is a male specimen with a label “Cumtypo/ comparat.” and another label representing the flag of Argentina without any indication. It could be the holotype specimen; it is in moderate to good conditions with the right antenna missing (Fig. 9).

Remarks. The specimen is associated with a label “*trifasciata* Burm[eister] R[epublic] A[rgentina]” (handwritten by Burmeister).

***Halesidota fuscipennis* Burmeister, 1878: 441**

Fig. 10

= *Hypocrisias jonesi* (Schaus, 1894): 230 (*Phaegoptera*) **syn. n.**

Current identity. *Hypocrisias fuscipennis* (Burmeister, 1878).

Material. Described from an unspecified number of specimens from Buénos-Ayres [Buenos Aires].

Type locality. Buénos-Ayres [Buenos Aires].

MACN. A male syntype included in the Burmeister collection with a green label with the inscription “Buenos Aires” and a red label with the inscription “Lectotype ♂ *Halesidota fuscipennis* Burmeister designated by Beccacece, Vincent & Navarro.” We hereby designate it as lectotype. [MACN]. It is in quite good conditions (Fig. 10). There are two paralectotypes: a male without labels in moderate to good conditions; a male with a green label with the inscription “Buenos Aires,” in moderate to poor condition, with no antennae, the apices of both forewings are missing and the right hindwing is ripped.

Remarks. The lectotype has a similar habitus to *Hypocrisias jonesi* (Schaus, 1894). This taxon was described from an unspecified number of specimens from Castro, Parana (Brazil). A male specimen, housed in USNM, was designated lectotype by Watson (1971). Comparison of the male genitalia of the lectotype dissected by Watson (1971) with the male genitalia from Buenos Aires and the nearby habitus justifies the synonymy of the two taxa. We therefore propose the synonymy given above.

***Halysidota infucata* Berg, 1882: 216**

Fig. 11

Current identity. *Leucanopsis infucata* (Berg, 1882), a junior subjective synonym of *Leucanopsis leucanina* (Felder & Rogenhofer, 1874).

Material. Described from a single male from “Territorios de las Misiones” (Province of Misiones, Argentina).

Type locality. “Territorios de las Misiones” (Province of Misiones, Argentina).

MACN. In the Berg collection there is a male specimen with a blue label “Misiones” / a red label with the inscription “TYPUS,” a white label with the inscription “Typus,” a white label with the inscription “*Halysidota infucata* Berg” (handwritten by Berg). This specimen is therefore the holotype. It is in rather poor conditions with no abdomen and the apices of the forewings are missing (Fig. 11).

Remarks. This species was synonymized with *Leucanopsis leucanina* from Colombia (Felder and Rogenhofer 1874) by Hampson (1901: 166). Based on the analysis of habitus and the type locality of both taxa, we conclude that these species are different and therefore we propose the following recombination: *Leucanopsis infucata* (Berg, 1882), **stat. rev.**

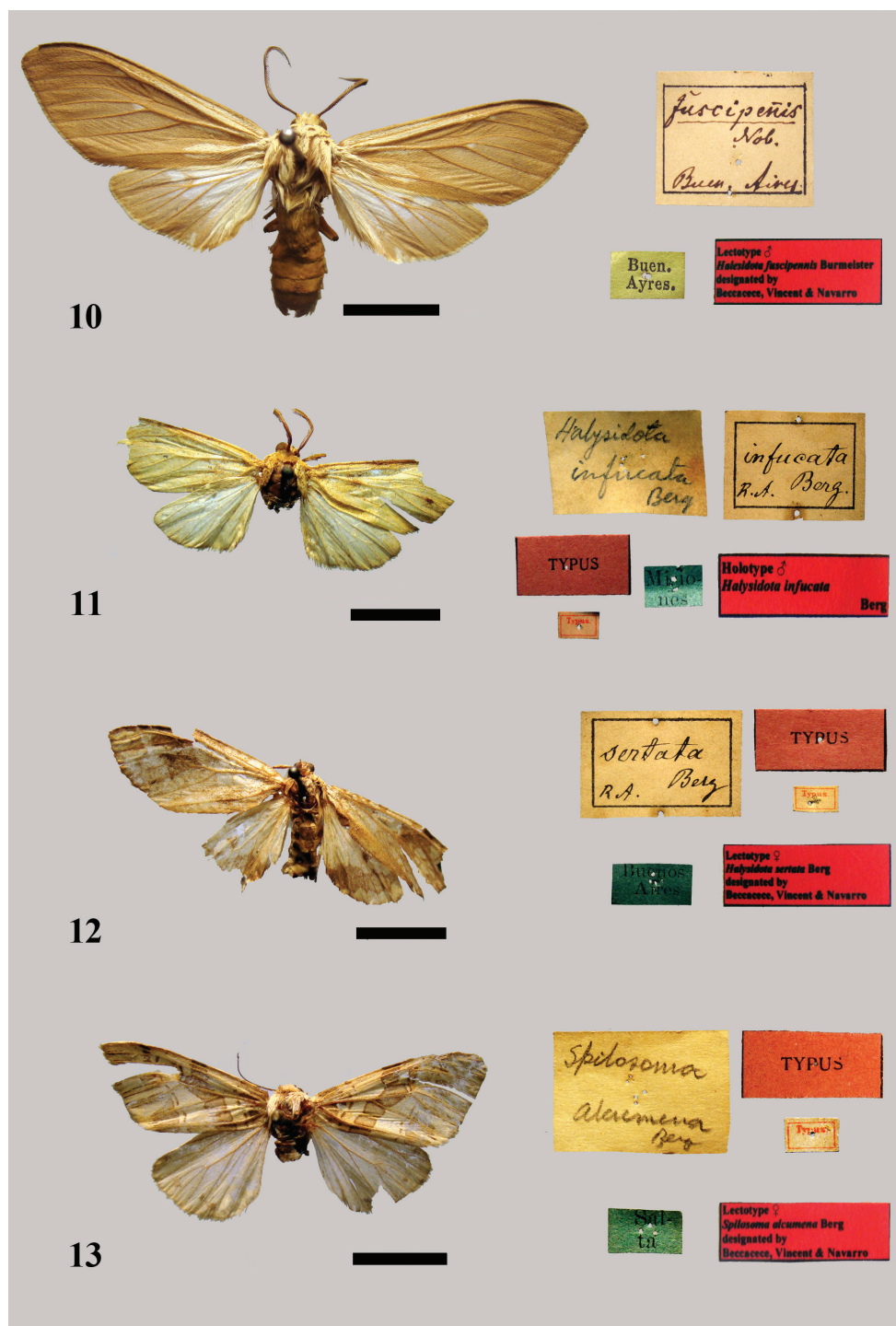


Figure 10–13. 10 Lectotype male *Halesidota fuscipennis* Burmeister 11 Holotype male *Halysidota infucata* Berg 12 Lectotype female *Halysidota sertata* Berg 13 Lectotype female *Spilosoma alcumena* Berg.

***Halysidota sertata* Berg, 1882: 214**

Fig. 12

Current identity. *Tessella sertata* (Berg, 1882).**Material.** Described from one male and one female from “los alrededores [surroundings] de Buenos Aires.”**Type locality.** Buenos Aires [Argentina].**MACN.** A female syntype in the Berg collection with a green label with the inscription “Buenos Aires,” a red label with the inscription “TYPUS,” a white label with the inscription “Typus” and a red label with the inscription “Lectotype ♀ *Halysidota sertata* Berg designated by Beccacece, Vincent & Navarro.” We hereby designate it as lectotype. [MACN]. It is in very poor condition, with no antennae, both wings are damaged and the right wings are folded backwards (Fig. 12).**Remarks.** Berg stated that the male specimen is preserved in the collection of M. Ruscheweyh. In Horn et al. (1990), a part of this collection may be in ZMHB. After verification by the second author, no corresponding specimen was located in this institution.**Arctiinae, Arctiini, Arctiina*****Spilosoma alcumena* Berg, 1882: 213**

Fig. 13

Current identity. *Isia alcumena alcumena* (Berg, 1882).**Material.** Described on the basis of a male specimen from Tucumán (City of San Miguel de Tucumán, Argentina) and a female specimen from Salta (City or province of Salta, Argentina).**Type locality.** Salta [Argentina].**MACN.** A female syntype housed in the Berg collection with a blue label with the inscription “Salta,” a red label with the inscription “TYPUS,” a white label with the inscription “Typus,” a white label that reads “*Spilosoma alcumena* Berg” (handwritten by Berg), and red label with the inscription “Lectotype ♀ *Spilosoma alcumena* Berg designated by Beccacece, Vincent & Navarro.” It is in bad condition, but it is recognizable: the abdomen and right antenna are missing and both forewing apices and the right hindwing are damaged (Fig. 13). The male, here designated as a paralectotype, bears a blue label with the inscription “Tucuman,” a white label with the inscription “Typus,” a white label with the number “11948” and a white label that reads “*Spilosoma Alcumena* Bov Berg” (handwritten by Berg). It is in moderate to good condition: it is missing the right antenna, the left antenna is broken and left hindwing is ripped.**Remarks.** Berg indicated that the male syntype was preserved in Gunther’s collection and the female syntype was in “la Universidad” [MACN], donated by himself. The male paralectotype was also deposited in the MACN.

***Ecpantheria kinkelini* Burmeister, 1879: 59**

Fig. 14

Current identity. *Hypercompe kinkelini* (Burmeister, 1879).

Material. Described on the basis of an unspecified number of male and female specimens from Palermo, near Buénos-Ayres [Buenos Aires].

Type locality. Palermo, Buénos-Ayres [Buenos Aires, Argentina].

MACN. In the Burmeister collection there are two specimens that apparently belong to the type-series: a male specimen with no label pinned on it; it is in good condition; a female specimen with a green label with the inscription “Buen[os] Aires,” which is in quite good condition (Fig. 14). The habitus and scale of the two specimens correspond to the original description and they are associated with a square label on the box that reads “Kinkelini Burm[eister] Buen[os] Air[es].” Therefore, we assume they are syntypes. We hereby designate the female specimen as lectotype in [MACN] with a red label with the inscription “Lectotype ♀ *Ecpantheria kinkelini* Burmeister designated by Beccacece, Vincent & Navarro.” The male specimen is designated as a paralectotype.

Remarks. The specific name is in honor of Kinkelin (collector of both specimens).

***Ecpantheria anomala* Burmeister, 1883: 40**

Fig. 15

Current identity. *Hypercompe anomala* (Burmeister, 1883).

Material. Described on the basis of an unspecified number of male specimens from Entre Ríos [province] (Argentina).

Type locality. Entre Ríos [province] [Argentina].

MACN. In the Burmeister collection there is a male specimen with no label pinned on it, but it is associated with a square label in the box that reads “anom[a]la / Burm[eister] / Entrer [Entre Ríos] / Kk [Kinkelin]” (handwritten by Burmeister) and a red label with the inscription “Lectotype ♂ *Ecpantheria anomala* Burmeister designated by Beccacece, Vincent & Navarro.” It presents the habitus and size that match Burmeister's description that feature in the original description. Therefore, we assume that it is a syntype. We hereby designated it as lectotype [MACN]. It is in good condition, with only the right antenna broken (Fig. 15).

***Antarctia severa* Berg, 1875a: 209**

Fig. 16

Current identity. *Paracles severa* (Berg, 1875a).

Material. Described from an unspecified number of specimens from Patagonia (Argentina).

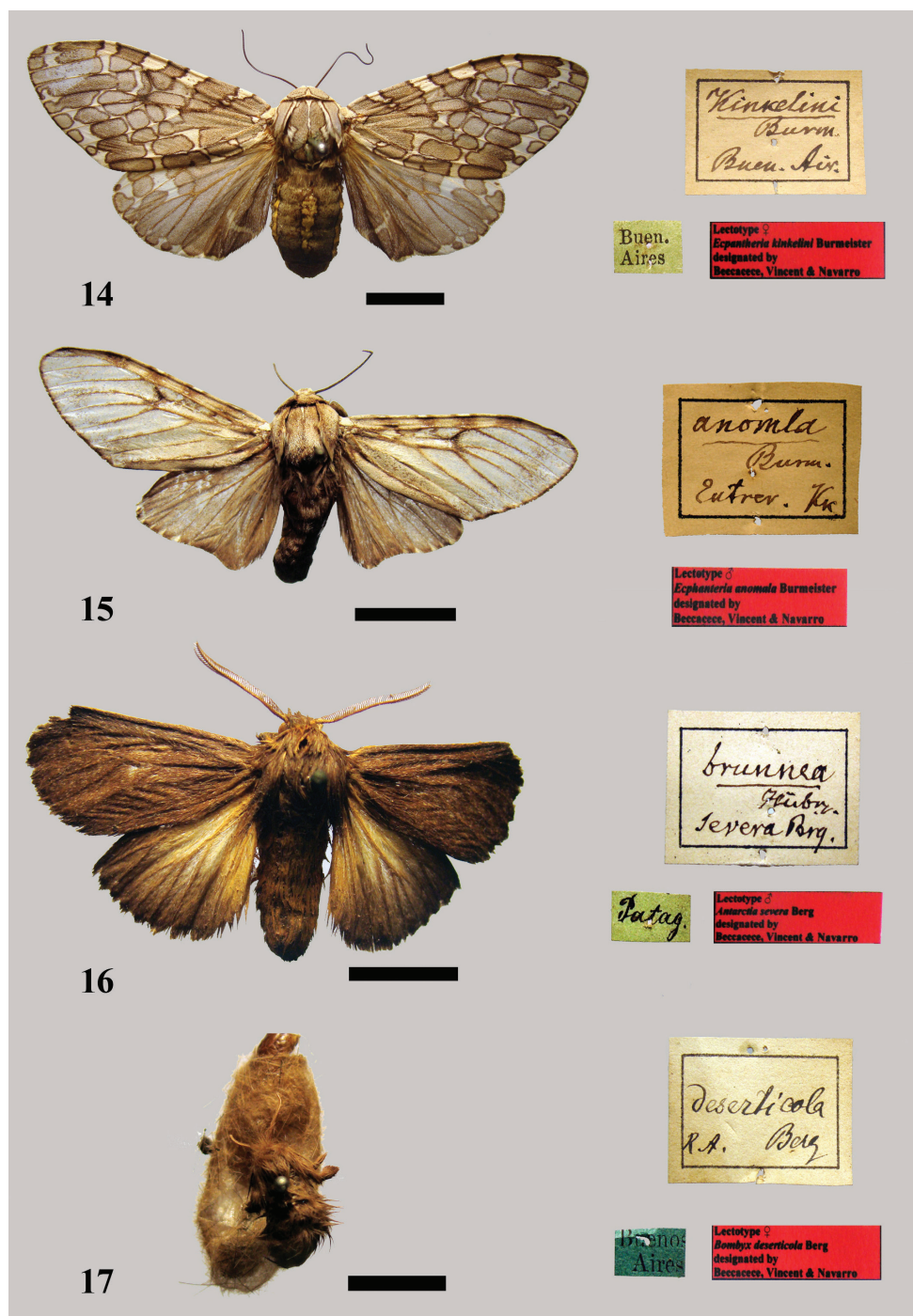


Figure 14–17. 14 Lectotype female *Ecpantheria kinkelini* Burmeister 15 Lectotype male *Ecpantheria anomala* Burmeister 16 Lectotype male *Antarctia severa* Berg 17 Lectotype female *Bombyx deserticola* Berg.

Type locality. Rio Santa Cruz [Santa Cruz province, Argentina]. See Remarks.

MACN. A male syntype included in the Burmeister collection with a green label with the inscription “Patag[onia]” and a red label with the inscription “Lectotype ♂ *Antarctia severa* Berg designated by Beccacece, Vincent & Navarro.” We hereby designate it as lectotype [MACN]. It is in quite good condition, although both tips of the antennae are broken (Fig. 16). We designate one paralectotype, a female specimen with a green label with the inscription “Patag[onia].” It is in moderate to good condition with no antennae, a torn inner base of the left hindwing and a small piece missing from the termen of the right hindwing.

Remarks. Burmeister (1878) indicated the collecting locality of the type specimens more precisely: “Berg discovered this species from Rio Santa Cruz in South Patagonia.”

***Bombyx deserticola* Berg, 1875a: 212**

Fig. 17

Current identity. *Paracles deserticola* (Berg, 1875a).

Material. Described from an unspecified number of female (wingless) specimens from the outfall of the Rio Negro (south of Buenos Aires province).

Type locality. outfall of the Rio Negro [south of Buenos Aires province, Argentina].

MACN. A wingless female syntype included in the Berg collection with a blue label with the inscription “Buenos Aires” and a red label with the inscription “Lectotype ♀ *Bombyx deserticola* Berg designated by Beccacece, Vincent & Navarro.” We hereby designate it as lectotype [MACN]. It is in very poor condition, missing the apical part of the left antenna and a pinned cocoon (Fig. 17). There are two possible paralectotypes: a wingless female with a data label reading “Buenos Aires;” it is almost totally damaged and externally unrecognizable; a wingless female with a data label reading “Buenos Aires,” “Cum typo/Comparat,” which is in moderate to good condition with no antennae. None of these specimens is labelled as a type, which is usual for Berg’s type material. In addition, in the Burmeister collection there are three female specimens: a wingless female with a data label reading “Córdoba” [Córdoba], which is in quite good conditions, but the location does not match the location of the type locality; a wingless female with a data label reading “Buen. Ayres.” [*Buenos aires*], which is in quite good conditions, with short antennae; the labelling is by Burmeister; a wingless female with no data label and another label reading “168,” which is in quite good condition and its habitus matches the species description. It is possibly one of the syntypes.

Remarks. Berg (1875a) described *Bombyx deserticola* in German, but without all the information; in a Spanish publication “Lepidópteros Patagónicos observados en el viage de 1874” (The Patagonian Lepidoptera observed in the voyage of 1874) Berg (1875b) indicated that only a female collected from Patagonia and another unspecified number from Buenos Aires were described as *Bombyx deserticola*. Moreover, in the

Spanish publication there is a note in the index in which Berg proposes this species as in genus *Trichosoma* Ramb[ur]. (*Ocnogyna* Led[erer].). In addition, in the Berg collection there are three male specimens: a male with labels reading “Typus,” “TYPUS,” “Buenos Aires,” “*Laora deserticola* Berg” (handwritten by Berg). It is in moderate condition with the distal half of the right antenna broken; a male specimen with labels reading “Cumtypo/comparat.” and “Buenos Aires,” which is in good condition; a male labelled “Cumtypo/comparat.” “Buenos Aires,” which is in poor condition with no abdomen and the distal of the right antenna broken. These three male specimens cannot be paralectotypes because the description is based only on wingless females.

***Palustra azollae* Berg, 1877a: 258**

Fig. 18

Current identity. *Paracles azollae* (Berg, 1877).

Material. Described from a male specimen from Tigre (north of Buenos Aires), 15 specimens from the south of Buenos Aires, and an unspecified number of specimens from the Riachuelo channels, close to the mouth of the Rio de la Plata. All the specimens were reared from caterpillars.

Type locality. Buenos Aires [Argentina].

MACN. a male syntype included in the Berg collection with a blue label with the inscription “Buenos Aires,” a red label with the inscription “TYPUS,” a white label with the inscription “Typus” and a red label with the inscription “Lectotype ♂ *Palustra azollae* Berg designated by Beccacece, Vincent & Navarro.” We hereby designate it as lectotype [MACN]. It is in moderate condition, missing the apical half of the right antenna (Fig. 18). We designate two paralectotypes: (1) a male with red label with the inscription “TYPUS,” a blue label with the inscription “Buenos Aires” and a white label “*azollae* Berg” (handwritten by Berg), which is in quite good condition; (2) a female specimen with a blue label with the inscription “Buenos Aires,” a red label with the inscription “TYPUS” and a white label with the inscription “Typus.” It is in moderate to poor condition, missing the right forewing and the right hindwing is damaged.

Remarks. In the Burmeister collection there are six specimens: a male specimen with a label “Buen. Ayres” [Buenos Aires], which is in quite good condition; a male without labels, which is in quite good condition, although the right antenna is missing; a male without labels, which is in moderate condition: the antennae are missing; a female with a label “Buen. Ayres” [Buenos Aires], which is in moderate condition because the abdomen is missing; a female without labels in good condition; a female without labels in good condition. These labelled specimens are not syntypes because they are labelled in Burmeister’s manner. On the other hand, we cannot confirm whether or not the other unlabelled specimens are types.

Paracles azollae Berg, 1877a was redescribed under the same name as new by Berg (1877b: 191).

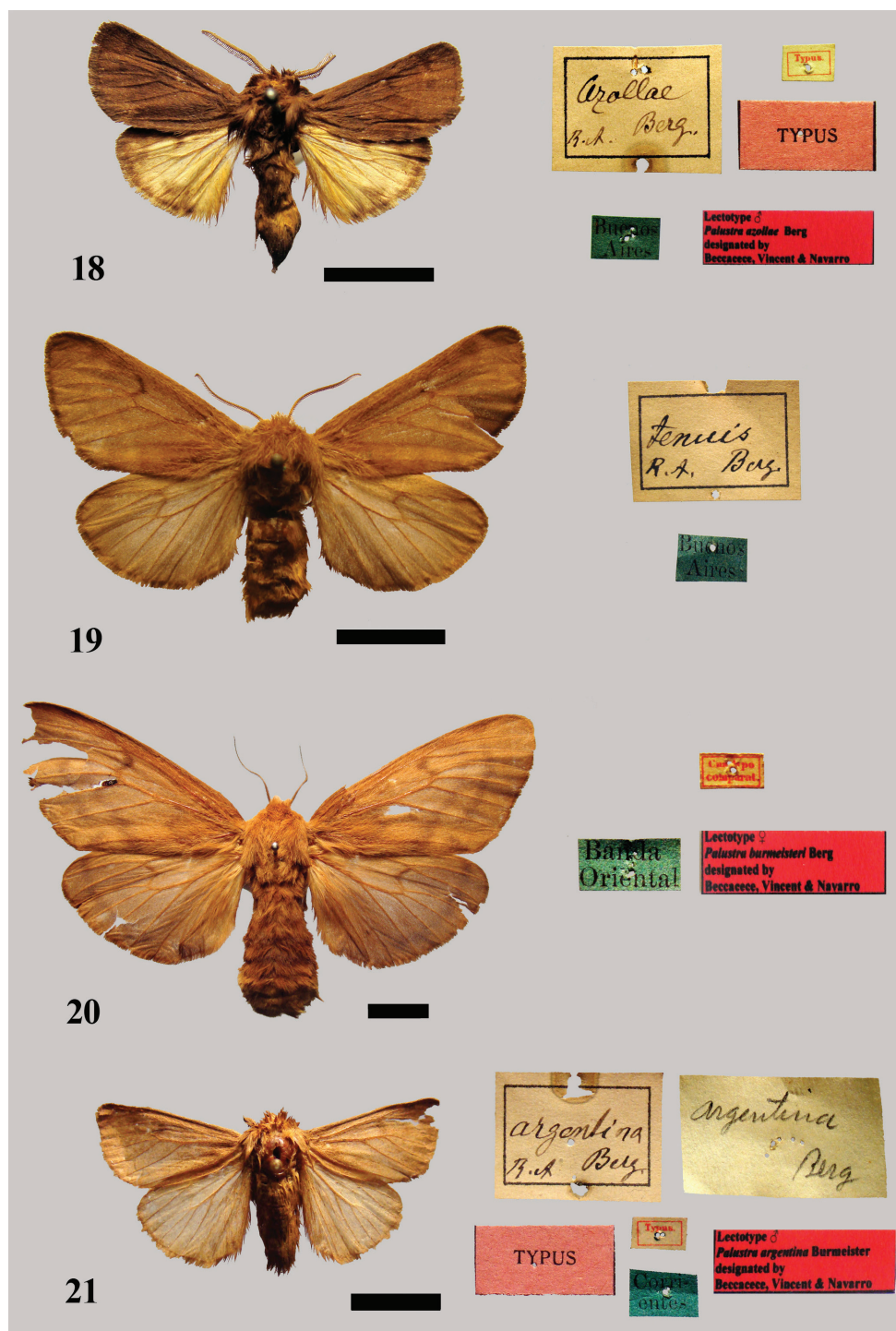


Figure 18–21. 18 Lectotype male *Palustra azollae* Berg 19 Possible syntype female of *Palustra tenuis* 20 Lectotype female *Palustra burmeisteri* Berg 21 Lectotype male *Palustra argentina* Berg.

***Palustra tenuis* Berg, 1877a: 259**

Fig. 19

Current identity. *Paracles tenuis tenuis* (Berg, 1877).**Material.** Described from a male and two females from Boca de Riachuelo [outfall of Riachuelo] near Buenos Ayres [Buenos Aires].**Type locality.** outfall of Riachuelo, near Buenos Ayres [Buenos Aires, Argentina].**MACN.** In the Berg collection there is a female specimen with a data label reading “Buenos Aires;” it is in quite good condition, although the right forewing is ripped (Fig. 19). This specimen is not labelled as type, as Berg’s type material usually is, however, it could be one of the female syntypes.**Remarks.** In the Burmeister collection there are three specimens labelled as *Palustra tenuis* Berg: a male specimen with a label “Buen. Ayres” [Buenos Aires], which is in quite good condition, although it has no antennae; a female specimen with no data label, a small piece missing at the right apex of the forewing as well as the left antenna; a female specimen with the data label “Buen. Ayres” [Buenos Aires], which is in quite good conditions, although a small piece is missing at the right apex of the forewing and the left hindwing is ripped. These specimens are not likely to be syntypes because they are not labelled in Berg’s manner. The aged condition and the decolored pattern of the possible female lectotype in the Berg collection could be confused with the female of *P. azollae* (Berg).*Palustra tenuis* Berg, 1877a was redescribed under the same name as new by Berg (1877b: 191).***Palustra burmeisteri* Berg, 1877c: 228**

Fig. 20

Current identity. *Paracles burmeisteri* (Berg, 1877).**Material.** Described from a female and a male (atrophied) specimen obtained after rearing caterpillars from the “Banda Oriental” [Eastern Band of Uruguay].**Type locality.** Banda Oriental [Eastern Band, Republic of Uruguay].**MACN.** In the Berg collection there are two specimens from the type locality: a female specimen with data labels reading “Cumtipo/comparat.,” “Banda Oriental.” It is in moderate to good conditions with the apex of the left forewing torn (Fig. 20). Its habitus is exactly like figure 1 in the original description. We hereby designate it as lectotype [MACN]. This female is labelled with a red label with the inscription “Lectotype ♀ *Palustra burmeisteri* Berg designated by Beccacece, Vincent & Navarro;” a male specimen with data labels reading “Banda oriental,” “*burmeisteri* Berg” (handwritten), in moderate to good conditions with no antennae nor right wing. This specimen does not bear a label of type. In the Burmeister collection there are two male and two female specimens without labels. There are only two labels in the box: “*burmeisteri* Berg, Rep.

Urug [Republic of Uruguay]" and "*Palustra* Don. [donated by] Berg." One of the male specimens is clearly atrophied. We assume that it is the other syntype (the atrophied male), we hereby designate it as a paralectotype.

Remarks. In the Berg collection the female specimen is in moderate to good condition, although it is missing a considerable portion of the apex of the right forewing and left hindwing, and bears no labels. The other male and two females in the Burmeister collection are not syntypes.

Palustra burmeisteri Berg, 1877c was redescribed under the same name as new by Berg (1878: 224).

***Palustra argentina* Berg, 1877c: 233**

Fig. 21

Current identity. *Paracles argentina* (Berg, 1877). It is a junior subjective synonym of *Paracles laboulbeni* (Bar, 1873).

Material. Described on the basis of six specimens from Corrientes (province of Corrientes, Argentina).

Type locality. Corrientes [province of Corrientes, Argentina].

MACN. a male syntype included in the Berg collection with a blue label with the inscription "Corrientes," a red label with the inscription "TYPUS," a white label with the inscription "Typus" and a white label with "*argentina* Berg" (handwritten by Berg), and a red label with the inscription "Lectotype ♂ *Palustra argentina* Berg designated by Beccacece, Vincent & Navarro." We hereby designate it as lectotype [MACN]. It is in moderate to good conditions, although it has no antennae and the apex of the right forewing is torn (Fig. 21). From the Burmeister collection we designate two paralectotypes: a male specimen with a blue label printed "Corrientes" and a white label with the inscription "Typus;" a female specimen with a blue label with the inscription "Corrientes" and a white label with the inscription "Typus." Both specimens are in moderate to good overall condition, although rather worn.

Remarks. In the Berg collection, there is a female specimen with a blue label with the inscription "Misiones," a red label with the inscription "TYPUS" and a white label with the inscription "Typus." It is in bad condition as it is missing the abdomen and the right antenna and the apices of both wings are damaged; according to the locality data, this specimen was incorrectly labelled as a type. *Paracles argentina* (Berg, 1877) was synonymized with *Paracles laboulbeni* (Bar, 1873) by Hampson (1901: 512). This latter species is from French Guiana and is characterized by the forewings having three transverse bands with little contrast. This feature is absent in the lectotype of *Paracles argentina*, so we revise the status of this species: *Paracles argentina* (Berg, 1877), **sp. rev.**

Palustra argentina Berg, 1877c was redescribed under the same name as new by Berg (1878: 227).

***Antarctia persimilis* Burmeister, 1878: 452**

Fig. 22

Current identity. *Paracles persimilis* (Burmeister, 1878).

Material. Described on the basis of a male and a female specimen from Rio de Janeiro (Brazil).

Type locality. Rio de Janeiro, Brasil.

MACN. In the Burmeister collection there is a single female specimen with no label pinned on it (Fig. 22). The only label associated with the specimen is the square white label with “*persimilis* Burm[eister] Brasil.” (Burmeister’s handwriting) and a red label with the inscription “Lectotype ♀ *Antarctia persimilis* Burmeister designated by Beccacece, Vincent & Navarro.” It is inferred that the female specimen belongs to the original type series and we hereby designate it as lectotype [MACN]. It is in good overall condition.

Remarks. The male syntype was not located.

***Antarctia multifarior* Burmeister, 1878: 452**

Fig. 23

Current identity. *Paracles multifarior* (Burmeister, 1878), a junior subjective synonym of *Paracles fusca* (Walker, 1856).

Material. Described on the basis of an unspecified number of specimens from Buénos-Ayres [Buenos Aires].

Type locality. Buénos-Ayres [Buenos Aires, Argentina].

MACN. In the Burmeister collection there are two male specimens with no label pinned on them. They are in quite good condition and have little information on the square label: “*multifarior* Berg Buen[os] Air[es]” (Burmeister’s handwriting) (Fig. 23). We hereby designate the first male specimen as lectotype in [MACN] with a red label with the inscription “Lectotype ♂ *Anctartia multifarior* Burmeister designated by Beccacece, Vincent & Navarro.” The other specimen is designated as a paralectotype.

Remarks. There is a female of *Paracles azollae* (Berg, 1877) incorrectly placed in the series below the main label.

***Antarctia costata* Burmeister, 1878: 451**

Fig. 24

Current identity. *Paracles costata* (Burmeister, 1878), senior synonym of *Paracles bergi* (Schaus, 1896).

Material. Described on the basis of a single specimen from Rio de Janeiro (Brazil).

Type locality. Rio de Janeiro [Brazil].

MACN. In the Burmeister collection there is a male specimen with a green label with the inscription “Rio d[e] Jan[eiro];” it is in moderate to good condition, but miss-

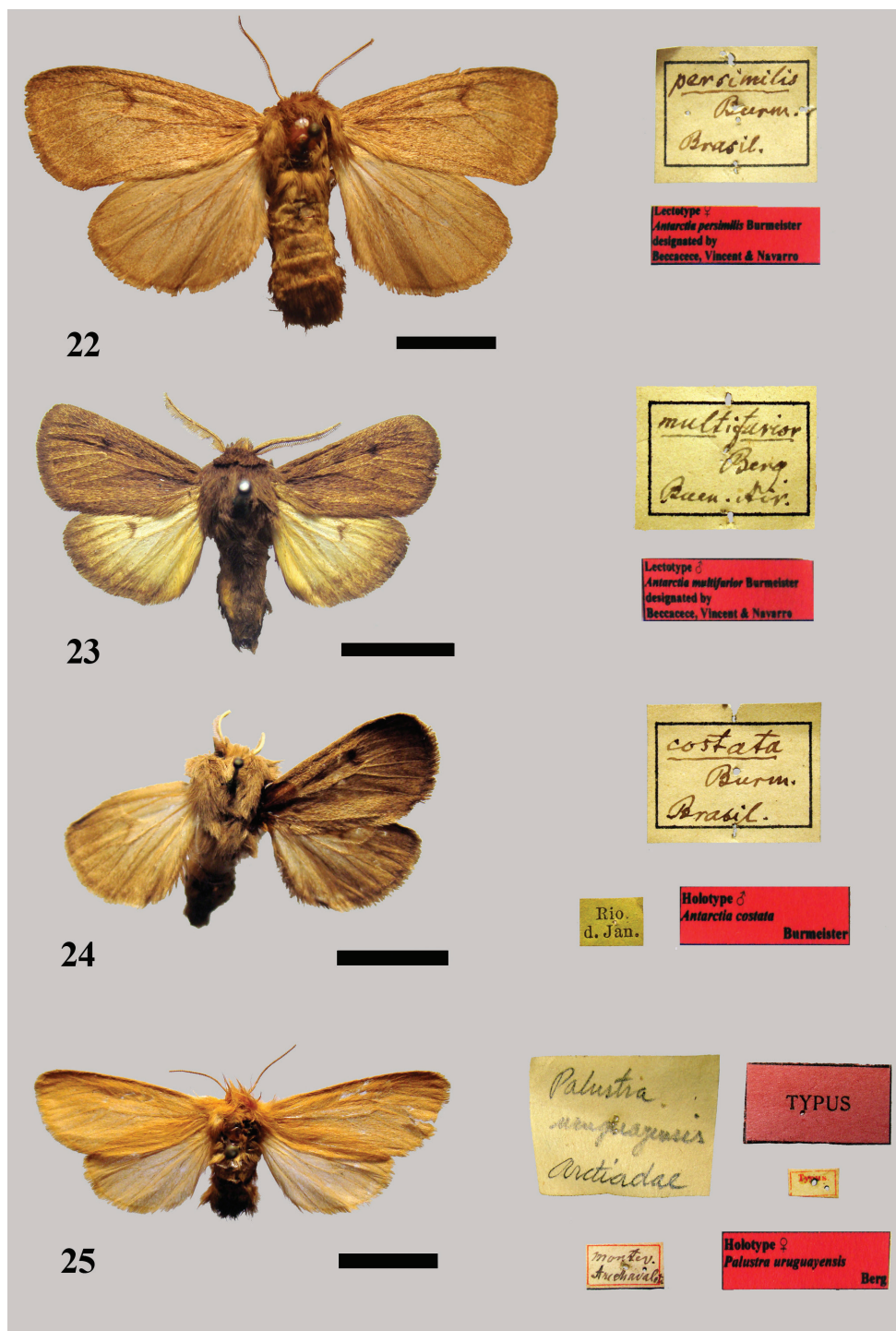


Figure 22–25. 22 Lectotype female *Antarctia persimilis* Burmeister 23 Lectotype male *Anarctia multiflorior* Burmeister 24 Holotype male *Anarctia costata* Burmeister 25 Holotype female *Palustria uruguayensis* Berg.

ing the left forewing (Fig. 24). Its habitus matches the original description and for this reason we believe that this specimen is the holotype. We label it with a white label with the inscription “Holotype ♂ *Antarctia costata* Burmeister.”

***Palustra uruguayensis* Berg, 1886: 212**

Fig. 25

Current identity. *Paracles uruguayensis* (Berg, 1886) is a junior synonym of *Paracles vulpina* (Hübner, [1825]).

Material. Described on the basis of a single female specimen from Respublica uruguayensis [Republic of Uruguay] Montevideo (Uruguay).

Type locality. Montevideo [Uruguay].

MACN. In the Berg collection there is a female specimen with a white label which reads “Montev[ideo] Arechavaleta col,” a red label with the inscription “TYPUS,” a white label with the inscription “Typus,” a white label that reads “*Palustra uruguayensis* arctiadae” (handwritten by Berg) and a red label with the inscription “Holotype ♀ *Palustra uruguayensis* Berg.” According to the original description, this female is the holotype. We labelled it and herewith recognize it as the holotype [MACN]. It is in good overall condition (Fig. 25).

Remarks. This species was synonymized with *Paracles vulpina* (Hübner, [1825]) by Hampson (1901: 448). Superficially, the figures of *A. vulpina* Hübner and the holotype of *P. uruguayensis* Berg have quite different appearances. The head and thorax of the male *A. vulpina* are bright red brown, the axis of the antenna is white; the abdomen has an orange dorsum. The forewing is bright red brown, the costal edge is yellowish white, and the cilia are white at the tips. The hindwings are white, the base of the inner area has some orange hair, the costa and veins towards the apex are brownish. The forewing of the female has a slightly paler costa, and the cilia are not white at the tips. The hindwing is pale brown (Hampson, 1901). The holotype female of *P. uruguayensis* Berg has a pale grey-yellow color pattern. The species is similar to *Paracles laboulbeni* (Bar, 1873). Therefore, we propose the two taxa are valid species with the following recombination: *Paracles uruguayensis* (Berg, 1886), **sp. rev.**

Arctiinae, Arctiini, Pericopina

***Eucharia centenaria* Burmeister, 1878: 436**

Fig. 26

Current identity. *Dysschema centenaria centenaria* (Burmeister, 1878).

Material. Described from a single male from Zárate (Province of Buenos Aires, Argentina).



Figure 26. Holotype male *Eucharha centenaria* Burmeister.

Type locality. Zárate [Province of Buenos Aires, Argentina].

MACN. In the Berg collection there is a male specimen with the following labels: “Cumtypo/comparat.” and “Zarate Kink[elin].” It could be the male holotype; it is in quite good overall condition (Fig. 13).

Remarks. In the original description Burmeister stated that the taxon was discovered and named by M. Kinkelin. We have not found a publication of Kinkelin describing the taxon. Burmeister apparently was the first to name and describe this taxon and is the sole author. The male specimen labelled “Cumtypo/comparat.” is probably the male holotype. The original description, type locality and collector are identical for this specimen.

Acknowledgements

We wish to thank Dr. Arturo Roig Alsina and MACN for allowing the study of the specimens in the Burmeister and Berg collections, to Lic. Hugo Castello for the comments on the labels and his assistance with Burmeister’s bibliography, to Prof. Cecilia Saleme de Dip (Facultad de Filosofía y Letras, Universidad Nacional de Tucumán, Argentina) for reading and correcting to the manuscript and to Dr. Adriana Zapata (Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba) and Johanna Valeria Rodríguez Ramírez for their help during the visit in MACN. Great thanks are due to the reviewers for valuable comments and many useful suggestions on the manuscript. This research was funded by CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina), which awarded a doctoral grant to HMB. We also wish to thank Consejo de Investigaciones de la Universidad Nacional de Tucumán (Project 26/G431) and CONICET (PIP N° 0696) for their support.

References

- Bar C (1873) Sur un genre nouveau de Lépidoptères de la tribu des Bombycidae et dont la chenille est aquatique. *Annales de la Société Entomologique de France* 3(5): 297–306.
- Beccacece H, Navarro F (in press) Redescrición de *Biturix rectilinea* (Burmeister, 1878) con comentarios sobre su posición taxonómica (Lepidoptera: Erebidae, Arctiinae).
- Berg C (1875a) Patagonische Lepidopteren. *Bulletin de la Société Impériale des Naturalistes de Moscou* 49: 191–245.
- Berg C (1875b) Lepidopteros Patagonicos observados en el viage de 1874. *Acta de la Academia Nacional de Ciencias Exactas* 1: 63–101.
- Berg C (1877a) In: Dohrn CA. Drei Leseblumen. *Stettiner Entomologische Zeitung* 38: 256–260.
- Berg C (1877b) Descriptions de deux nouveaux Lépidoptères de la famille des Arctiadae (*Palustra azollae* et *Palustra tenuis*). *Annales de la Société Entomologique de France* (5) 7: 189–194.
- Berg C (1877c) Estudios Lepidopterológicos acerca de la fauna Argentina y oriental. *Anales de la Sociedad Científica Argentina* 3: 228–242.
- Berg C (1878) Lepidopterologische Studien I. Neue *Palustra*-Arten, deren Raupen im Wasser leben. *Stettiner Entomologische Zeitung* 39: 221–230.
- Berg C (1882) Farrago Lepidopterologica. Contribuciones al estudio de la fauna Argentina y paises limitrofes. *Anales de la Sociedad Científica Argentina* 13: 213–223.
- Berg C (1886) Communication. *Annales de la Société Entomologique de France* (6) 5: 212–213.
- Berg C (1895a) Notice nécrologique sur le docteur Hermann Burmeister. *Annales de la Société Entomologique de France* 64: 705–712.
- Berg C (1895b) Carlos German Conrado Burmeister. Reseña biografica. Con retrato. *Anales del Museo Nacional de Buenos Aires* 4: 315–357.
- Burmeister CHC (1832–1855) *Handbuch der Entomologie. Zweiter Band. Besondere Entomologie*. Berlin, Enslin.
- Burmeister CHC (1878) Description physique de la République Argentine: d'après des observations personnelles et étrangères 5(1). F. Savy, Paris, 524 pp.
- Burmeister CHC (1879) Atlas de la description physique de la République Argentine 5(2). Coni, Buenos Aires, 64 pp.
- Burmeister CHC (1883) Revisión del género *Ecpantheria*. *Anales del Museo Nacional de Buenos Aires* 3: 19–44.
- Felder C, Rogenhofer AF (1874) Reise der österreichischen Fregatte Novara um die Erde. *Zoologkcher Theil 2(Abtheilung 2)*: 75–120. [pls.]
- Gaede M (1923) Alte und neue Arctiinae des Berliner Zoologischen Museums. *Entomologische Rundschau* 40: 2–3, 27–28.
- Gallardo A (1902) El Doctor Carlos Berg. *Apuntes Biograficos*. *Anales de la Sociedad Científica Argentina* 53: 98–114.
- Hampson GF (1901) *Catalogue of the Lepidoptera Phalaenae in the British Museum*. 3, London, xix + 690 pp.
- Horn W, Kahle I, Friese G, Gaedike R (1990) *Collectiones entomologicae. Ein Kompendium über den Verbleib entomologischer Sammlungen der Welt bis 1960. Teil I: A bis K*.

Akademie der Landwirtschaftswissenschaften der Deutschen Demokratischen Republik edition, Berlin, 200 pp.

Hübner J [1825] Sammlung exotischer Schmetterlinge 2: pl. [193], f. 1–4.

Schaus W (1894) New species of Heterocera from tropical America. Proceedings of the Zoological Society of London 1894: 225–243.

Schaus W (1896) New species of American Heterocera. Journal of the New York Entomological Society 4: 130–145.

Watson A (1971) An illustrated catalogue of the Neotropical Arctiinae types in the United States National Museum (Lepidoptera: Arctiidae), part I. Smith. Contributions to Zoology 50: 1–361. doi: 10.5479/si.00810282.50

Watson A, Goodger DT (1986) Catalogue of the Neotropical Tiger-moths. Department of Entomology, British Museum (Natural History). Occasional Papers on Systematics Entomology 1: 1–71.

Taxonomy and biogeography of the Nearctic *Raphia* Hübner (Lepidoptera, Noctuidae, Raphiinae)

B. Christian Schmidt¹, Gary G. Anweiler²

¹ Canadian Food Inspection Agency, Canadian National Collection of Insects, Arachnids and Nematodes, K.W. Neatby Bldg., 960 Carling Ave., Ottawa, ON, Canada K1A 0C6 ² E.H. Strickland Entomological Museum, 218 Earth Sciences Building, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada, T6G 2E9

Corresponding author: B. Christian Schmidt (chris.schmidt@inspection.gc.ca)

Academic editor: D. Lafontaine | Received 14 March 2014 | Accepted 19 April 2014 | Published 27 June 2014

<http://zoobank.org/2F467B1A-F770-4D5A-98B3-C4905BF74B08>

Citation: Schmidt BC, Anweiler GG (2014) Taxonomy and biogeography of the Nearctic *Raphia* Hübner (Lepidoptera, Noctuidae, Raphiinae). In: Schmidt BC, Lafontaine JD (Eds) Contributions to the systematics of New World macro-moths V. ZooKeys 421: 91–113. doi: 10.3897/zookeys.421.7517

Abstract

The taxonomic status and biogeography of the North American *Raphia* species is reviewed using adult morphology, larval host plants, geographic phenotypic variation, and variation of mtDNA COI barcode sequences. Lack of diagnostic morphological differences, combined with relatively low mtDNA barcode divergences and clinal phenotypic variation in key geographic regions indicate that the six previously recognized species of North American *Raphia* are best interpreted as parapatric subspecies. *Raphia frater abrupta* Grote, **stat. n.**, *R. f. coloradensis* Putnam-Cramer, **stat. r.**, *R. f. piazzzi* Hill, **stat. n.**, and *R. f. elbea* Smith, **stat. n.**, are accordingly revised to subspecies of *R. frater* Grote. Type locality restrictions are provided for *Raphia abrupta* and *Raphia frater* and a neotype is designated for *Raphia frater* var. *coloradensis*.

Keywords

DNA barcode, *Populus*, incipient species, subspecies, parapatry

Introduction

Raphia Hübner is a small genus of the Holarctic region, with a single African species (Poole 1989) questionably congeneric. As the sole genus currently comprising the Raphiinae, the phylogenetic placement of *Raphia* has an interesting history. Most early

works included the genus in older concepts of the Pantheinae. Smith (in Smith and Dyar 1898) excluded *Raphia* from the Pantheinae, but remained uncertain of its affinities within the Noctuidae. Hampson similarly excluded *Raphia* from the Pantheinae (Hampson 1913) and Acronictinae (Hampson 1909), and although never published, *Raphia* would presumably have been included in Hampson's volume covering "Ophi-derinae" (Kitching 1984), a catch-all subfamily for noctuoids with fully quadrifine hindwing venation and lacking other specialized features emphasized by Hampson. Forbes (1954) and Franclemont and Todd (1983) maintained *Raphia* in Pantheinae, and it was not until recent times that Beck (1996) proposed a separate subfamily to accommodate *Raphia*. Two additional genera were recently thought to be related to *Raphia*: *Diloba* Boisduval (Fibiger et al. 2009) and *Aon* Neumoegen (Fibiger and Lafontaine 2005), the former resulting in a family-level synonymy of Raphiinae under Dilobinae (Fibiger et al. 2009). Molecular study and re-assessment of morphological traits has since shown that Raphiinae and Dilobinae are best retained as valid subfamilies (Zahiri et al. 2013). Similarly, *Aon* has subsequently been reclassified as belonging to Erebiidae: Hypocalinae (Lafontaine and Schmidt 2010).

Three *Raphia* species occur in temperate Asia, one in southern Europe (Poole 1989), and until now six species were recognized in North America (Lafontaine and Schmidt 2010). The current species concepts of Nearctic *Raphia* are essentially unchanged from those proposed by Smith (1908), although *R. coloradensis* was revised to the synonymy of *R. frater* by Schmidt and Anweiler (2010) and *R. piazzzi* (Hill 1927), described after Smith's work. Hence, over a century has elapsed since Smith's comprehensive synopsis of the Nearctic species. In this study, we revise the taxonomy of the six North American *Raphia* taxa based on geographic variation in adult phenotype, genitalia morphology, mtDNA barcode variation, and larval host plant use.

Methods and materials

Adult genitalia were prepared following the methods of Lafontaine (2004). Cleaned, stained genitalia were stored and examined in 30% ethanol, and slide-mounted in Euparal before being photographed using a Nikon D200 digital camera. Distribution maps were generated using SimpleMappr (<http://www.simplemappr.net/>). Tree distribution maps were adapted from USGS (2013).

We examined approximately 4000 specimens during the course of this study, primarily those of the CNC, EME, MEM, USNM, and UASM. Specimen repository abbreviations are as follows:

- AMNH** American Museum of Natural History, New York;
- ANSP** Academy of Natural Sciences, Philadelphia, PA;
- BIO** Biodiversity Institute of Ontario, Guelph, Ontario;
- BMNH** The Natural History Museum (statutorily British Museum [Natural History]), London;

| | |
|-------------|---|
| CNC | Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa; |
| CSU | Colorado State University, Fort Collins; |
| EME | Essig Museum of Entomology, University of California, Berkeley, California; |
| MEM | Mississippi Entomological Museum, Mississippi State, MS; |
| UASM | University of Alberta Strickland Museum, Edmonton, Alberta; |
| USNM | National Museum of Natural History (formerly United States National Museum), Washington, D.C. |

DNA extraction, PCR amplification, and sequencing of the COI barcode region were performed at the Canadian Centre for DNA Barcoding (CCDB) and followed standard protocols (Hebert et al. 2013; <http://www.ccdb.ca/resources.php>). Only sequence records greater than 500bp (range 500bp – 658bp) are included.

Results and discussion

Morphology. Comparison of 20 genitalia dissections of each sex, representing all geographic entities, failed to reveal any diagnostic differences. The shape of the male valve apex and clasper varied slightly, but do so even within a single population. The shape of the inflated vesica, the most important diagnostic character in many noctuid species complexes, showed no discernible differences. Female genitalia were similarly conservative in variation. The European *R. hybris* Hübner, which is externally very similar to *R. frater* (and is in fact virtually indistinguishable from some *R. f. coloradensis* phenotypes), differs from *R. frater* in valve shape, vesica structure (including presence of spinules that are absent in *R. frater*) and shape and size of the corpus bursae. This indicates that *Raphia* genitalic morphology is not unusually homogeneous, where interspecific differences might be lacking.

The North American *Raphia* species have previously been delineated based on wing colour and pattern (Smith 1908), and geographic variation is considerable (Fig. 1). The most important forewing characters include ground colour, extent of medio-anal black shading, shape of the antemedial band, and the amount of fuscous shading of the hindwing. The colour of the prothoracic setae and overall size also vary.

Raphia has an extensive North American distribution, occupying virtually all biomes. Phenotypes are generally quite consistent regionally, but can appear drastically different in geographically disparate areas, which led early authors such as Smith (1908) to recognize multiple North American species. To assess phenotypic and mtDNA variation in these contact zones, we therefore attempted to locate and study specimens from key geographic regions where either two or more taxa would be expected to occur sympatrically or transition from one phenotype to another. The most comprehensive data were available for four such regions: **a**) the central Great Plains and **b**) the north-eastern U.S., both where nominal ssp. *frater* interacts with ssp. *abrupta*; **b**) southern New Mexico where ssp. *elbea* meets ssp. *coloradensis*, and **c**) the Pacific Northwest / northern Rocky Mountains where ssp. *coloradensis*, *frater* and *elbea* meet (Figs 1, 3).

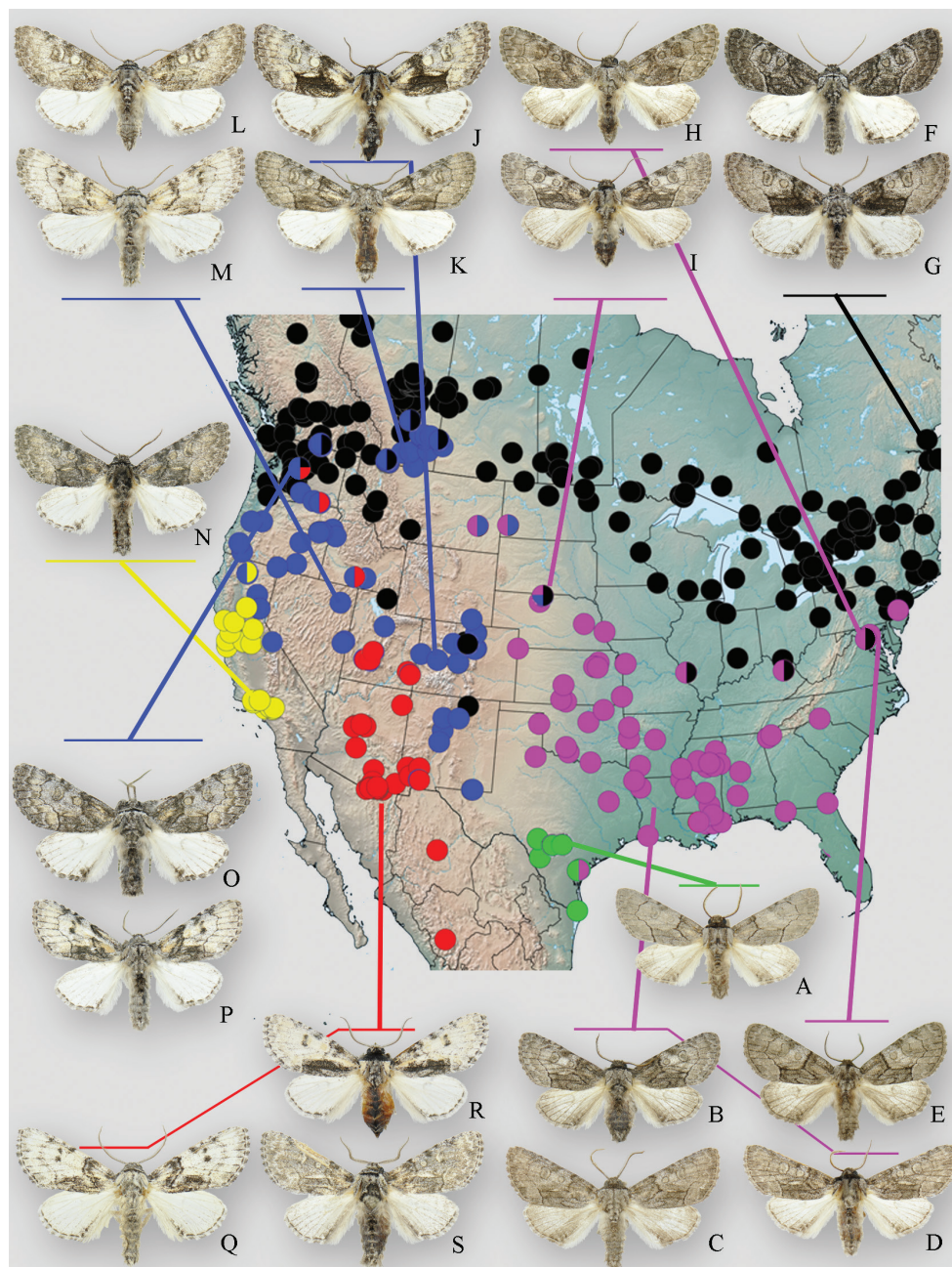


Figure 1. Geographic distribution and phenotypic variation of *Raphia frater* subspecies. Circles indicate specimens examined during this study: green – subsp. *piazzi*; pink – subsp. *abrupta*; black – subsp. *frater*; blue – subsp. *coloradensis*; yellow – subsp. *cinderella*. Multi-coloured circles indicate transitional populations and/or phenotypically intermediate specimens between respective subspecies. **a** *R. f. piazzi* (Zavallo Co., TX) **b** *R. f. abrupta* (Oktibeha Co., MS) **c** *R. f. abrupta* (Cottle Co., TX) **d** *R. f. abrupta* (Cottle Co., TX) **e** *R. f. abrupta* (Montgomery Co., MD) **f, g** *R. f. frater* (Edmunston, NB) **h** *R. f. abrupta* – *frater* intermediate (Anne Arundel Co., MD) **i** *R. f. abrupta* – *frater* – *coloradensis* intermediate from highly variable population in Cherry Co., NE **j** *R. f. coloradensis* (Alamosa Co., CO) **k** *R. f. coloradensis* (Milk River valley, AB) **l** *R. f. coloradensis* (Sanpete Co., UT) **m** *R. f. coloradensis* (Elko Co., NV) **n** *R. f. cinderella* (Ventura Co., CA) **o, p** *R. f. coloradensis* – *frater* intermediates (Chelan Co., WA) **q** *R. f. elbea* (Cochise Co., AZ) **r** *R. f. elbea* (San Juan Co., UT) **s** *R. f. elbea* (Santa Cruz Co., AZ). All specimens are males.

In the central Great Plains, a large series of over 60 specimens from northern Nebraska (Cherry Co.) is so variable that scarcely two individuals are alike, varying from the granular, dark grey forewing and white hindwing of ssp. *frater*, to the even, light grey forewing and slightly fuscous hindwing of *R. f. abrupta*; an intermediate specimen is shown in Fig. 1i. Some individuals show the blotchy black and grey pattern (with a contrasting black medio-anal shade) characteristic of *R. f. coloradensis*. A shorter series from Kansas (Riley Co.) falls within the variation of the Nebraska population. Interestingly, Smith (1908) remarked that Denver, Colorado specimens varied more towards ssp. *abrupta* than ssp. *coloradensis*. Single specimens from southeastern Montana and southwestern North Dakota have relatively pale forewings, like ssp. *coloradensis*, but some have fuscous hindwing shading and a dark prothoracic collar like *abrupta*. The zone of clinal variation may therefore be more extensive than the specimens from the few available sites in the northern Great Plains indicate, so further surveying in the region from southeastern Montana and southwestern North Dakota southward to western Nebraska / Kansas and eastern Colorado (particularly along major river corridors) would be helpful. Such a large transition zone appears to be the result of continuous, flat topography with a single, widespread *Populus* L. species (*P. deltoides* Bartr.) that is utilized by both ssp. *coloradensis* (to the northwest) and ssp. *abrupta* (to the southeast). This transition zone corresponds closely with the suture zone first proposed by Remington (1968) and recently verified by others (Swenson 2010 and references therein).

The nature of the ssp. *abrupta* – *frater* interface is somewhat different in the Northeast, and is seemingly more influenced by topography and host plant distribution (Fig. 2); at least three *Populus* species occur regionally among topography ranging from coastal floodplains to the Appalachian Mountains. Specimens from the Pocono Mtns. of Pennsylvania are *R. f. frater*, whereas nearby central Maryland (Anne Arundel Co.) specimens (Fig. 1h) show transitional features in having a forewing pattern much like ssp. *frater*, but with a fuscous hindwing and a darker prothoracic collar characteristic of ssp. *abrupta*. Coastal Maryland (Montgomery Co.) specimens are typical *R. f. abrupta* (Fig. 1e). As discussed below, the transition zone between ssp. *frater* and ssp. *abrupta* seems to be mediated by habitat and host plant differences, with *frater* largely associated with aspen (*P. tremuloides* Michx. and *P. grandidentata* Michx.; Fig. 2) and ssp. *abrupta* with cottonwood (*P. deltoides*; Fig. 2). Study of the populations on either side

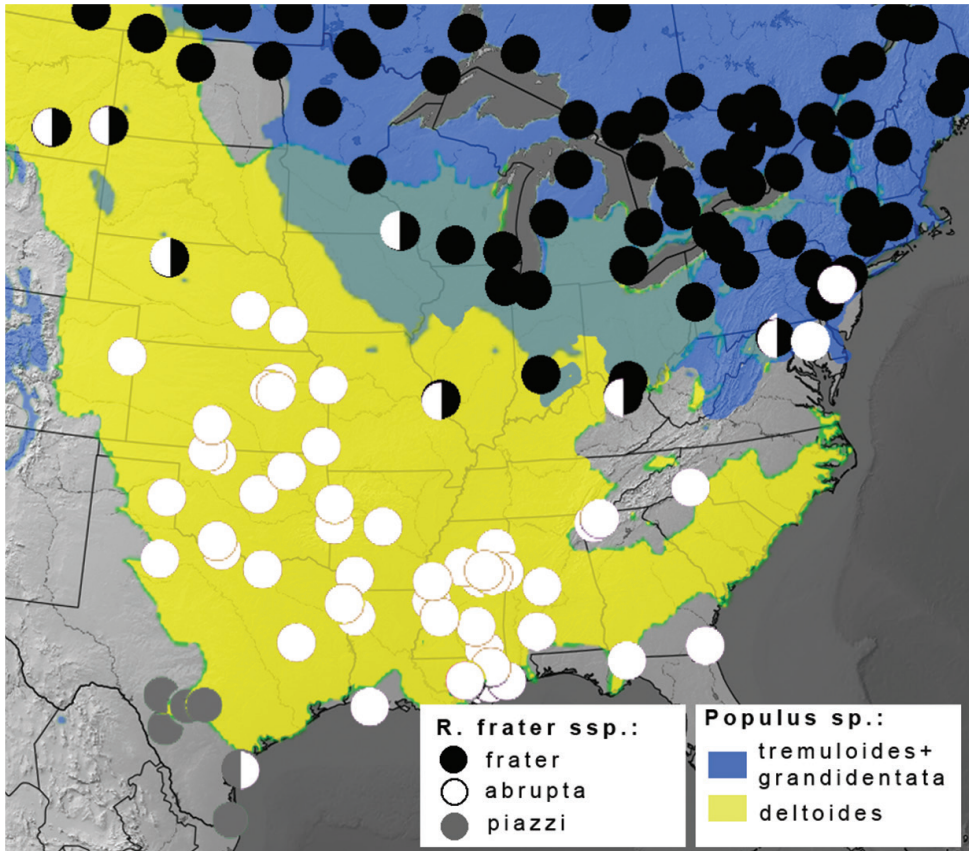


Figure 2. Distribution of *Raphia frater* subspecies (circles) relative to range of *Populus* larval host plants (coloured shading) in eastern North America. Black circles - subsp. *frater*; white circles – subsp. *abrupta*; grey circles – subsp. *piazzii*; half-circles represent transitional populations and/or phenotypically intermediate specimens. Blue shading – combined ranges of *Populus tremuloides* and *P. grandidentata*; yellow shading – *P. deltoides*; range overlap depicted in green. *Populus* ranges adapted from USGS (2013).

of the Ohio River is needed because *frater* occurs throughout Ohio (Rings et al. 1992), whereas the few northeastern Kentucky specimens that were examined are mostly like ssp. *abrupta*, but show some ssp. *frater* traits, including a mostly white hindwing. The Ohio River valley is an important suture zone between other biota, but the relative limits of *R. f. frater* and ssp. *abrupta* from the northern Appalachians eastward appear to be further south than recognized suture zones (Swenson 2010).

In southern New Mexico where *elbea* and *coloradensis* meet, *elbea* is known from the Mimbres Mountains (Grant Co.) in the southwest, with the nearest documented *coloradensis* locations 180 km to the northeast in the Rio Grande valley, and 300 km to the east in Eddy County (Fig. 1). The phenotypic transition between the two taxa is more abrupt in southern New Mexico than it is in the Great Basin where *elbea* imperceptibly transitions to the very pale Great Basin forms of *coloradensis*. A series from

Twin Falls, Idaho, and some individuals from Leavenworth, Washington (Fig. 1p), are indistinguishable from Arizona *elbea* (Fig. 1q). *Raphia f. elbea* therefore grades into *R. f. coloradensis* in low-elevation habitats of the northern Great Basin. Specimens from the Eddy Co., New Mexico population are most like *coloradensis*, but some individuals are again indistinguishable from *elbea*. The mtDNA haplotypes associate this population with *coloradensis* (Fig. 3), and the available larval hosts are *Populus angustifolia* James and *P. deltoides* (National Park Service 2014), but not *P. fremonti* Wats. with which *elbea* is most often associated. Analysis of *Raphia* populations from the lower Rio Grande valley of New Mexico is desirable given the geographically intermediate position between *elbea* and *coloradensis*, and the presence of *Populus fremonti* (Fig. 3).

Populations at the edges of the Great Basin can be extremely variable, much like the situation between *abrupta* and *frater* in the north-central Great Plains. Series of specimens from Waterton Lakes, Alberta; Okanagan Valley, British Columbia; Baker County, Oregon; and Leavenworth, Washington range from the typical dark grey *frater* to pale yellowish *coloradensis* (Fig. 1). The Leavenworth population is remarkable in that it exhibits phenotypes ranging from *frater* to *coloradensis* (Fig 1o) and *elbea* (Fig 1p).

The geographic structure of California populations is not well documented; typical *cinderella* occurs from the San Francisco Bay area southward through the Central Valley to Los Angeles Co., but *R. frater* is apparently absent from southeastern California and the southern Sierra Nevada. Northern California (including the Sierra Nevada) specimens are most like Great Basin *coloradensis* but the transition from *cinderella* to this paler form is subtle, with Siskiyou Mountains material appearing intermediate. The Siskiyou Mountains are part of a northern California – southern Oregon suture zone also identified for other flora and fauna (see Swenson 2010 and references therein). Areas in central Texas where *abrupta* and *piazzi* meet, and eastern New Mexico/west Texas where the ranges of *abrupta*, *coloradensis* and *elbea* converge, remain unstudied.

Extreme phenotypic variation is therefore the modal geographic pattern at suture zones. In all cases where we examined suture zones between putative taxa, phenotype variation was moderate to extreme, and specimens could not consistently be assigned to existing taxonomic categories. Similarly, mtDNA variation patterns show no evidence of sympatric, reproductively isolated taxa, as discussed below.

Host plants. 72% of the 132 larval collections of *R. frater* from across Canada summarized by Prentice (1962) came from trembling aspen, 17% from other *Populus* species (*P. balsamifera* L., *P. trichocarpa* Torr. & Gray, *P. grandidentata*, *P. 'x canadensis'* (Alt.), *P. nigra* L. var. *italica* du Roi), and 3% from *Salix* spp. Three records from white birch and one from alder (both Betulaceae) reported by Prentice are exceptional and possibly accidental. Wagner et al. (2011) consider *Populus* to be the main hosts, and question the validity of records from birch and alder. The closely-related European species, *R. hybris*, is restricted to *Populus*. *Raphia* larvae possess an unusually large number of proleg crochets (Beck 1996), a trait also seen in the *Populus*-feeding genus *Ufeus* Grote (Noctuidae: Noctuinae); this trait is postulated to be an adaptation to maintaining a grip on the leaves of aspen species (Lafontaine and Walsh 2013), which tremble even in slight breezes. Based on these data, *Populus*, and to a lesser extent *Salix*

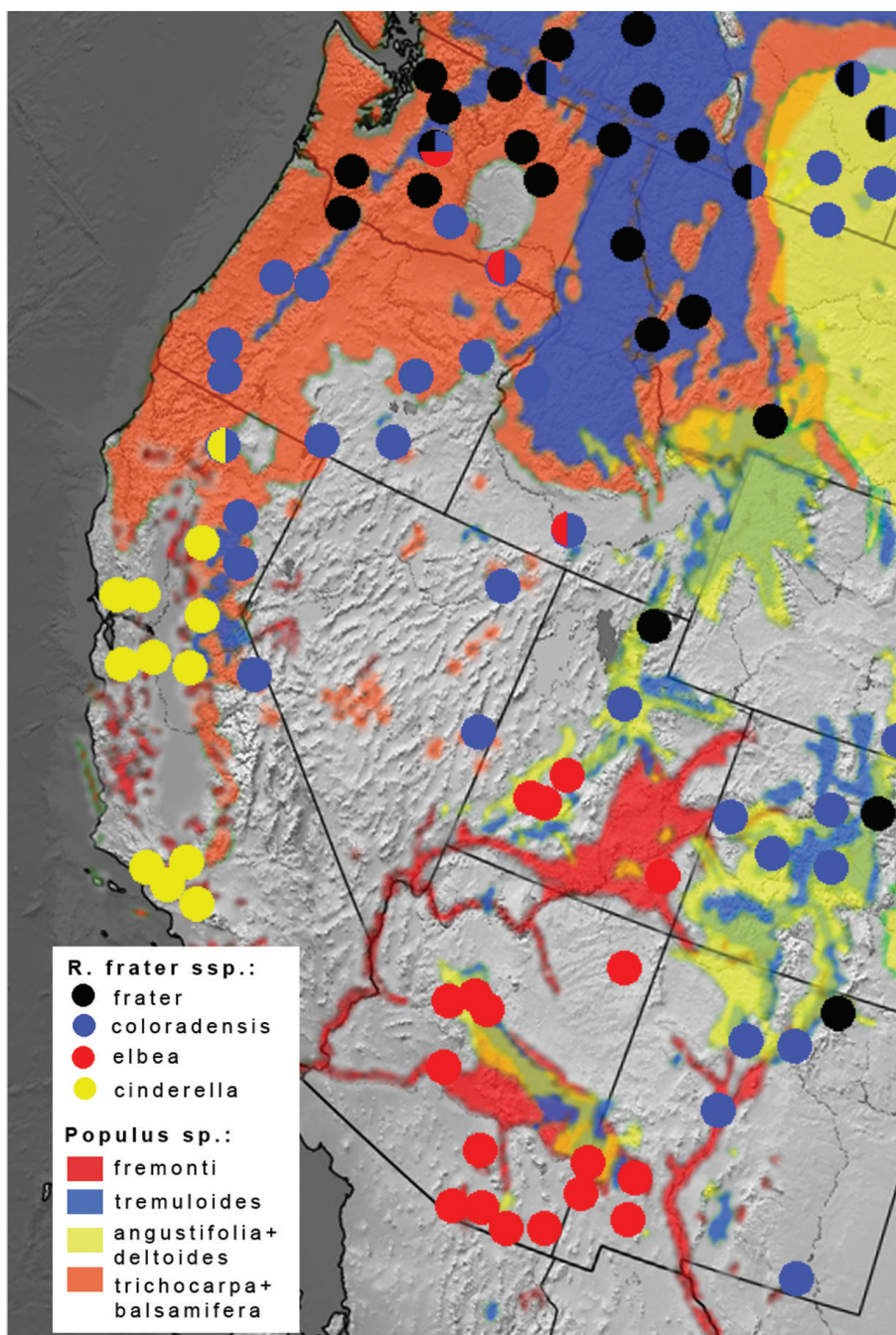


Figure 3. Distribution of *Raphia frater* subspecies (circles) relative to range of *Populus* species (coloured shading) in western North America. Half-circles represent transitional populations and/or phenotypically intermediate specimens. Ranges for *P. trichocarpa* + *P. balsamifera* and *P. angustifolia* + *P. deltoides* are combined, with both *P. balsamifera* and *P. deltoides* occurring in Alberta – Montana (upper right). *Populus* ranges adapted from USGS (2013).

L. (both Salicaceae), are certainly the primary and probably the only larval host plants. *Salix* may be used only incidentally or in certain regions/habitats; the parallel paucity of *Raphia* and *Populus* occurrence in the central Appalachian region is notable (Fig. 2). Eight species of *Populus* occur in North America, divided into four sections: *Leucoides* Spach (*P. heterophylla* L.), *Aigeiros* Duby (*P. deltoides*, *P. fremonti*), *Tacamahaca* Spach (*P. balsamifera*, *P. trichocarpa*, *P. angustifolia*) and *Populus* L. (*P. grandidentata*, *P. tremuloides*). One additional species, *P. mexicana* Wesm. of central Mexico, is the sole constituent of section *Abaso* Eckenwalder (Eckenwalder 1996).

Although it is reasonably certain that *Raphia frater* larvae are Salicaceae specialists, the geographic variation in host use and extent of specialization is not well understood. Nonetheless, it is possible to extrapolate broader host use patterns based on larval collections, host plant distributions and habitat associations. Below, we outline some potential scenarios of host use among *R. frater* subspecies.

Host plant records for *R. f. frater* (Prentice 1962) indicate that *P. tremuloides* is probably the dominant, and certainly the most geographically widespread host (with the caveat that the high proportion of trembling aspen collections may simply reflect sampling bias). In eastern North America, the southern range limit of *R. f. frater* corresponds closely with the combined southern limits of the two aspen species (section *Populus*: *P. tremuloides* and *P. grandidentata*; Fig. 2). *Raphia frater* populations in riparian habitats of southern Alberta, where *P. tremuloides* is scarce or absent, are associated with other *Populus* species that form a complex zone of hybridization and overlap among four species (*P. deltoides*, *P. balsamifera*, *P. trichocarpa*, and *P. angustifolia*) along the major river valleys (Brayshaw 1965, Floate 2004). In this region *Raphia f. frater* phenotypes transition to *R. f. coloradensis* (Fig. 3). The northernmost extent of *P. deltoides* and *P. deltoides* × *balsamifera* hybrids in the Red Deer River valley at about 52° latitude (Floate 2004) also coincides with the northernmost extent of *R. f. coloradensis*-like phenotypes; north of there where *P. tremuloides* is the dominant species of the Aspen Parkland ecoregion, only pure *R. f. frater* phenotypes occur. Similarly, transitional *frater-coloradensis* populations occur in southwestern Alberta, southern British Columbia and central Washington at the range edges of *P. tremuloides*, where *P. trichocarpa* becomes the dominant *Populus* (Fig. 3). In northern Labrador, *R. f. frater* is at its northeastern range limit (not shown), occurring beyond the range of *Populus*; *Salix* species are the presumed hosts.

Throughout most of the range of *R. f. abrupta*, *P. deltoides* is the only *Populus* species present. Swamp cottonwood (*P. heterophylla*) has a small eastern North American range, occurring primarily along the Mississippi and Ohio River valleys and along the Atlantic seaboard (see e.g., Sibley 2009, USGS 2013), so this may serve as a host in some areas. The hosts for the southwest Texas taxon *R. f. piazzzi* are unknown, and may constitute willows rather than *Populus*, the latter being rare or absent where *R. f. piazzzi* occurs (Fig. 3).

In the Pacific Northwest, *R. f. frater* is associated with *P. tremuloides* in northern Washington and British Columbia, with *R. f. coloradensis* of dry, low-elevation habitats associated with *P. trichocarpa* (L. Crabo, pers. comm.). Crumb (1956) documented a larval collection from the latter species in south-central Washington. Throughout most of the Pacific Northwest, the only *Populus* species are *P. tremuloides* at upper elevations,

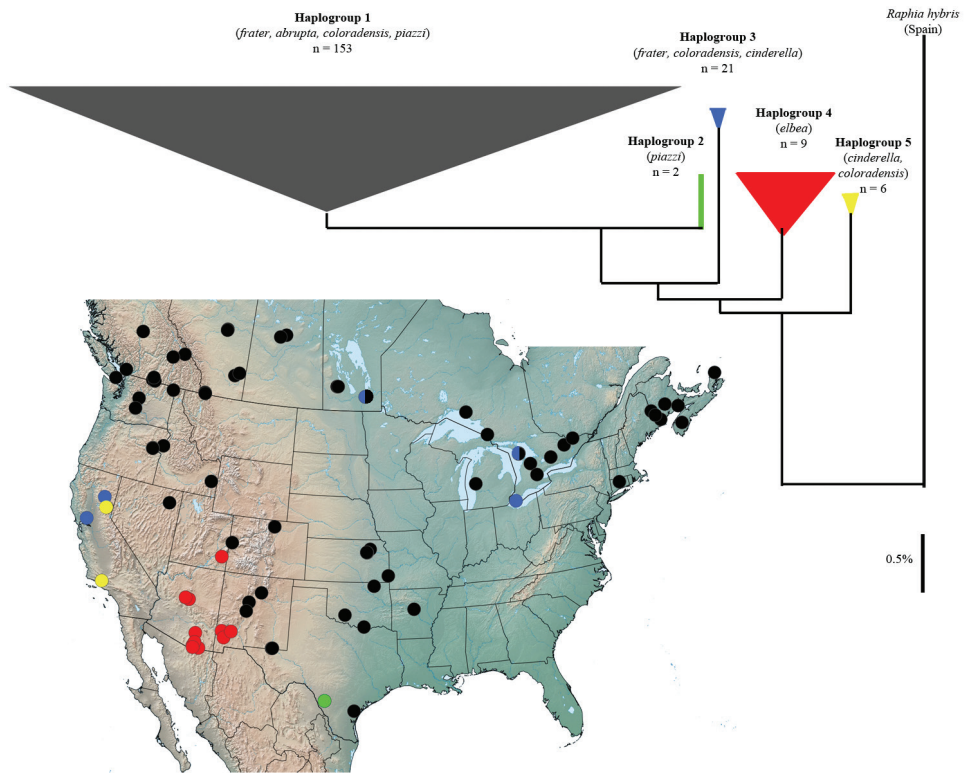


Figure 4. Neighbour-joining tree and associated sampling sites of mtDNA barcode haplotypes in *R. frater*. Haplogroup colour corresponds to that of sampling sites. Subspecies assignment based on morphology and sample size is indicated for each haplogroup. Width of triangles is proportional to number of haplotypes, height represents maximum divergence within haplogroup.

and *P. trichocarpa* in low-elevation riparian habitats and drier soils in moist regions (Fig. 3). A third species, *P. angustifolia*, occurs locally in the eastern parts of the Pacific Northwest, with habitats similar to *P. trichocarpa*. There are no specific host records for the Californian *R. f. cinderella*, with both *P. trichocarpa* and *P. fremonti* being the most likely hosts. Along the east slopes of the Oregon Cascade Ranges to the north, *R. f. coloradensis* associates with *P. trichocarpa* (L. Crabo, pers. comm.) Dyar (1894) cites “poplar” as a foodplant for larvae from Yosemite. Subspecies *coloradensis* in the Sierra Nevada, to the east of the central Californian range of *cinderella*, is associated with *P. tremuloides*.

Arizona populations of *R. f. elbea* feed on *P. fremonti* (Crumb 1956; D. Wagner, pers. comm.), and again this is the only available *Populus* in much of the range of ssp. *elbea*, excepting the higher elevations in the mountain ranges of central Arizona where *P. tremuloides* and *P. angustifolia* occur (Fig. 3). A population of *R. f. coloradensis* in the Rio Grande valley of central New Mexico is also associated with riparian *P. fremonti* (Fig. 3). Aspen-associated, *R. f. frater*-like populations may occur at high elevations in Arizona, similar to the situation in Colorado, but this has not been documented. This

raises the interesting possibility that *frater* occurs at higher elevations, with *elbea* occurring in the low-elevation floodplain. Surveying at the uppermost elevations of the Chiricahua and Santa Catalina Mountains of southeastern Arizona where aspen occurs have so far not yielded *Raphia* (BCS unpubl. data), but the more expansive range of *P. tremuloides* along, for example, the Mogollon Rim is poorly surveyed.

In summary, larval host plant associations of *R. frater* populations shows some broad congruencies between subspecies and *Populus* species distributions, but with limited evidence for high host fidelity: range edges of *R. frater* subspecies generally do not closely follow those of the various *Populus* hosts, suggesting that *Populus* availability rather than high host fidelity may be the limiting factor to *Raphia* distribution, and that climatic and topographic effects have a greater selective influence than does host plant specialization. To what extent these congruencies reflect common co-evolutionary trajectories, and what factors drive intraspecific divergence, would be a fascinating and fruitful area of study.

Molecular variation. The deepest splits in mtDNA barcode variation (alluded to previously in Lafontaine and Schmidt 2010) segregate North American *Raphia* into four groups, but only one of these is private to a recognizable taxon (*R. f. elbea*). None of the remaining subspecies exhibited discrete haplotypic variation. Based on analysis of 192 specimens from localities across the range of *R. frater* representing all subspecies (Suppl. material 1), haplotypes segregated into five groups: **1**) a large group from across most of the eastern, northern and central range portions that includes *R. f. frater*, *R. f. coloradensis*, *R. f. abrupta* and *R. f. piazzzi*, varying by up to ~1.3% (Fig. 4); **2**) a discrete group closest to haplogroup 1, consisting of two *R. f. piazzzi* specimens (Fig. 4); **3**) a divergent group of geographically disparate samples of Eastern *R. f. frater* (Ontario, Manitoba) and Californian *R. f. cinderella* specimens, differing by a minimum of ~2.2% from all other groups (Fig. 4); **4**) a group private to *R. f. elbea* (Arizona, New Mexico, Utah) with a minimum ~1.0% divergence; **5**) A group of Californian *R. f. cinderella* with a minimum divergence of ~1.8% from all other haplotypes.

The combination of California and eastern Canada samples in haplogroup 3 to the exclusion of all others was quite unexpected, given the geographic structuring of other haplogroups. Two haplogroup-3 populations (Bird Hill, Manitoba; Bruce Peninsula, Ontario) also exhibited group 1 haplotypes (Fig. 4), the only sampled populations to yield more than one haplogroup. Representative specimens from these sites were of the same phenotype and from the same sampling event. This haplogroup could therefore be a retained ancestral mtDNA polymorphism, or indicative of *Wolbachia*-induced mtDNA lineage sorting similar to that documented by Kodandaramaiah et al. (2013). Determining the underlying cause of this interesting variation will require study using nuclear gene markers and *Wolbachia* assays.

Considering the general lack of taxonomic resolution of North American *Raphia* in the barcode sequence, and comparing divergences among Palaearctic *Raphia* as a metric of mean species divergences within the genus, mtDNA variation is most parsimonious with a geographically structured, single-species interpretation. The contrast between often considerably different adult phenotypes and lack of significant mtDNA and morphological differentiation may reflect strong regional selection on bark-cryptic wing patterns, which in turn is dependent on dominant host trees that vary according to regional host preferences.

Systematics

Raphia Hübner, [1821]

Rhaphia Agassiz, 1847. An unjustified emendation of *Raphia* Hübner, [1821].

Anodonta Rambur, 1858. Type species: *Noctua hybris* Hübner, [1813], by monotypy.

A junior homonym of *Anodonta* Lamarck, 1799 [Mollusca].

Certila Walker, 1865. Type species: *Certila flexuosa* Walker, by monotypy. *Certila flexuosa* is a junior subjective synonym of *Raphia frater* Grote.

Saligena Walker, 1865. Type species: *Saligena personata* Walker, 1865, by monotypy.

Saligena personata is a junior subjective synonym of *Raphia frater* Grote.

Type species. *Noctua hybris* Hübner, [1813] by subsequent designation by Grote (1874).

Raphia frater Grote

Diagnosis. Despite variation in adult facies and lack of a particular diagnostic trait, *R. frater* is recognizable by the combination of a broad, rounded forewing, often conspicuous antemedial and postmedial band, obsolete medial band (rarely faint), an orbicular, reniform and usually also a claviform stigma that are clearly outlined, black shading in the anal angle of the hindwing, and the conspicuously bipectinate male antennae. *Pseudopanthea palata* (Grote) and *Colocasia* Ochseneimer species share some superficial similarities with *Raphia frater*, but attention to the above-stated characters relative to those in *Pseudopanthea* McDunnough and *Colocasia* Ochseneimer will provide an easy diagnosis of this unique species.

Description. **Head** – Male antennae bipectinate, anterior rami 3× longer than segment length, posterior rami 3.3× longer; female antennae simple; eyes round, with short, sparse interfacetal setae, visible only at high magnification; labial palpus with second segment clothed in long strap-like scales ventrally; third segment 0.6 × length of second segment (when denuded) and smoothly scaled; occiput and frons with mix of grey and black scales, frons with transverse line of black scales; frons rounded and moderately protuberant when denuded. **Thorax** – vestiture dark grey to yellowish grey, thoracic collar sometimes contrastingly darker than dorsum; tarsi smoothly scaled, with transverse bands of black and light to dark grey; tibia with similar scaling but with faint or indistinct banding; femur with long, shaggy hair-like scales. **Abdomen** – lacking specialized secondary sexual structures such as coremata; vestiture of smooth, short grey scales; small, rounded dorsal tufts on segments A3, A4 and A5, consisting of densely set spatulate scales. **Forewing** – ground colour varies from a dark charcoal grey to pale yellowish ochre; antemedial band a parallel-sided, double black line, varying from slightly irregular and rounded to nearly linear, acute, and angled at the cubital vein; medial band obsolete, usually reduced to a black bar or two diffuse lines at costa adjacent to reniform stigma, but band sometimes visible as

a faint, diffuse black line extending from bottom of reniform stigma to anal margin; postmedial band a single black line, sinuate and slightly sagittate at veins (often faint or absent in ssp. *coloradensis* and *elbea*), expanding to diffuse black patch at costa; orbicular stigma paler than ground colour, with black border and often with a diffuse dark pupil (orbicular often absent entirely in ssp. *coloradensis* and *elbea*); reniform stigma paler than ground colour, with a black border (border often lacking in *coloradensis* and *elbea*) and a diffuse black central crescent; subterminal band absent, faint, or diffusely sagittate with paler distal edging; terminal area often darker grey than subterminal area. Average size is greatest in subspecies *frater*, while *abrupta* and *piazzi* are smallest; forewing length varies from 16.2 mm and 18.5 mm in male and female *R. f. frater* to 13.7 mm and 15.2 mm in male and female *R. f. abrupta*, respectively. **Hindwing** – ground colour varying from white, white and dusted with fuscous grey (ssp. *frater*, *coloradensis*, *elbea*, *cinderella*, *piazzi*), or entirely pale fuscous grey (ssp. *abrupta*), females with more fuscous than males; crescentic discal spot diffuse or absent; postmedial band faint or absent, although nearly always with a contiguous diffuse black patch at anal angle. **Male genitalia** (Fig. 5) – uncus slightly compressed dorsoventrally, with slight medial bulge, apex blunt; valva tapering more or less evenly to a rounded point, sacculus poorly differentiated from remaining valva; ampulla long and flattened, $0.7 \times$ length of valva width, projecting mesially; aedeagus stout and sausage shaped, $2.1 \times$ longer than wide; vesica a simple kidney-shaped, unarmed chamber equal in length to aedeagus, tapering gradually into ductus. **Female genitalia** (Fig. 5) – bursa copulatrix membranous, lacking apparent differential sclerotization, including ostium, ante- and postvaginal plate; ductus bursae a simple rugose tube, $3.3 \times$ longer than diameter, connecting subbasally to corpus bursae; corpus bursae a simple kidney-shaped chamber, slighter wider over apical two-thirds; ductus seminalis arising from basal end of corpus bursae, caudad of ductus bursae; papillae anales short, bluntly rounded, with a broadly joined base, with two types of unusual, modified setae: 1) a dense band of thin, evenly curved setae arising from base of papillae and curving up to caudal margin, outer surface of lobe virtually encircled by a dense setal crown; and 2) highly modified thick, spatulate setae densely set along caudal margin of lobe. **Immature stages** – larva described by Thaxter (1883) based on eastern specimens, and by Dyar (1894) from Yosemite, California (possibly referable to *R. f. cinderella*). Illustrations in McCabe (1991) (head capsule and mandible), Wagner (2005) and Wagner et al. (2011). Mature larva stout, tapered only slightly anteriorly, bluish green to apple green with a slightly translucent quality, pinacula yellow, a dorsal transverse yellow band on A1, A5 and A8 extends to just above spiracle; T2 with short horn-like process middorsally, reddish with yellow base; these bands with whitish anterior border, those on A5 and A8 partially bordered with reddish orange; prolegs green, anal prolegs with yellow and reddish orange; head whitish green, usually retracted into T1, ocelli black, labrum whitish; total length 40 to 30 mm. Thaxter (1883) states that male larvae are more slender and smaller. Cocoon tough and firm, incorporating debris; pupa cylindrical with a rounded abdomen, cremaster short but broad and thick, lacking hooks. Eggs laid in small clusters or

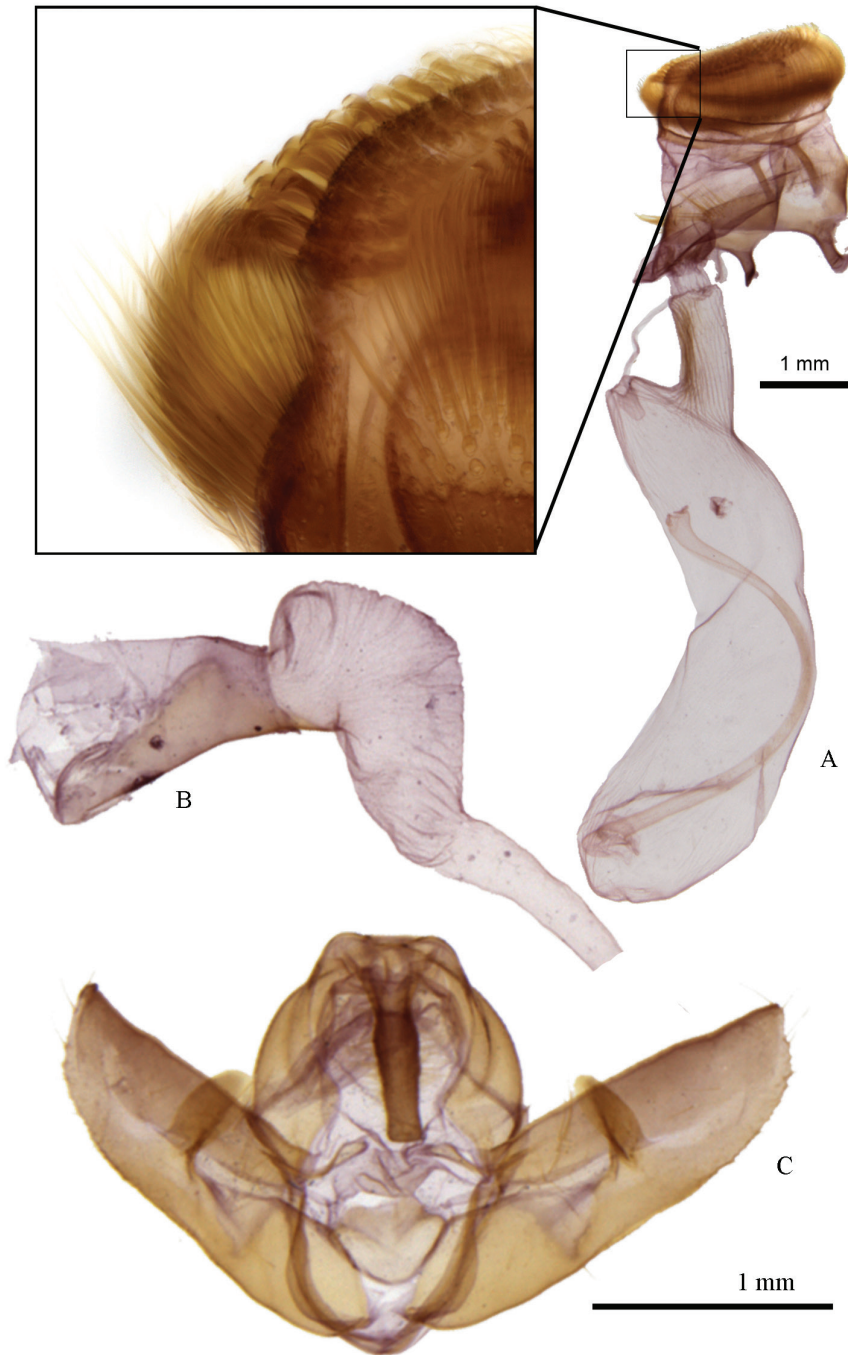


Figure 5. Genitalia of *Raphia frater*. **a** female (Konza Prairie Biol. Stn., Riley Co., KS; leg. Metlevski), with inset showing apical spatulate setae and subapical dense setal crown of papillae anales **b** male vesica **c** male genital capsule (Pitchfork Ranch, Grant Co., NM; leg. C. Ferris); note magnification difference between sexes.

overlapping in linear groups; early instars much more elongate ‘semi-loopers’ with A3 and A4 prolegs reduced (Wagner et al. 2011). Larvae rest along midrib of leaf underside. Comparison among larvae of Californian *R. frater* (Dyar, 1894), *R. f. frater*, *R. f. abrupta* and *R. f. elbea* indicate no discernible differences among these subspecies.

Biology and distribution. *Raphia frater* occurs in virtually all wooded or shrubby habitats of the boreal region since the larval hosts form a dominant part of most non-coniferous forest types. It can be one of the most common late spring noctuids in aspen-dominated boreal forests of central Canada. In the West it becomes increasingly more restricted to riparian areas, particularly major river systems in drier regions of the Pacific Northwest and the desert of the Southwest. *Raphia frater* has a nearly trans-continental distribution, absent only from the arctic and most of the subarctic. The records from northern subarctic Labrador are surprising, but are based on three CNC specimens from two localities, so the data appear to be authentic. Handfield (2011) cites records from the northeast shore of the St. Lawrence, but the species is not known from Newfoundland. The range is essentially continuous south to northern Mexico, although very spotty throughout the Atlantic states, and spotty or absent in the central to southern Appalachians. Nominal *R. f. frater* occurs across the boreal region south to the northeastern States, southern Great Lakes region, and northern Rockies / Pacific Northwest; *R. f. abrupta* occurs from the Great Plains southward to eastern Texas and eastward to the Atlantic seaboard; *R. f. coloradensis* occurs from western California to the eastern slope of the Rockies; *R. f. elbea* occurs from at least southeastern Utah through Arizona, southwestern New Mexico and into Mexico; *R. f. cinderella* is restricted to western and central California; and *R. f. piazzzi* occurs from the Edwards Plateau into southern Texas. *Raphia frater* is univoltine across the boreal region and most of the west, with peak flight activity from late May to July. It is bivoltine in the eastern U.S., flying mostly in April to May, and July to August. In the Deep South, *R. f. abrupta* has three abundance peaks: March, May and a smaller flight (partial third brood?) in September (Brou 2014). Larvae are most common from late July to mid-August in Canada (Prentice 1962).

***Raphia frater frater* Grote**

Figs 1f, 1g, 2, 3

Raphia frater Grote, 1864

Saligena personata Walker, 1865

Type material. *Raphia frater* Grote, 1864 – # 7675 [ANSP]. Type locality: Middle States [eastern USA]; here restricted to Mount Pocono, Monroe Co., Pennsylvania. Grote (1864) simply stated the type locality as “Middle States,” and no additional information is available on the holotype label data. We interpret this as referring to the region south of the New England States, and north of the southern States. Given the complex variation of North American *R. frater*, it is advisable to restrict the type locality. As Grote’s material likely

originated from the eastern United States, we restrict the Type locality to Mount Pocono, Monroe Co., Pennsylvania, from which we examined typical *R. frater frater* specimens. *Raphia frater* and *R. abrupta* are the oldest available names for this species, and were published simultaneously. As first revisers, we designate *frater* as the senior name (ICZN, Article 24.2.2). Syn. *Saligena personata* Walker, 1865 - [BMNH]. Type locality: United States.

Diagnosis and description. The nominal subspecies of *R. frater* typically has an even, powdery, dark grey forewing ground colour with all of the markings complete, consisting of the antemedial and postmedial band, and the orbicular, reniform and usually the claviform stigmas. Average forewing length is 16.3 mm ($n = 9$) in males, 18.6 mm in females ($n = 9$). The male hindwing is white with little or no dusting of black scales in the subterminal area, and with a pronounced, diffusely-edged black patch in the anal angle, this often with an adjacent black line formed by the terminus of the postmedial band; females usually have some fuscous scales on the hindwing, especially on a slight postmedial band. This subspecies generally lacks the form with contrastingly darker medio-anal and costal black patches that is prevalent in *R. f. coloradensis*, but it does occur rarely even in Atlantic Canada (Fig. 1g). The yellowish-ochre forewing scales typical of *R. f. coloradensis* are absent. *Raphia f. abrupta* differs in having a more angulate and linear antemedial band, a paler grey and less powdery-appearing forewing, duskier hindwing, and smaller size. As discussed in the section on *Raphia frater*, geographically intermediate populations are extremely variable with respect to these traits, and are considered to be transitional between subspecies *frater* and *coloradensis/abrupta*, the only two subspecies abutting the range of *R. f. frater*.

Biology and distribution. *Raphia f. frater* is primarily a boreal taxon, especially common in aspen (*Populus tremuloides* and *P. grandidentata*) dominated forests and the Aspen Parkland ecoregion of the Prairie Provinces. In the East, it extends south of the Great Lakes region into Pennsylvania, Ohio and Indiana, but apparently not southward into the southern Appalachians, which are essentially devoid of *Raphia* records. The transition zone between *R. f. frater* and *R. f. abrupta* extends from Maryland westward roughly along the Ohio River Valley to east-central Missouri, then northwestward through the northern Great Plains. The southeastern range edge of *R. f. frater* is virtually identical to that of both trembling and bigtooth aspens (Fig. 2). In the West, *R. f. frater* occurs south along mid-elevation mountain ranges of the Pacific Northwest into Washington, and southward along the Rocky Mountains. Specimens from high elevations in Colorado (Gilpin Co., 9500') and New Mexico (Sangre de Cristo Mtns., 7900') are of the typical *frater* phenotype, the *coloradensis* phenotypes occurring at lower elevations.

***Raphia frater abrupta* Grote, stat. n.**

Figs 1b–e, 2

Raphia abrupta Grote, 1864

Certila flexuosa Walker, 1865

Type material. *Raphia abrupta* - female holotype # 7675 [ANSP]. Type locality: not given; here restricted to Sycamore Landing, Seneca, Montgomery Co., Maryland. The female type bears no locality or collector label data, and since this is a widespread, geographically variable taxon, we restrict the type locality to Sycamore Landing, Seneca, Montgomery Co., Maryland; a series in USNM from this locality, collected by D. C. Ferguson, is phenotypically more similar to the female type than specimens from the Great Plains; it is also more likely that the holotype originated from the eastern US rather than the Great Plains, which were not well collected in the mid 1800's.

Certila flexuosa Walker - [BMNH; not examined]. Type locality: North America.

Diagnosis and description. *Raphia frater abrupta* replaces *R. f. frater* from the central Great Plains eastward to the mid-Atlantic seaboard, and southward to eastern Texas and Florida. It is on average smaller with a more evenly-coloured forewing, a more linear, angulate antemedial band and a fuscous hindwing. Average forewing length is 13.7 mm ($n = 9$) in males, 15.2 mm in females ($n = 9$). The thoracic collar is often darker than the dorsal thorax, not concolorous as in *R. f. frater*. The wing facies of subspecies *abrupta* is in many ways intermediate between *R. f. piazzzi* of central and southern Texas and *R. f. frater* to the north, but the exact nature of the interface between *abrupta* and *piazzi* in Texas remains unstudied.

Biology and distribution. Subspecies *abrupta* occurs south of the range of the aspen species favoured by *R. f. frater* larvae, and its riparian haunts suggest it feeds on eastern cottonwood (*Populus deltoides*), the only *Populus* species in much of its range. Swamp cottonwood (*P. heterophylla*) and willows (*Salix* spp.) may also be suitable hosts. This subspecies is apparently rare on the Atlantic seaboard and absent altogether in the Appalachians. We examined only a single historical specimen from New Jersey (Trenton), with records north of there assignable to *R. f. frater*. All Ohio records were attributed to *R. f. frater* by Rings et al. (1992), although specimens with a pale grey forewing and dusky hindwing, traits of the *abrupta* phenotype, rarely occur as far north as southernmost Ontario (Toronto) and southeastern Minnesota (Fillmore Co.).

***Raphia frater piazzzi* Hill**

Figs 1a, 2

Paphia [sic] *piazzi* Hill, 1927.

Type material. Holotype male [USNM]. Type locality: Brownsville, Texas [USA].

Diagnosis and description. *Raphia frater piazzzi* is the least-known member of the group with a restricted distribution in central and southern Texas. Most similar in size and facies to *R. f. abrupta*, it is distinguished from that subspecies by the paler, more evenly grey forewing with sharper transverse lines than in *R. f. abrupta*. The biology and biogeographic relationship to *R. f. abrupta*, which occurs to the northeast of *piazzi*'s range, is not known, and very few specimens of this taxon are present in collec-

tions. An additional enigma is whether or not Rio Grande *piazzi* populations interact with the vastly-different looking Sonoran *R. f. elbea*.

Biology and distribution. Described from southernmost Texas, this subspecies is otherwise known only from the Edwards Plateau region; a single specimen from Sinton County to the southeast is phenotypically intermediate between *abrupta* and *piazzi*, but clearly more field work is needed to establish the limits of both subspecies. mtDNA barcode data of three *piazzi* specimens (Sinton Co. and Zavalla Co.) are very similar to the haplotypes of *R. f. abrupta*, *R. f. frater*, and *R. f. coloradensis*.

Remarks. We were unable to obtain DNA sequence from topotypical specimens of *piazzi* from the lower Rio Grande near Brownsville, Texas. The unique haplotype of the Edwards Plateau specimens (Fig. 4) may represent nominal *piazzi*, but could equally represent a unique genetic lineage from the Edwards Plateau, with its unique fauna much of which is not shared with the Rio Grande fauna.

***Raphia frater coloradensis* Putnam-Cramer, stat. n.**

Figs 1j–m, 1o, 3

Raphia frater var. *coloradensis* Putnam-Cramer, 1886

Raphia pallula H. Edwards, 1886, **syn. nov.**

Type material. *Raphia frater* var. *coloradensis* - Neotype female, here designated [CNC]. Type locality: Deer Creek Cyn. Park, 39°33.18'N 105°08.49'W, 5950', SW Littleton, Jefferson Co., Colorado. None of the original types, three males and four females “taken in Colorado by D. Bruce,” could be located and are presumed lost. The primary type of *Xylena thoracica* Putnam-Cramer, the only other noctuid named by Putnam-Cramer, is housed at USNM. Prior to 1886, D. Bruce collected in the mountains and foothills near Denver (Brown 1966), and we accordingly select a specimen from the same region to designate as **neotype**: “Colorado: Jefferson Co. / 39°33.18'N 105°08.49'W / Deer Creek Cyn. Park / SW Littleton, w of hogback / 16–17 June 2008, 5950' elev / riparian area s. of road / leg: Chuck Harp uv trap”; “Neotype / *Raphia frater* var. / *coloradensis* Putnam-Cramer / Schmidt and Anweiler 2014.”

Raphia pallula - Holotype female [AMNH]. Type locality: Siskiyou Co., California [USA]. Published several months after *coloradensis* Putnam-Cramer, Edwards was apparently not aware of Putnam-Cramer's name as it is not mentioned in his description.

Diagnosis and description. Within the range of *coloradensis*, specimens identical to the typical boreal *R. f. frater* are often present; in the most arid parts of the range of *coloradensis* in the southern Great Basin, *coloradensis* is more consistently pale ochre yellow with obsolete transverse lines and diffuse black costal/reniform blotches, overall very similar to *elbea*, but with less pronounced costal and reniform dark patches. Average forewing length is 14.9 mm ($n = 9$) in males, 16.8 mm in females ($n = 6$).

Biology and distribution. This subspecies occurs from southernmost British Columbia / Alberta to New Mexico, Utah, and California. It is most commonly associated

with riparian, low-elevation habitats. Northern populations fly from late May to July in a single generation. Flight dates spanning from May into August in the Great Basin and Southern Rocky mountain region indicate a second or partial second generation.

Remarks. *Raphia frater coloradensis* is the most weakly-differentiated subspecies, and may simply be an ecologically induced phenotype of *R. f. frater* that occurs in the warmer, drier regions of the West. Several populations, spanning a large geographical area, have been identified that exhibit a large range of phenotypic variation, as discussed above in the 'Morphology' section. Specimens from Siskiyou Co., California and the east slope of the northern Sierra Nevada (Sierra Co.) are phenotypically very similar to Great Basin *coloradensis*, and we therefore treat *pallula* as a junior subjective synonym. DNA barcodes of two specimens from the northern Sierra Nevada (Sierra Co.) belonged to the *frater-coloradensis-abrupta* haplogroup (Fig. 4).

***Raphia frater cinderella* Smith, stat. n.**

Figs 1n, 3

Raphia cinderella Smith, 1903.

Type material. A male lectotype was designated by Todd (1982) [AMNH]. Type locality: Los Angeles Co., Cal. [California, USA].

Diagnosis and description. *Raphia frater cinderella* is a Californian subspecies that is similar in size and colour to *R. f. coloradensis*, but with a more diffuse, poorly contrasting forewing pattern that usually lacks the pronouncedly darker reniform and costal dark patches. The forewing ground colour is also pale powdery grey, not pale ochre as it often is in *coloradensis*. The two taxa appear to intergrade in the Siskiyou and northern Sierra Nevada.

Biology and distribution. The range of this subspecies is restricted to central and southern California west of the Sierra Nevada. Fremont Cottonwood and willows are the most likely larval hosts, although records specific to this subspecies are lacking. Most collection dates are from June; Records from Stanislaus Co. for April - May and July may indicate a second generation.

***Raphia frater elbea* Smith, stat. n.**

Figs 1q-s, 3

Raphia elbea Smith, 1908

Type material. A male lectotype was designated by Todd (1982) [AMNH]. Type locality: Deming, [Luna Co.,], New Mexico [USA].

Diagnosis and description. *Raphia frater elbea* is most similar to the pale yellowish-ochre forms of *R. f. coloradensis*, but differ from that subspecies in having both the costal and reniform dark patches more prominent; when present, the black medio-anal

patch is also darker and more elongate; additionally, *R. f. elbea* appears to exhibit a unique, divergent mtDNA haplotype group.

Biology and distribution. This subspecies occurs from southeastern Utah and western New Mexico southward through Arizona into northern Mexico. In southeastern Arizona it occurs in riparian areas in association with the larval host, *Populus fremonti*. Flight records are from February to October, with most being from March to May and August to September, indicating at least two generations annually.

Conclusions

The North American *Raphia* populations exhibit considerable geographic variation in phenotype, previously segregated into six species. Despite these geographically structured phenotypic differences, diagnostic morphological differences in genitalia and larvae are not evident. Scrutiny of geographic contact zones between putative taxa revealed populations with extensive phenotypic and conservative molecular variation, rather than bimodal phenotypic variation coupled with deep molecular divergences that would be expected for sympatric, reproductively isolated taxa. *Raphia frater* larvae are not highly restricted to a host species or genus, but do specialize on *Populus* and *Salix*, with a pattern of regional host availability and possibly also preference. Differences in host plant suitability among the various species of Salicaceae remain unstudied. Assessment of morphology, mtDNA variation, and biogeography therefore leads us to conclude that the geographic segregates of North American *Raphia* are best treated as subspecies of a single species. The regional adaptation to habitats representing nearly all North American biomes, combined with relatively discrete geographic ranges of unique adult phenotypes, suggest a pattern of young or incipient species in the *R. frater* group.

The taxonomy and biogeography of the North American *Raphia* populations is a complex interplay between topography, host plant use, phenotypic variation and evolutionary history. This study is only the first attempt at a better understanding of this interesting group. Many questions remain unanswered: what are the exact geospatial and host plant patterns of the contact zone between *R. f. abrupta* and *R. f. frater*? Is there geographic overlap with altitudinal segregation in the West between aspen-feeding *frater* and cottonwood feeding *elbea*? Does the mtDNA haplogroup 3 represent *Wolbachia* infection? Do the lower Rio Grande / Edwards Plateau *piazzi* populations grade into *abrupta*? *Raphia* would provide a fertile area of study in understanding large-scale patterns of host plant use and biogeography of a widely distributed continental Lepidopteran.

Acknowledgements

We thank James Adams, Charles Bordelon, Vernon A. Brou Jr., Richard Brown, Lars Crabo, Terhune Dickel, Cliff Ferris, Ed Knudson, Paul Opler, Jan Metlevski, Eric Metzler, Hugo Kons, Bruce Walsh and Chuck Harp for generously providing specimens

and/or data used in this study, and Jocelyn Gill for preparing the specimen images. Discussions with Lars Crabo and Don Lafontaine on *Raphia* biogeography and species limits provided insight and guidance during this project. Evgeny Zakharov, Paul Hebert and other members of the Barcode of Life Project at the University of Guelph, Ontario, Canada, provided DNA data. Molecular analyses were carried out through grants from the National Science and Engineering Research Council of Canada and Genome Canada through the Ontario Genomics Institute.

References

- Agassiz JLR (1847) Nomenclator Zoologicus Index Universalis, continens nomina systematica classium, ordinem, familiarum et generum Animalium omnium, tam viventium quam fossilium, secundum ordinem alphabeticum unicum disposita, adjectis homonymiis plantarum, nec non variis adnotationibus et emendationibus. Fasciculus XII. In: Nomenclator Zoologicus continens nomina systematica generum animalium tam viventium quam fossilium, secundum ordinem alphabeticum disposita, adjectis auctoribus, libris, in quibus reperiuntur, anno editionis, etymologia et familiis, ad quas pertinent, in singulis classibus. Jent et Gassmann, Soloduri, viii + 393 pp.
- Beck H (1996) Systematische Liste der Noctuidae Europas (Lepidoptera, Noctuidae). Neue Entomologische Nachrichten 36: 1–122.
- Brayshaw TC (1965) Native poplars of southern Alberta and their hybrids. Canadian Department of Forestry, Ottawa. Publ. 1109.
- Brown FM (1966) David Bruce (1833–1903) and other entomological collectors in Colorado. Journal of the New York Entomological Society 74: 126–133.
- Brou VA Jr (2014) *Raphia abrupta* in Louisiana. Southern Lepidopterists' News 35: 173–174.
- Crumb SE (1956) The larvae of the Phalaenidae. United States Department of Agriculture Technical Bulletin 1135: 1–356.
- Dyar HG (1894) Some undescribed stages of Noctuidae larvae. The Canadian Entomologist 26: 17–21. doi: 10.4039/Ent2617-1
- Eckenwalder JE (1996) Systematics and evolution of *Populus*. In: Stettler RF, Bradshaw HD, Heilman PE, Hinckley TM (Eds) Biology of *Populus* and its implications for management and conservation. NRC Research Press, Ottawa, 7–32.
- Edwards H (1886) Apparently new forms of American Lepidoptera. Entomologica Americana 2: 165–171.
- Fibiger M, Lafontaine JD (2005) A review of the higher classification of the Noctuoidea (Lepidoptera) – with special reference to the Holarctic fauna. Esperiana 11: 7–92.
- Fibiger M, Ronkay L, Steiner A, Zilli A (2009) Noctuidae Europaeae. Vol. 11, Pantheinae, Dilobinae, Acronictinae, Eustrotiinae, Nolinae, Bagisarinae, Acontiinae, Metoponiinae, Heliothinae, and Bryophilinae. Entomological Press, Sorø, 504 pp.
- Floate KD (2004) Extent and patterns of hybridization among the three species of *Populus* that constitute the riparian forest of southern Alberta, Canada. Canadian Journal of Botany, 82: 253–264. doi: 10.1139/b03-135

- Forbes WTM (1954) Lepidoptera of New York and neighboring states. Part 3 Noctuidae. Cornell University Agriculture Experiment Station, Memoir 329: 1–433.
- Franclemont JG, Todd EL (1983) Noctuidae. In: Hodges RW, Dominick T, Davis DR, Ferguson DC, Franclemont JG, Munroe EG, Powell JA (1983) Check List of the Lepidoptera of America North of Mexico. E. W. Classey Ltd, London and The Wedge Entomological Research Foundation Washington, 284 pp.
- Grote AR (1864) Descriptions of North American Lepidoptera – no. 2. Proceedings of the Entomological Society of Philadelphia 2: 433–441.
- Grote AR (1874) List of the Noctuidae of North America. Bulletin of the Buffalo Society of Natural Sciences 2: 1–77.
- Hampson GF (1909) Catalogue of the Lepidoptera Phalaenae in the British Museum 8: 1–583.
- Hampson GF (1913) Catalogue of the Lepidoptera Phalaenae in the British Museum 13: 1–609.
- Handfield L (2011) Le guide des papillons du Québec. Version scientifique, Broquet, Ottawa, 1352 pp.
- Hebert PDN, deWaard JR, Zakharov EV, Prosser SWJ, Sones JE, McKeown JTA, Mantle B, La Salle J (2013) A DNA ‘Barcode Blitz’: Rapid digitization and sequencing of a natural history collection. PLoS ONE 8: e68535. doi: 10.1371/journal.pone.0068535
- Hill CA (1927) Three new moths from the southwest. Bulletin of the Southern California Academy of Sciences 26: 6–7.
- Hübner J (1813) Sammlung Europäischer Schmettlinge. Vol. 4. Eulen. Augsburg, 2–81.
- Hübner J (1821) Verzeichniss bekannter Schmettlinge. Augsburg, 431 pp.
- Kitching IJ (1984) An historical review of the higher classification of the Noctuidae (Lepidoptera). Bulletin of the British Museum (Natural History) (Entomology) 49: 153–234.
- Kodandaramaiah U, Simonsen TJ, Bromilow S, Wahlberg N, Sperling, F (2013) Deceptive single-locus taxonomy and phylogeography: *Wolbachia*-associated divergence in mitochondrial DNA is not reflected in morphology and nuclear markers in a butterfly species. Ecology and Evolution 3: 5167–5176. doi: 10.1002/ece3.886
- Lafontaine JD (2004) Noctuoidea: Noctuidae (part) – Agrotini. In: Hodges RW (Ed) The Moths of North America. Fascicle 27.1. The Wedge Entomological Research Foundation, Washington, 394 pp.
- Lafontaine JD, Schmidt BC (2010) Annotated check list of the Noctuoidea (Insecta, Lepidoptera) of North America north of Mexico. ZooKeys 40: 1–239. doi: 10.3897/zookeys.40.414
- Lafontaine JD, Walsh JB (2013) A revision of the genus *Ufeus* Grote with the description of a new species from Arizona (Lepidoptera, Noctuidae, Noctuinae, Xylenini, Ufeina). ZooKeys 264: 193–207. doi: 10.3897/zookeys.264.3526
- McCabe TL (1991) Atlas of Adirondack Caterpillars: With a Host List, Rearing Notes, and a Selected Bibliography of Works Depicting Caterpillars. New York State Museum Bulletin 470: 1–114.
- National Park Service (2014) Checklist of the Vascular Plants of Carlsbad Caverns National Park. http://www.nps.gov/cave/planyourvisit/upload/2007_CAVE_Plants.pdf [accessed 5 March 2014]
- Poole RW (1989) Lepidopterorum Catalogus (New Series). Fascicle 118 Noctuidae, Parts 1–3. E.J. Brill, New York, 1314 pp.

- Prentice RM (1962) Forest Lepidoptera of Canada reported by the Forest Insect Survey, Vol. 2: Nycteolidae, Notodontidae, Noctuidae, Liparidae. Canada Dept. of Forestry, Forest Entomology and Pathology Branch, Publication No. 1013, 77–281.
- Putnam-Cramer AW (1886) Two new varieties of noctuids. *Entomologica Americana* 2: 1–142.
- Rambur JP (1858) Catalogue Systématique des Lépidoptères de l'Andalousie. JB Bailliere, Paris, 422 pp. [22 plates]
- Remington CL (1968) Suture-zones of hybrid interaction between recently joined biotas. In: Dobzhansky T, Hecht MK, Steere WC (Eds) *Evolutionary Biology*. Plenum, New York, 321–428. doi: 10.1007/978-1-4684-8094-8_8
- Rings RW, Metzler EH, Arnold FJ, Harris DH (1992) The owlet moths of Ohio Order Lepidoptera Family Noctuidae. *Ohio Biological Survey Bulletin, New Series* 9(2): 1–219. [pl. 1–16]
- Schmidt BC, Anweiler GG (2010) Taxonomic changes to Lepidoptera: Macro-moths. In: Pohl GR, Anweiler GG, Schmidt BC, Kondla NG (Eds) *An annotated list of the Lepidoptera of Alberta, Canada*. *ZooKeys* 38: 497–509. doi: 10.3897/zookeys.38.383
- Sibley DA (2009) *The Sibley Guide to Trees*. Alfred E. Knopf, New York, 426 pp.
- Smith JB (1903) New noctuids for 1903, no. 4, with notes on certain described species. *Transactions of the American Entomological Society* 29: 191–224.
- Smith JB (1908) New species of Noctuidae for 1908. I. With notes *Charadra*, *Raphia* and *Pseudanarta*. *Journal of the Entomological Society of New York* 16: 79–98.
- Smith JB, Dyar HG (1898) Contributions toward a monograph of the Lepidopterous family Noctuidae of boreal North America. A Revision of the species of *Acronycta* (Ochsenheimer) and of certain allied genera. *Proceedings of the United States National Museum* 21 (1140): 1–194. doi: 10.5479/si.00963801.21-1140.1
- Swenson NG (2010) Mapping the suturing of a continental biota. *Molecular Ecology* 19: 5324–5327. doi: 10.1111/j.1365-294X.2010.04880.x
- Thaxter R (1883) Descriptions of noctuid larvae found on Cutts' Island, Maine. *Papilio* 3: 10–19.
- USGS (2013) Digital Representations of Tree Species Range Maps from “Atlas of United States Trees” by Elbert L. Little, Jr. (and other publications). <http://esp.cr.usgs.gov/data/little/> [accessed 10 November 2010]
- Todd EL (1982) The noctuid type material of J. B. Smith (Lepidoptera). *United States Department of Agriculture Technical Bulletin* 1645: 1–228.
- Wagner DL (2005) *Caterpillars of eastern North America: a guide to identification and natural history*. Princeton University Press, Princeton, NJ, 512 pp.
- Wagner DL, Schweitzer DF, Sullivan JB, Reardon RC (2011) *Owlet Caterpillars of Eastern North America*. Princeton University Press, Princeton, NJ, 576 pp.
- Walker FD (1865) *List of the Specimens of Lepidopterous Insects in the Collection of the British Museum* 32. British Museum, London, 448 pp.
- Zahiri R, Lafontaine JD, Schmidt, BC, Holloway JD, Kitching IJ, Mutanen M, Wahlberg N (2013) Relationships of the basal lineages of Noctuidae (Lepidoptera, Noctuoidea) based on eight gene regions. *Zoologica Scripta* 42: 488–507. doi: 10.1111/zsc.12022

Supplementary material I

Table S1. Specimen data for mtDNA barcode vouchers.

Authors: B. Christian Schmidt, Gary G. Anweiler

Data type: data spreadsheet

Explanation note: Haplogroup numbers refer to those given in Fig. 4; Abbreviations for specimen depositories are as given in Methods and materials section.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: doi: 10.3897/zookeys.421.7517.app1

Polyphyly of Lichen-cryptic Dagger Moths: synonymy of *Agriopodes* Hampson and description of a new basal acronictine genus, *Chloronycta*, gen. n. (Lepidoptera, Noctuidae)

B. Christian Schmidt¹, David L. Wagner², Brigitte V. Zacharczenko²,
Reza Zahiri³, Gary G. Anweiler⁴

1 Canadian Food Inspection Agency, Canadian National Collection of Insects, Arachnids, and Nematodes, K.W. Neatby Bldg., 960 Carling Ave., Ottawa, ON, Canada K1A 0C6 **2** Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269 **3** Biodiversity Institute of Ontario, University of Guelph, Guelph, Ontario, Canada **4** E.H. Strickland Entomological Museum, 218 Earth Sciences Building, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada, T6G 2E9

Corresponding author: B. Christian Schmidt (chris.schmidt@inspection.gc.ca)

Academic editor: D. Lafontaine | Received 4 March 2014 | Accepted 2 May 2014 | Published 27 June 2014

<http://zoobank.org/B69FD062-806F-4AE7-8C68-1F8FD650D2A7>

Citation: Schmidt BC (2014) Polyphyly of Lichen-cryptic Dagger Moths: synonymy of *Agriopodes* Hampson and description of a new basal acronictine genus, *Chloronycta*, gen. n. (Lepidoptera, Noctuidae). In: Schmidt BC, Lafontaine JD (Eds) Contributions to the systematics of New World macro-moths V. ZooKeys 421: 115–137. doi: 10.3897/zookeys.421.7424

Abstract

The taxonomic composition and systematic position of *Agriopodes* Hampson is examined through an integrated approach using adult and larval morphology, biology, and molecular sequence data. The type-species of *Agriopodes*, *Moma fallax* Herrich-Schäffer is shown to be derived within the *Acronicta grisea* Walker species-group; accordingly, *Agriopodes* is relegated to synonymy under *Acronicta* Ochsenheimer, **syn. n.** (Acronictinae). Additionally, molecular markers and morphology show that *Agriopodes* is not monophyletic: *Agriopodes tybo* (Barnes) is not closely related to *A. fallax* nor to *Acronicta*, and is transferred to a new genus, *Chloronycta* Schmidt & Anweiler, **gen. n.** The immature stages of *Chloronycta tybo* **comb. n.** are described and illustrated for the first time. Although previously treated as a valid species, we show that *Agriopodes geminata* (Smith) represents the northern terminus of clinal variation in wing pattern of *A. fallax* and synonymize *A. geminata* under *A. fallax* (**syn. n.**). The history and identity of *Agriopodes corticosa* (Boisduval), a *nomen dubium*, is discussed.

Keywords

Agriopodes fallax, *Agriopodes geminata*, *Agriopodes tybo*, dagger moths, *Fraxinus*, Arizona

Introduction

The New World genus *Agriopodes* Hampson (Noctuidae, Acronictinae) has included as many as seven species, united by their striking lichen-mimicking colours of green, white and black. As we show here, their similarity in colour pattern is convergent, and represents a common evolutionary trajectory repeated multiple times across the Noctuoidea. The superficial nature of their shared pattern elements is reflected in the taxonomic history of *Agriopodes*, with species previously removed from the genus now distributed among three different subfamilies outside the Acronictinae (Lafontaine and Schmidt 2010). When Hampson (1909) described *Agriopodes*, he included four species, *A. fallax* (Herrich-Schäffer), *A. geminata* (Smith), *A. tybo* (Barnes) and *A. viridata* (Harvey). As was typical of taxonomic works of Hampson's, his generic diagnosis relied on external characters such as wing venation and pattern, scale vestiture, palpi and antennal structure; at the subfamily level within the Noctuidae, these characters can be misleading phylogenetically (Kitching and Rawlins 1998; Fibiger and Lafontaine 2005). Genitalic dissections were not studied by Hampson and his contemporaries as this methodology was still in its infancy.

Barnes and McDunnough (1917) added three more species to *Agriopodes*: *A. lepidula* (Grote), *A. teratophora* (Herrich-Schäffer) and *A. corticosa* (Guenée), an arrangement maintained by McDunnough (1938), except that *A. lepidula* was transferred to *Leuconycta* Hampson (now Condicinae). Franclemont and Todd (1983) retained *fallax*, *geminata*, *tybo* and *teratophora* in *Agriopodes*; transferred *viridata* to *Cryphia* Hübner (now Bryophilinae); and treated *A. corticosa* as a non-North American species of unknown identity. Franclemont and Todd (1983) apparently overlooked Forbes' (1954) transfer of *teratophora* to *Erastria* Ochseneheimer (now *Anterastria* Sugi in Noctuinae). Poole's (1989) global Noctuidae catalogue maintained Franclemont and Todd's concept of *Agriopodes* but also included *jucundella* Dyar, which had been transferred to *Cryphia* by Ferguson (1988) the previous year. Presently, this species is placed as "*Elaphria*" *jucundella* in Noctuinae, Elaphriini (Lafontaine and Schmidt 2010).

As part of an ongoing revision of the North American Acronictinae (Schmidt and Anweiler in prep.), we examined the four remaining species of *Agriopodes* (*fallax*, *geminata*, *tybo* and *corticosa*), and it soon became evident that the monophyly of *Agriopodes* was still problematic. Forbes (1954) expressed doubt that *A. fallax*, the type-species of *Agriopodes*, was distinct from *Acronicta*. He stated that it was "hardly distinguishable... [and] not really distinct from *Apatela* [= *Acronicta*]," but retained *Agriopodes* as a valid genus based on the mesothoracic scale tufts and green colouration of the adult, both characters that appear in other *Acronicta* but to lesser degrees. The larval habitus of *A. fallax* is not immediately recognizable as belonging to a particular group of *Acronicta* but is certainly within the range of morphological variation encompassed by the genus (see Wagner et al. 2011). The species status of *A. geminata* poses another problem, be-

ing very similar to *A. fallax*, but thought to occur as a disjunct population in Manitoba and Saskatchewan beyond the eastern North American range of *A. fallax*. *Agriopodes tybo*, a Sonoran species reaching the U.S. in southeastern Arizona, is shown below to be unrelated to *A. fallax*, and we propose a new genus for it and describe the immature stages. Lastly, we review the status of *Bryophila corticosa* Guenée, purportedly described from North America and placed in *Agriopodes* by McDunnough (1938).

Methods and materials

Morphology. Adult genitalia were prepared using standard methods, described in detail by Lafontaine (2004). Cleaned, stained genitalia were stored and examined in 30% ethanol and slide-mounted in Euparal before being photographed. As Acronictinae, Pantheinae, Balsinae and Raphiinae (the latter included in Dilobinae by Fibiger et al. 2009) are thought to be closely related, we examined the external and genitalic morphology of nearly all New World species presently included in these subfamilies, the vast majority of which are North American (Poole 1989; Lafontaine and Schmidt 2010). We also examined representative species of European and Asian taxa, including type-species of all European (Fibiger et al. 2009) and most Asian acronictine genera (Holloway 2011; Inoue et al. 1982; Kononenko and Han 2007).

Molecular analysis. We compared molecular variation of *Agriopodes fallax* to other Acronictinae using eight gene regions, namely *cytochrome c oxidase subunit 1* (COI) (1477 bp) from the mitochondrial genome and *elongation factor-1 α* (EF-1 α) (1240 bp), *ribosomal protein S5* (RpS5) (617 bp), *carbamoylphosphate synthase domain protein* (CAD) (859 bp), *cytosolic malate dehydrogenase* (MDH) (407 bp), *glyceraldehyde-3-phosphate dehydrogenase* (GAPDH) (691 bp), *isocitrate dehydrogenase* (IDH) (716 bp) and *wingless* (400 bp) genes from the nuclear genome. All genes are single-copy, protein-coding exons and have previously been found to be highly informative in phylogenetic analyses of Lepidoptera at multiple taxonomic levels (Zahiri et al. 2011, 2012, 2013a, b). Voucher data for DNA samples are given in Table 1.

We also examined molecular variation in *A. fallax*, *A. geminata*, *A. tybo*, and more than 80 species of North American Acronictinae, including exemplars from all recognized genera and species groups, using the barcode region (658 bp) of COI gene (Hebert et al. 2003). DNA was extracted from one or two legs removed from a dried specimen and processed at the Canadian Centre for DNA Barcoding, Guelph, Ontario. DNA extraction, amplification and sequencing protocols for the Barcode of Life initiative are given in Hebert et al. (2003). Haplotypes of all barcode sequences were compared initially with phylograms constructed using the (Kimura 2-parameter) neighbor-joining method as implemented on the BOLD website (Ratnasingham and Hebert 2007).

Phylogenetic analysis. Data matrices (6407 bp total) were analysed by non-model-based (parsimony) with equal weighting and model-based evolutionary methods (Bayesian Inference, BI). Parsimony analyses used New Technology heuristic searches

Table 1. Specimen voucher data and GenBank accession numbers for samples used in phylogenetic analysis. Dash indicates DNA markers that did not amplify.

| Code | Genus | Species | Country | CAD | COL-BEGIN | COL-END | EF1A-BEGIN | EF1A-END | GAPDH | IDH | MDH | RPS5 | WINGLESS |
|---------|---------------------|--------------------|---------|----------|-----------|----------|------------|----------|----------|----------|----------|----------|----------|
| MM06745 | <i>Craniophora</i> | <i>ligusri</i> | FINLAND | HQ006948 | HQ006148 | HQ006855 | HQ006246 | HQ006341 | HQ006432 | HQ006498 | HQ006577 | HQ006665 | HQ006757 |
| RZ619 | <i>Harrismammia</i> | <i>tristigmata</i> | USA | – | KC819665 | KC819683 | KC819699 | KC819716 | KC819732 | KC819747 | KC819762 | KC819779 | – |
| RZ620 | <i>Polygrammate</i> | <i>hebraicum</i> | USA | KC819652 | KC819666 | KC819684 | KC819700 | KC819717 | KC819733 | KC819748 | KC819763 | KC819780 | KC819797 |
| RZ607 | <i>Acronicta</i> | <i>modica</i> | USA | – | KJ726386 | KJ726386 | KJ726393 | KJ726393 | KJ726400 | KJ726407 | KJ726416 | KJ726419 | KJ726432 |
| RZ597 | <i>Acronicta</i> | <i>americana</i> | USA | – | KC819662 | KC819680 | KC819696 | KC819713 | KC819729 | KC819744 | KC819760 | KC819776 | KC819794 |
| MM01529 | <i>Acronicta</i> | <i>runicis</i> | FINLAND | GU828163 | GU828666 | GU828464 | GU828997 | GU829280 | GU829792 | GU830053 | GU830372 | GU830662 | GU829551 |
| RZ602 | <i>Acronicta</i> | <i>impletea</i> | USA | KJ726383 | KJ726387 | KJ726387 | KJ726399 | KJ726399 | KJ726401 | – | KJ726417 | KJ726423 | KJ726426 |
| RZ599 | <i>Acronicta</i> | <i>fragilis</i> | USA | KJ726384 | KJ726388 | KJ726388 | KJ726394 | KJ726394 | KJ726402 | KJ726408 | – | KJ726425 | KJ726427 |
| RZ616 | <i>Agriopodes</i> | <i>fallax</i> | USA | – | KC819667 | KC819685 | KC819701 | KC819718 | KC819734 | KC819749 | KC819764 | KC819781 | KC819798 |
| RZ611 | <i>Acronicta</i> | <i>superans</i> | USA | – | KJ726389 | KJ726389 | KJ726395 | KJ726395 | KJ726403 | KJ726409 | KJ726413 | KJ726420 | KJ726430 |
| RZ615 | <i>Acronicta</i> | <i>grisea</i> | USA | – | KJ726390 | KJ726390 | KJ726396 | KJ726396 | KJ726404 | KJ726410 | KJ726414 | KJ726421 | KJ726431 |
| RZ612 | <i>Acronicta</i> | <i>tritona</i> | USA | – | KJ726391 | KJ726391 | KJ726397 | KJ726397 | KJ726405 | KJ726411 | KJ726418 | KJ726422 | KJ726428 |
| RZ613 | <i>Acronicta</i> | <i>vinnula</i> | USA | KJ726385 | KJ726392 | KJ726392 | KJ726398 | KJ726398 | KJ726406 | KJ726412 | KJ726415 | KJ726424 | KJ726429 |

(consisted of Tree Fusion, Ratchet, Tree Drifting and Sectorial searches) implemented in the program TNT v1.1 (Goloboff et al. 2003). The analysis was run with default parameters applied until the most parsimonious tree was found 1000 times. BI analyses implemented using MrBayes v3.1 (Ronquist et al. 2005). Data sets were partitioned by gene region into eight partitions. For the model of sequence evolution, a GTR + Γ model was selected as the most appropriate model for each gene partition based on the Akaike Information Criterion using FindModel (<http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html>). The Bayesian analyses were run for 5 million generations, with every 1000th generation sampled. Clade robustness was estimated by posterior probabilities (i.e., PP) in MrBayes. Convergence was determined when the average standard deviation of split frequencies went below 0.05 and the PSRF (Potential Scale Reduction Factor) approached 1, and both runs had properly converged to a stationary distribution after a burn-in stage (of 5,000 sampled generations).

Immature stages. Last instars of *A. fallax* from 10 km E of Indian Lakes, Hamilton Co., New York were compared with those of all North American genera of Acronictinae, most species of Nearctic *Acronicta* and images of both the European (Beck 1999) and Japanese (Sugi 1987) Acronictinae. Larvae and eggs of *A. tybo* were collected from Velvet Ash (*Fraxinus velutina* Torr., Oleaceae) near the American Museum of Natural History Southwestern Research Station, Cave Creek Canyon, Cochise Co., Arizona, and subsequently reared indoors on White Ash (*Fraxinus americana* L.) and Green Ash (*Fraxinus pennsylvanica* Marsh.).

Results and discussion

Molecular analysis. Phylogenetic analyses of the multi-gene dataset resolved a well-supported monophyletic *Acronicta* clade with the inclusion of *A. fallax*, which placed as the sister species to a group consisting of *A. superans* Guenée, *A. grisea* Walker, *A. tritona* (Hübner) and *A. vinnula* (Grote) (Fig. 1). As discussed below, these four species represent two structurally delimited groups, with *grisea*, *tritona* and *vinnula* in the *tritona*-group and *superans* in the *hasta*-group (Schmidt and Anweiler unpubl. data).

Barcode variation showed that the single sample of *Agriopodes geminata* (641 bp) was very similar to haplotypes of *A. fallax* from ON, MI, FL, GA and OK, differing by 2–3 bp; comparison to barcode variation across *A. fallax* in the BOLD database ($n = 25$) indicated intraspecific variation of up to approximately 1.6% (Ratnasingham and Hebert 2007).

Agriopodes tybo barcode sequence showed little affinity to any sampled Acronictinae, differing by at least 8% from all other sequences in the BOLD database, which contains approximately 7300 species representing 250 genera of Noctuidae globally (BOLD). To explore a potential relationship of *A. tybo* to Amphipyryinae, Psaphidini, we compared *A. tybo* to a dataset constrained to Nearctic psaphidine genera (58 species and 29 genera), but minimum divergences were similarly upwards of 7%; as might be expected, nodes of intergeneric relationships were unsupported (data not shown). Barcode sequence of *A. tybo* was not found to be phylogenetically informative as to prob-

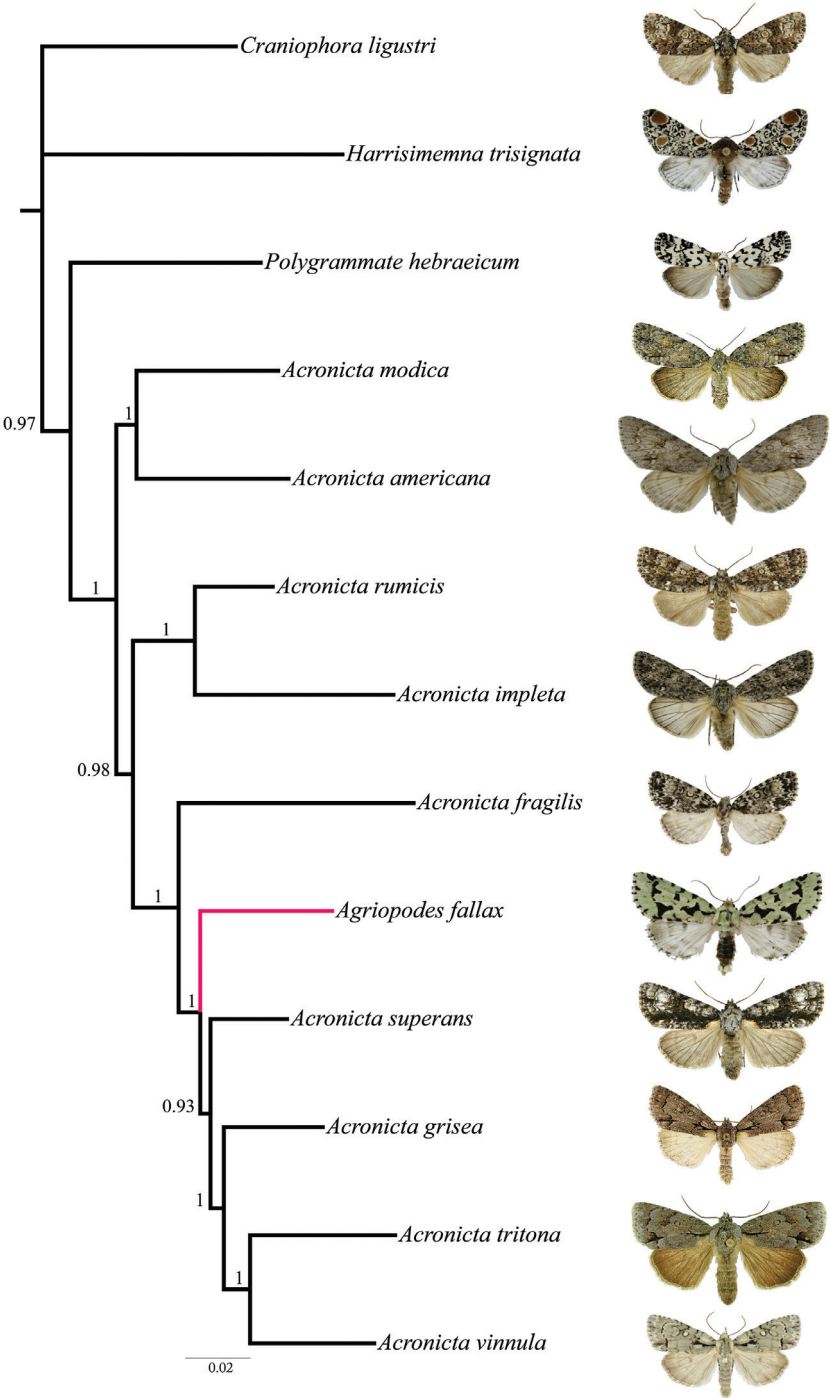


Figure 1. Phylogenetic placement of *Agriopodes fallax* (terminal branch in red) relative to 12 additional acronictine taxa, based on Bayesian analysis of eight gene regions. Bootstrap support values >50% are given for internal branches.

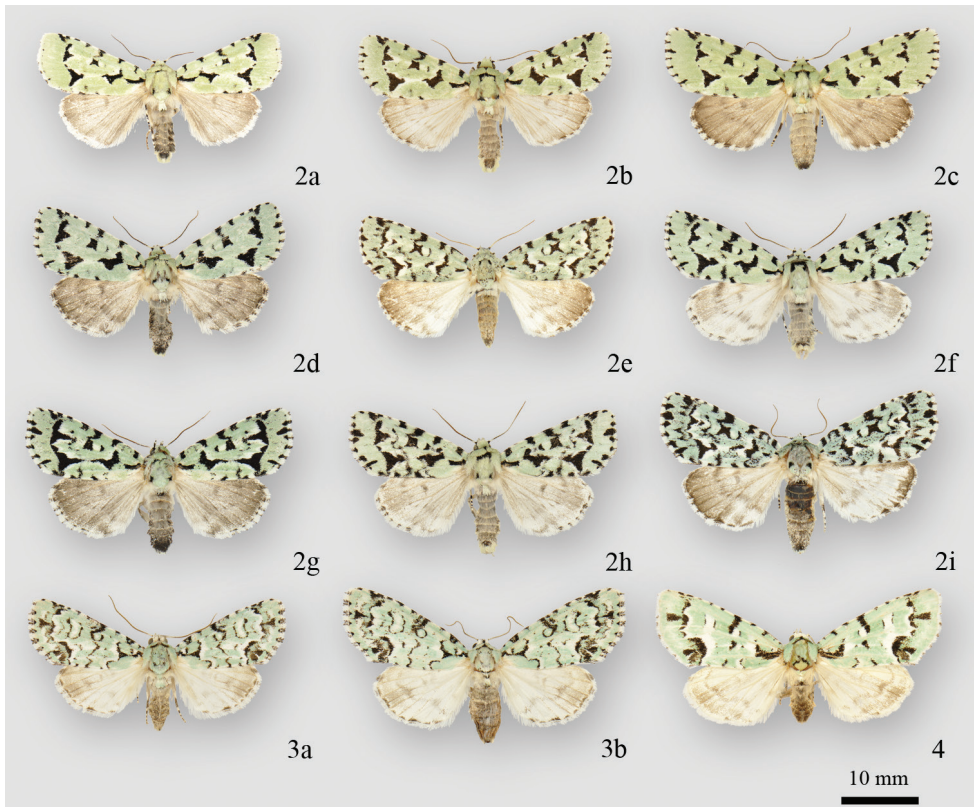
able subfamily membership. The generic placement of *A. tybo* is currently the focus of an expanded study by Wagner et al. (in prep.).

***Acronicta fallax* comb. n.**

Figs 2, 5, 9, 13

Adult morphology. The fate of the genus *Agriopodes* is anchored to the phylogenetic position of *A. fallax*, its type-species. Comparison of genitalic structure of *A. fallax* to all North American and most Eurasian Acronictinae species reveals that genitalic features are most consistent with those found across an endemic North American group of *Acronicta* species, consisting of *A. tritona*, *A. grisea*, *A. falcula* (Grote), *A. lithospila* Grote, *A. hamamelis* Guenée, *A. mansueta* Smith, *A. paralella* (Grote) and *A. vinnula*, here termed the *tritona*-group. Structural synapomorphies for these species are primarily those of the male genitalia (Fig. 5), including a short, claw-like clasper and a broad shield-like juxta (wider than long), with strap-like dorso-lateral extensions. The male vesica structure is moderately complex and consists of a sausage-shaped main chamber that curves ventrally then right laterally, which is armed with short, spade- to thorn-like spines to longer attenuated spines. The size and position of the vesica diverticula are unique, with thumb-like diverticula consistently present in the basal and sub-basal positions, and smaller diverticula variably present in the medial and apical positions. In females, the corpus bursae is relatively broad and rounded, shaped like a heart or a boxing glove with the appendix bursae forming the 'thumb' (Fig. 9). Females of the *tritona*-group (Figs 10, 11) lack the dense, persistent patch of fine, felt-like hairs between the 8th tergite and sternite that is present in the *Acronicta hasta*-group. The *hasta*-group contains at least 14 species, largely corresponding to "Group II" of Forbes (1954). As also suggested by the placement of *A. superans* in our tree (Fig. 1), the *hasta*-group is related to the *tritona*-group, but exhibits a number of distinctive autapomorphies not present in either the *tritona*-group or *A. fallax*, such as a unique hourglass-shaped juxta; modification of the quadrate ventral process of the clasper into a broad, scoop-like flange and a dorsally curved pollex; and as noted above, a patch of persistent felt-like setae on the female A8 pleuron.

Structurally, *A. fallax* shows clear affinities to *A. grisea* and *A. falcula* of the *tritona*-group; the valve, clasper and uncus are much like those of *A. grisea*, with the clasper apex slightly less curved. The dorsolateral straps of the juxta are spinulose, and the medioventral portion of the juxta is produced into a rounded knob that is unique to *A. fallax*, although *A. tritona* shows a rudimentary form of this. Aedeagus and vesica structure of *A. fallax* are also similar to those of *A. grisea* and *A. falcula*, with two basal, unarmed diverticuli, a spinose main chamber, and a finely spinulose distal portion of the main chamber. The large spine field is composed of short, broad-based spines basally, and rounded, spade-like spines distally, similar to those found in *A. tritona*. The female genitalic structure of *A. fallax* is most similar to *A. grisea* (Fig. 10). Larval morphology does not offer support for a special association among *A. fallax* and *tritona*



Figures 2–4. *Acronicta* and *Chloronycta* adults. **2a** *Acronicta fallax* male (North Port, FL) **2b** *Acronicta fallax* male (Hillsboro, MO) **2c** *Acronicta fallax* female (Hillsboro, MO) **2d** *Acronicta fallax* female (Backus Woods, ON) **2e** *Acronicta fallax* male (Cartwright, MB) **2f** *Acronicta fallax* male Edmunston, NB) **2g** *Acronicta fallax* female (Ottawa, ON) **2h** *Acronicta fallax* male (La Verendrye Reserve, QC) **2i** *Acronicta fallax* male (Crooked Lake, SK) **3a** *Chloronycta tybo* male (Huachuca Mtns, AZ) **3b** *Chloronycta tybo* female (Cave Ck. Cyn., Chiricahua Mtns, AZ) **4** *Chloronycta* sp. female (Turundeo, MEX).

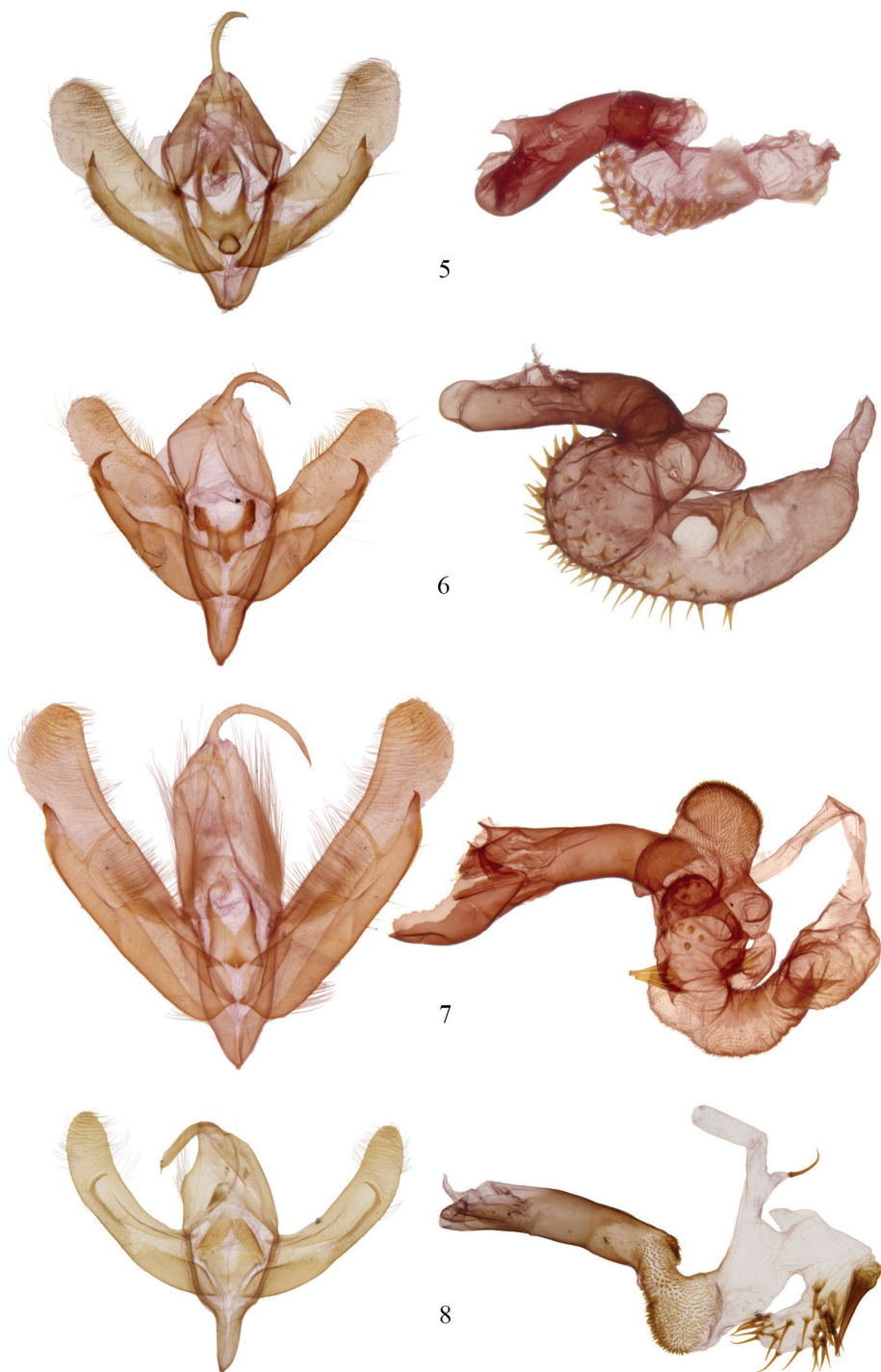
falcula / *grisea*, although there is greater similarity of *fallax* to the *tritona* group than to larvae of the *hasta*-group.

Many *Acronicta* species bear a prominent black basal, anal and apical forewing dash; the basal and anal dashes are sometimes transected by a crescentic line resulting in a dagger-like mark (hence the common name dagger moths). These forewing dashes typical of *Acronicta* are also present in modified form in *A. fallax*, with the apical and anal dash (dagger marks) broadly joined to the postmedial line to form two roughly triangular postmedial patches. The basal dash is short and thick; and there is a black rectangular bar connecting the orbicular and reniform spots; the orbicular and reniform spots are occasionally and then only incompletely outlined. Unlike the green psaphidines (Amphipyridae, Psaphidini: *Feralia* Grote and *Miracavira* Franclemont), the green pigment of *A. fallax* is not sensitive to moisture degradation, where green changes to yellow upon exposure to high humidity (dried specimens of *A. fallax* can

usually be moisture-relaxed without loss of green colouration). This suggests a fundamental biochemical difference in the green pigment of *Acronicta* (found in *A. fallax* and *A. vinnula*) compared to that of psaphidines.

Larval morphology and biology. The immature stages of *A. fallax* were described by Dyar (1899), and Crumb (1956) gives a brief description based on a preserved larva. Illustrations are in Wagner et al. (2011) and McCabe (1991; head capsule and mandible). Dyar described the waxy-white egg as a flattened dome with about 48 radial ridges lacking transverse striae, 2 mm across and 1 mm in height—characters consistent with those of *Acronicta*. *Agriopodes fallax* shares structural similarities with members of the *A. hasta* and *A. tritona* species groups; head often with 6–8 dark (snow-flake-shaped) spots over each somewhat quadrangular lobe, D1 borne from small wart on T1, and the ground colour tends to be green and body height highest through the anterior abdominal segments in both clades. Superficially, *A. fallax* shares greatest similarity with larvae of *A. vinnula* and kin, a member of the *tritona*-group, although we cannot identify its sister taxon with certainty based on our knowledge of its morphology, behavior and natural history.

The mature larva is bright lime to yellowish green with a whitish middorsal and somewhat broader subdorsal stripe, with body tapering posteriorly. The integument is covered with abundant, minute secondary setae in the form of spinules that are slightly thickened basally, giving the integument a velvety texture. With the exception of the D1 pinaculum on T1, which is brownish to red and borne from a small wart, the pinacula are nearly obsolete in the last instar, i.e. flattened, faintly brown or concolourous, and with short setae (pinacula are more elevated and reddish brown with longer setae in middle instars). The greenish head sometimes has paired dark spots above the frons and a field of 6–8 darker spots over each lobe, laterad to apex of frons. The head, usually retracted into the thorax, has a rough, granular surface but lacks secondary setae, and is about 4 mm wide when mature. The thoracic shield is lightly sclerotized; prothorax with XD setae longest on body, extending well forward; XD1 and D1 solitary; D2 setal cluster shifted forward and grouping with XD2 seta; SD and L setae grouped, each comprised of 8–11 setae. Nearly all primary setae are replaced with open but defined clusters of 6–12 setae. Abdomen with D, SD, and L setal clusters more or less vertically aligned; D2 in typical position on A7–A10; solitary seta present below L2 group, well forward of spiracle; L3 group a diffuse set of 9–12 setae; numerous setae in each subventral cluster. A8 spiracle approximately 2 × diameter of those on preceding segments. The anal plate and pinacula are ill defined or undifferentiated, with limits defined by clusters of microspinules, which are largest (some tooth-like) over the anal plate. Prolegs with 23–28 crochets. Length of larva at maturity is 28–30 mm. The prepupal larva turns waxy red, and tunnels into soft wood or spins a flimsy cocoon in a crevice. The larva feeds from the leaf underside of *Viburnum* species, including *V. dentatum* L. (Dyar 1899) and *Viburnum nudum cassinoides* (L.) Torr. & A. Gray (Wagner et al. 2011). Undoubtedly, other *Viburnum* species are used also, particularly by northern populations beyond the range of *V. dentatum* and *V. nudum*. A record for poplars (*Populus* sp.) as a host cited by Tietz (1972) is certainly erroneous.



Figures 5–8. *Acronicta* and *Chloronycta* male genitalia. **5** *Acronicta fallax* **6** *Acronicta grisea* **7** *Acronicta tritona* **8** *Chloronycta tybo*. Reproduced to scale.

***Agriopodes geminata* (Smith)**

Moma geminata Smith, 1903

Remarks. *Acronicta fallax* exhibits a moderate range of geographic variation (Fig. 2), with a gradual increase in size and extent of forewing black markings with increasing latitude. The northwestern-most populations from Manitoba, Saskatchewan and eastern Alberta mark the extreme end of this cline, and have been treated as a separate species, *Agriopodes geminata*. We can find no consistent differences in genitalic structure between *A. fallax* and *A. geminata*, and differences in COI barcodes fall well within the range of variation of *A. fallax*, as discussed above. We therefore consider *geminata* to be a geographic form of *A. fallax* (syn. n.). *Acronicta geminata* Draudt, 1950 of China is a junior secondary homonym of *Acronicta geminata* (Smith), but since we treat the latter as a junior subjective synonym of *A. fallax*, no replacement name for *Acronicta geminata* Draudt is necessary.

***Agriopodes corticosa* (Guenée)**

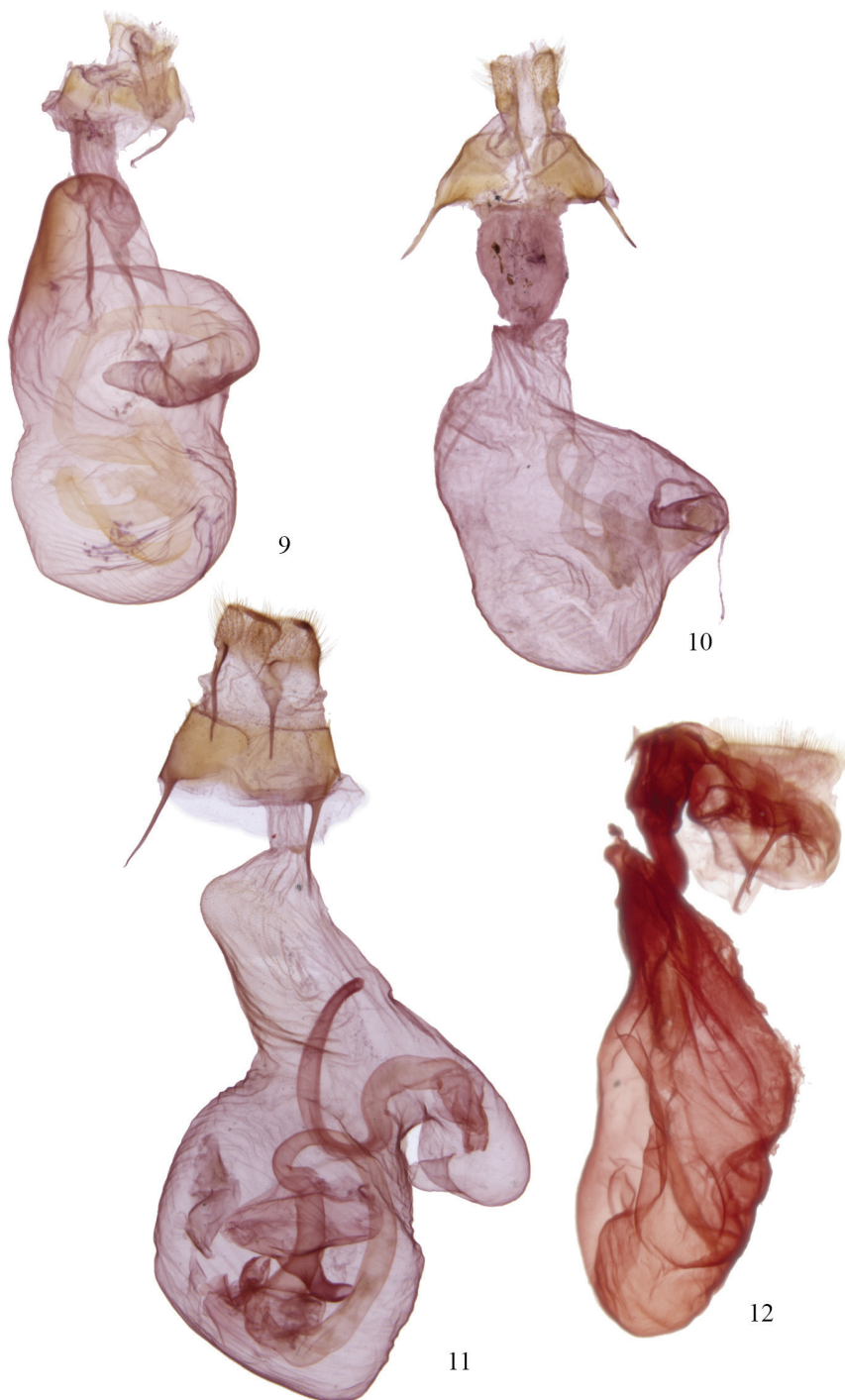
Bryophila corticosa Guenée, 1852

Remarks. The identity of this taxon remains an enigma. We have been unsuccessful in locating type specimens in collections housing Guenée types (The Natural History Museum, London; National Museum of Natural History, Washington, D.C.), and the specimens are presumed to be lost. No illustration accompanied the description, a translation of which follows (our comments in square brackets):

“Same size as [*Noctua*] *Glandifera* [a junior subjective synonym of *Nyctobrya muralis* (Forster, 1771; Bryophilinae), diagnosed by Guenée in the account previous to *corticosa*]. Forewings broad, scaly, variably coloured with greenish white, light brown and black, and with all of the lines black. Basal space also greenish white, with the basal line and one spot at the costal border black. Median space of a grey brown, with the disc [claviform spot] lightly dusted with a fawn color; terminal space spotted with brown. The subterminal line very dark black, very undulated, and more or less parallel to the postmedial line. Fringe whitish, streaked with many fine black lines. Hindwings pearly white, with a blackish shade at the base of the interior [anal] angle and extending nearly halfway along the wing. Underside of the abdomen white. Body rather big. Antennae long.

North America. Boisduval collection. Two specimens.”

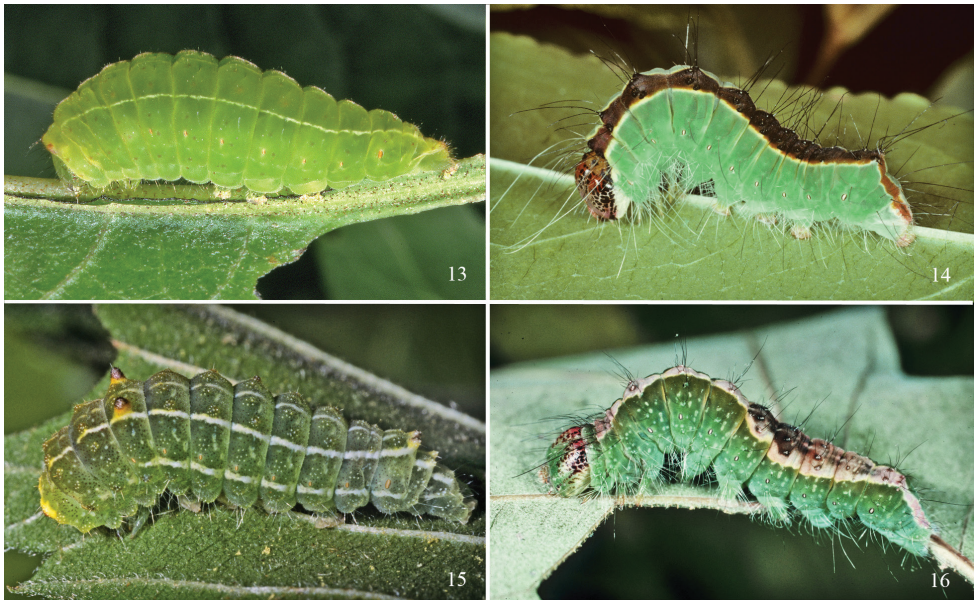
Since its description, the identity of this taxon has been uncertain, and it has often been omitted entirely (e.g., Hampson 1908, 1909). Guenée originally associated it with *Bryophila* Treitschke, and nearly all of Guenée’s *Bryophila* species are currently placed in Bryophilinae (Fibiger et al. 2009), although three Nearctic “*Bryophila*” species are now placed in Noctuidae, Xylenini (*Chytonix palliatricula* (Guenée)) and



Figures 9–12. *Acronicta* and *Chloronycta* female genitalia. **9** *Acronicta fallax* **10** *Acronicta grisea* **11** *Acronicta tritona* **12** *Chloronycta tybo*.

Acronictinae (*Cerma cora* Hübner and *Polygrammate hebraeicum* Hübner) (Lafontaine and Schmidt 2010). Dyar (1902) listed it as *Jaspidia corticosa* (Guenée) along with species now in *Leuconycta*, *Cryphia*, and *Anterastris*. Hampson (1909) established *Agriopodes* but overlooked *corticosa*, and Barnes and McDunnough (1917) subsequently expanded Hampson's concept of *Agriopodes* to include *corticosa* for reasons that are unclear, except perhaps that they felt the original description of *corticosa* rendered it closest to *A. fallax*. The placement of *corticosa* in *Agriopodes* was maintained by Poole (1989). Hodges et al. (1983: p. ix) excluded *Agriopodes corticosa* from the North American fauna based on an assessment that it most likely represented an Asian or South American species.

The description, comparison to *Nyctobrya muralis* (Forster) (see e.g., Fibiger et al. 2009: pl.12 Figs 42–48), and inclusion of other externally similar species (primarily European Bryophilinae) in Guenée's concept of *Bryophila*, leave little doubt that *corticosa* is a greenish-white and black noctuid, probably with a lichen-mimicking pattern (i.e., one that occurs uncommonly but repeatedly in unrelated noctuid lineages). If one assumes the North American origin of the type as correct, there are only a few species that *corticosa* could possibly refer to. All of the approximately 200 North American taxa named by Guenée during this time occur in eastern North America, and none is strictly western, although Boisduval, the source of the *corticosa* types, was describing Californian species at this time. Eastern North American noctuids with pale green forewing patterning include *Feralia* (three species), *Leuconycta* (two species), and *Acronicta fallax*. Guenée named and described *Feralia jocosus* under a different family seven pages after *corticosa*, so in addition to the differences in *Feralia* facies to Guenée's *corticosa* description, *Feralia* can safely be ruled out as a candidate for the identity of *corticosa*. Similarly, *Leuconycta diphtheroides* (Guenée) was described by Guenée four pages after *corticosa*, so this species, and the externally similar *L. lepidula* (Grote), are unlikely candidates for *corticosa*. This leaves the possibility of *A. fallax* as the true identity of *corticosa*, an interesting prospect since *corticosa* would be the senior name. A number of points in Guenée's description of *corticosa*, however, cannot be construed as *A. fallax* characters, most notably the mention of brown colouration in the forewing, presence of a claviform spot, an undulating postmedial line, a white hindwing with dark scaling only at the anal margin, and a smaller wingspan. Expanding the possibilities for the identity of *corticosa* to western North American species likewise provides no further leads; the Nearctic *Cryphia* (endemic to the West) and southwestern *Bryophila* do not match Guenée's description. No European species easily fit the description either, and Guenée gave a diagnosis of all other European Bryophilinae known at that time, so he would have recognized them as such, or at least compared *corticosa* to other European species. The only thing that seems certain is that *Bryophila corticosa* is not identifiable as a European or North American species, as Franclemont and Todd [1983] also concluded, and there is no justification for maintaining it as a species of *Agriopodes*. We therefore consider *Bryophila corticosa*, comb. rev., a *nomen dubium* that cannot be placed in any noctuid subfamily.



Figures 13–16. *Acronicta* last instar larvae. **13** *Acronicta fallax* (Norfolk, CT) **14** *Acronicta superans* (Norfolk, CT) **15** *Acronicta vinnula* (Coventry, CT) **16** *Acronicta lithospila* (Martha's Vineyard, MA).

Fate of *Agriopodes*

The handsome green-mottled forewing colour and pattern of *Agriopodes* have resulted in a century of erroneous systematic placement of the eight species included at one time or another in this genus. Despite the remarkable divergence in wing pattern from other *Acronicta* species, our genitalic, external morphological, larval, and molecular character evidence confidently places *A. fallax* as an *Acronicta*.

The taxonomic fate of *Agriopodes* is complicated somewhat by the broad scope of the genus *Acronicta*. Beck (1999) took the extreme approach of splitting 13 European *Acronicta* species into nine genera, whereas a conservative approach of a single genus with six subgenera was subsequently proposed by Fibiger et al. (2009). Generic or subgeneric division for the North American *Acronicta* has not been proposed but an expanded concept of the genus is generally consistent with the view of Forbes (1954), who recognized five informal species-groups within *Acronicta*. A subgeneric classification similar to the divisions proposed by Fibiger et al. (2009) is being developed for the Nearctic, and reconciled with the Eurasian fauna (Schmidt and Anweiler, in prep.). We do not formally propose *Agriopodes* as a subgenus here, as it requires addressing the remaining genus-group names and more than 80 North American species of *Acronicta*.

***Chloronycta* Schmidt & Anweiler, gen. n.**

<http://zoobank.org/D57F9ACB-5959-4966-BC64-E3D754B69BBE>

Gender. Feminine.

Type species. *Moma tybo* Barnes, 1904.

Diagnosis. Two species are included in *Chloronycta*, *C. tybo* and an undescribed Mexican species near *C. tybo*, known to us from only one female specimen (Fig. 4) and therefore it is not formally described here. The only Nearctic species externally similar to *Chloronycta* is *Acronicta fallax*, but *Chloronycta* lacks the black bar between the reniform and orbicular spots, has the reniform and orbicular stigma finely outlined in black, and has various black markings in the subterminal space, which is entirely green in *A. fallax*. The two genera do not overlap in range, with *Chloronycta* essentially a Mexican taxon reaching southeastern Arizona, and *A. fallax* restricted to deciduous forests of eastern North America. Genitalic structure of the two genera is very different (Figs 5, 8, 9, 12). The main diagnostic characters for *Chloronycta* are 1) forewing ground colour pale bluish green and white, the green colouration not degrading to yellowish with exposure to moisture; 2) valve apex with flattened, corona-like setae; 3) vesica with a single long spine isolated at the base of the ductus ejaculatorius; 4) tympanal sclerite consisting of rounded, adjoining nodules, not flange- or scoop-like.

Description. Head. Antenna of male simple-prismatic, such that ventral margin appears slightly serrate when viewed laterally, evenly ciliate laterally and ventrally; female antenna similar but with segments less produced ventrally; antenna with dorsal scales grey, grading to white scales over basal third, with scattered black scales; haustellum normal, approximately equal in length to that of thorax; eye smooth, round; labial palpus with 3rd segment $0.4 \times$ length of 2nd segment; 1st segment clothed with black spatulate scales dorsally and longer, strap-like white scales ventrally; 2nd segment with short, spatulate white scales apically and basally and with black scales forming broad, dark band medially; 3rd segment with short spatulate white scales and scattered black scales; frons with short, appressed, spatulate scales and longer strap-like scales forming a medial crest near ventral margin; scales of frons white, except for a patch of black scales medio-laterally; occiput with longer spatulate white scales, with black scales forming a black medial crest-like line. Thorax. Prothoracic collar with pale bluish-green spatulate scales, bordered dorsally and along eye margin by narrower black scales; mesothorax, metathorax and tegula clothed in bluish-green spatulate scales, margin of tegula with longer hair-like scales; mesothorax with paired patch of subdorsal black scales at posterior margin; tympanal sclerite raised, rounded and spade-like; prothoracic leg with brown-black and white scaling, femur brown black dorsally and greyish white ventrally; tibia black, with a transverse medial and apical band of white scales; epiphysis $0.5 \times$ length of tibia; tarsal segments black scaled, with a distal band of white scales; scaling pattern of meso- and metathoracic legs similar to that of prothoracic leg; tibial spines white scaled, tibial spine formula

0-2-4. Abdomen. Clothed in a mix of brownish-grey and whitish scales, which are short, spatulate and closely appressed; A1 with a dorsal tuft of long spatulate, bluish-green scales; terminal scales white and hair-like; A8 sternites and tergites normal. Male genitalia (Fig. 8). Uncus rod-like, about $5-6 \times$ as long as wide, with a short, curved terminal spine; tegumen roughly rhomboid and broad, $2.3 \times$ longer than wide; vinculum with saccus well developed, base slightly constricted, $2.5 \times$ longer than base width; valves relatively simple, straplike and parallel sided, about $4.5 \times$ longer than wide, evenly curved in a shallow arc; sacculus moderately developed, clasper well developed but thin, slightly curved with a sharp terminus, located $4/5$ distance to valve apex, ampulla absent; area between clasper and terminus covered in long fine setae, setae on outer $2/3$ thicker and flattened; setae near margin of apex more robust and lance-like, directed towards base of valve; juxta well sclerotized, spinose and rasp-like dorsolaterally, dorsal margin divided; aedeagus $4.5 \times$ longer than wide, nearly straight, slightly decurved ventrally; basal half of vesica angled slightly downward, densely clothed with small but prominent spines, curving dorsad and expanding into a large medioventral diverticulum, this about as wide as long, with 15–20 long prominent spines and two to three massive, partially fused spines at base; vesica narrows abruptly beyond diverticulum, extending anteriorly, poorly differentiated from ductus ejaculatorius; a single prominent, elongate, curved spine arising from small narrow pouch near vesica terminus / base of ductus. Female genitalia (Fig. 12). Corpus bursae elongate globose, $1.25 \times$ longer than wide, with invaginated sclerotized area dorsally at base of ductus bursae; appendix bursae dorsal and to right of ductus bursae, small and indistinct, tapering abruptly to ductus seminalis; ductus bursae membranous, rugose, $1.5 \times$ longer than wide; ostium bursae moderately sclerotized, with v-shaped ventral notch; antevaginal plate somewhat sclerotized and covered with dense, minute setae, projecting caudad as a somewhat pointed scoop; apophyses short, posterior apophysis $0.8 \times$ and anterior apophysis $0.7 \times$ height of papillae; papillae anales densely setose, margin quadrangular with slightly protuberant ventrocaudal angle.

Biology and distribution. *Chloronycta* occurs in the mountainous regions from Mexico to south-eastern Arizona and southwestern New Mexico, where it reaches the northern terminus of its core range in the Sierra Madre Occidental. *Chloronycta tybo* occurs in canyons and mid-elevation wooded habitats, particularly riparian corridors where the larval host plant, *Fraxinus velutina*, grows. The larva and host plant of *Chloronycta tybo* are described here for the first time. The larval description under *A. tybo* in Powell and Opler (2009), based on an account by J. A. Comstock, actually refers to Comstock's (1957) description of *Agriopodes viridata* (Harvey), now placed in the genus *Bryolymnia* (Noctuidae, Elaphriini; Lafontaine et al. 2010).

The first two larval instars (Fig. 17) are leaf skeletonizers that remove patches of leaf tissue from the lower leaf surface. Middle (Fig. 18) and late instars feed from a leaf edge, always from the underside of a blade.

Ultimate instar larva (Fig. 19) (total length to 26 mm, $n = 3$) waxy green, integument translucent, body thickest through A3–A5, strongly tapered rearward. Broken middorsal

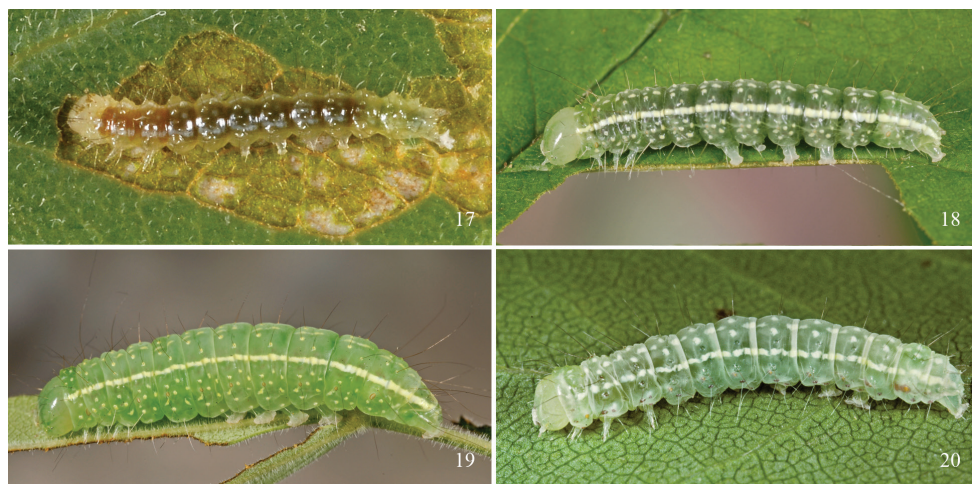
stripe composed of single lines on T2, T3, and A9, and anterior and posterior lines on A1–A8; broad, creamy subdorsal stripe that gradually widens posteriorly, extending from T1 through to and including anal plate. D1 and D2 pinacula free on all segments. Primary setae only, these fine; D, SD, L, and SV group setae borne from cream-yellow, pimple-like pinacula embedded within a pale yellow spot; longest setae black. One additional yellow subventral spot on T1–T3; four additional yellow lateral spots on A1–A8. D2 on T2 extending well forward of head. D2 on all abdominal segments $1.5 \times$ longer than D1. SD1 and L2 very long on abdominal segments, circa $2 \times$ length of an abdominal segment. D2 setae on A9 and A10 elongate, trailing behind body. Prolegs with 32–35 crochets. Spiracles tan yellow with brown peritreme. Entire integument microspinulose. Head immaculate pale green, shiny, translucent; labrum creamy. Prepupal larva flushed with red.

Prepupae tunnel into punky wood when available to form a pupal crypt, largely free of silk, with the exception of that used to weave the frass-silk cover that renders the pupal chamber essentially invisible to the untrained eye.

Remarks. Few acronictine groups have appreciable Neotropical representation (there are no confirmed South American Acronictinae). The majority of species are temperate and cold temperate; one exception in the New World is the *Acronicta theodora* Schaus group, which reaches Costa Rica. Acronictine genera are most diverse in temperate Asia but many genera, subgenera and species-groups are shared between the two realms (e.g. *Harrisimemna* Grote, *Simyra* Ochseneimer and *Acronicta* subgenera *Acronicta*, *Jocheara* Hübner, and *Hyboma* Hübner). *Chloronycta* may also be derived from an Asian ancestral group, although there are admittedly no obvious sister taxa—*Moma* Hübner and *Nacna* Fletcher are similar in facies, but neither belong to the Acronictinae (Wagner et al., in prep).

Despite the very similar forewing colouration of *Chloronycta* to *Acronicta fallax* the two share no uniquely derived structural traits; DNA barcode sequence also does not support an association between with these taxa. Genitalic structure in *Chloronycta* is unique among Acronictinae, and no close relatives are evident. The simple valve structure, short sacculus process along the ventral valve margin, and weakly-developed corona are shared by the Asian acronictine genus *Subleuconycta* Kozhanchikov (Kononenko and Han 2007). Larvae of this Old World genus are not known.

As there are no unequivocal adult or larval autapomorphies for Acronictinae (Kitching and Rawlins 1998; Wagner 2007a, b), we also examined the possibility of *C. tybo* belonging to other basal trifine subfamilies, most notably the Amphipyridae, Psaphidini, which share some similarities with *C. tybo* (elongate valve, flattened setae forming valve corona, green forewing colouration, elongate tegumen). As is the case for Acronictinae (Beck 1999; Wagner 2007a, b), the best diagnostic characters for Psaphidini are those of the immature stages (Wagner et al. 2008). The larva of *C. tybo* shares a number of similarities with those of *Comachara* Franclemont and *Polygrammate* Hübner (Fig. 20; Wagner et al. 2011); all three genera share a similar ground colour; long, slender, darkened dorsal setae; proportionately large, pale green, smooth and unmarked head capsule; thickened subdorsal line and broken middorsal stripe represented by anterior and posterior fragments. Most significantly among the shared features, the first two



Figures 17–20. *Chloronycta tybo* (Cave Creek Canyon, AZ) and *Polygrammate hebraicum* (Cosby, TN) larvae. **17** *C. tybo* early instar **18** *C. tybo* penultimate instar **19** *C. tybo* ultimate instar **20** *P. hebraicum* ultimate instar. In addition to overall resemblance, note similarities in dorsal pattern elements, as well as head allometry, colouration, and luster (particularly between penultimate instar of *C. tybo* and ultimate instar *P. hebraicum*).

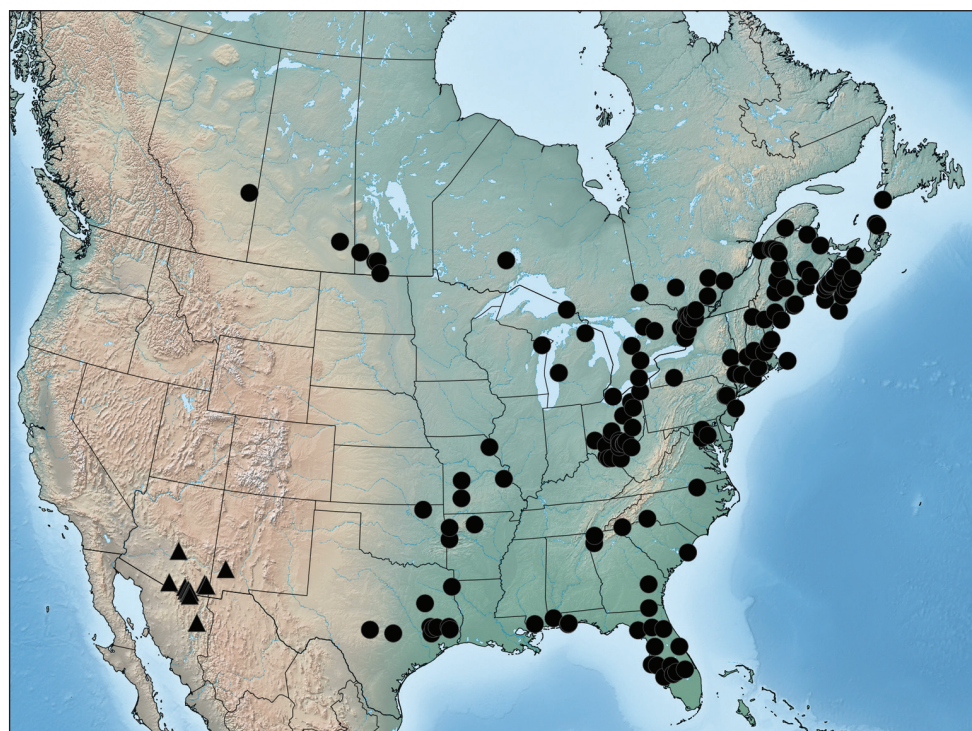


Figure 21. Distribution of *Acronicta fallax* (circles) and *Chloronycta tybo* (triangles) based on material examined in this study.

sets of prolegs are somewhat reduced in size in all three genera. However, the absence of secondary setae immediately differentiates *C. tybo* from all other North American Acronictinae except *Cerma*. Behavioral characters linking *Chloronycta tybo* to many Acronictinae include the wood-tunneling habits of the prepupae; mature larvae excavate pupal chambers in punky wood, then seal the entrance with a sheeting of silk and frass in the same fashion as various acronictine genera. However, while tunneling into wood, *Chloronycta tybo* larvae do not roll the frass shavings into balls as do some basal members of the Acronictinae (e. g., *Comachara*, *Harrisimemna*, and *Polygrammate*) (Wagner 2007a, b). *Chloronycta tybo* turns reddish as a prepupa, as do nearly all wood-tunneling Acronictinae.

The following adult characters associate *Chloronycta* with the Acronictinae: 1) a black 'eye-stripe,' which in the natural resting position of the moth is formed by black scaling on the middle of labial palpus segment 2, on the prothoracic collar behind the eye, and extending into the basal dash of the forewing; 2) dorsal tuft of scales on A1 (occurring also in unrelated subfamilies such as Plusiinae, but absent in Psaphidini); 3) legs strongly banded in black and white, shared with other acronictines including *Polygrammate*, *Harrisimemna*, and *Cerma* (Wagner 2007a, b), but absent in most Amphipyrrinae, Psaphidini (present in *Feralia* and *Miracavira*); 4) flattened, dome-shaped eggs; and 5) Oleaceae as a larval host plant family. The use of *Fraxinus* is very rare among noctuids, only six other North American species (none acronictines) are known to do so (Wagner 2007; Wagner, in prep.). Yet, a number of Asian acronictine genera (*Craniophora* Snellen, *Acronicta* subgenus *Plataplecta* Butler, *Thalatha* Walker, *Thalathoides* Holloway) specialize on this family (Holloway 1989), suggesting an ancient link between *Chloronycta* and the diverse Oleaceae-feeding genera of eastern Asia.

The discovery of a weakly-developed valval corona is noteworthy as all Acronictinae were previously thought to lack this structure (Fibiger and Lafontaine 2005; Lafontaine and Fibiger 2006). If placed correctly in the Acronictinae, the Asian *Subleuconycta* would provide a further example of a corona (Kononenko and Han 2007) in the dagger subfamily. The confirmed presence of this male genitalic trait considerably strengthens the hypothesis that Acronictinae are related to the Amphipyrrinae-group of noctuid subfamilies, and that the presence of secondary larval setae, shared with the more basal Pantheinae lineages, is homoplasious (Zahiri et al. 2013b).

Conclusions

Examination of morphological and molecular data shows that *A. fallax* is phylogenetically rooted to the *Acronicta tritonalhasta* groups, and that *A. fallax* and *A. geminata* are conspecific. Accordingly, we place *Agriopodes* within the current concept of *Acronicta* as a synonym. In contrast, *Chloronycta tybo* is not closely related to *A. fallax*, *Acronicta*, or, evidently, any other genus of Acronictinae, although available evidence places it in the subfamily in the vicinity of basal genera such as *Polygrammate*. Additional morphological and molecular studies with greater taxon sampling are needed to determine its phyloge-

netic position within basal noctuids. *Bryophila corticosa*, previously included in *Agriopodes*, cannot currently be associated with any known Noctuidae species (or subfamily), and remains a *nomen dubium*. The following nomenclatural changes are proposed:

***Acronicta* Ochsenheimer**

Agriopodes Hampson, 1908, *Catalogue of the Lepidoptera Phalaenae in the British Museum* 7: 16. **syn. n.**

Type species. *Moma fallax* Herrich-Schäffer, 1854, by subsequent designation by Hampson 1909, *ibidem*, 8: 37.

***Acronicta fallax* (Herrich-Schäffer), comb. n.**

Diphthera fallax Herrich-Schäffer, [1854], Sammlung neuer oder wenig bekannter aussereuropäische Schmetterlinge 1: pl. 42, f. 211, wrapper.

Type locality. Tennessee, [USA]. [types lost]

Moma geminata Smith, 1903, Journal of the New York Entomological Society 11: 1. **syn. n.**

Type locality. Cartwright, Manitoba [Canada]. [American Museum of Natural History, New York]

***Chloronycta* Schmidt & Anweiler, gen. n.**

Type species. *Moma tybo* Barnes, 1904

***Chloronycta tybo* (Barnes, 1904), comb. n.**

Moma tybo Barnes, 1904, Canadian Entomologist, 36: 166.

Type locality. Cochise Co., Arizona. [National Museum of Natural History, Washington, D.C.]

Within the Noctuoidea, green and black lichen patterning has arisen at least nine separate times in North American taxa: *Afrida* Möschler (Nolidae), *Acronicta* (Acronictinae), *Bryolymnia* and “*Elaphria*” *cyanympa* (Noctuinae, Elaphriini), *Leuconycta* (Condicinae), *Cryphia* (Bryophilinae) and *Feralia*, *Miracavira*, *Emarginea* Guenée (Amphipyriinae, Psaphidini). There are likely also multiple independent derivations in the biochemistry of green-scale pigmentation, since green pigments are moisture sensitive in, for example, psaphidines and geometrines (Geometridae), but not in acronictines. The green pigment may be a novel autapomorphy for the Acronictinae, parallel to the geoverdin pigment present in Geometridae, Geometrinae (Cook et al. 1994).

Acknowledgements

We thank Tim McCabe for the loan of *Agriopodes fallax* larvae, and Jocelyn Gill for preparing the specimen images. Louis Handfield and Suzanne Fauteux kindly translated French text. Evgeny Zakharov, Paul Hebert and other members of the Barcode

of Life Project at the University of Guelph, Ontario, Canada, provided DNA data. Molecular analyses were carried out through grants from the National Science and Engineering Research Council of Canada and Genome Canada through the Ontario Genomics Institute. Jadranka Rota and Niklas Walberg facilitated our efforts during the collection and analysis of the nuclear data reported here. Sam Jaffe was the first to alert us to the presence of *Chloronycta tybo* larvae on ash at Herb Martyr Campground near the Southwest Research Station, Arizona. Lastly, we thank James Adams and an anonymous reviewer for reviewing the manuscript.

References

- Barnes W, McDunnough J (1917) Check list of the Lepidoptera of boreal America. Herald Press, Decatur, 200 pp. doi: 10.5962/bhl.title.10097
- Beck H (1999) Die Larven der Europäischen Noctuidae – Revision der Systematik der Noctuidae (Lepidoptera, Noctuidae). *Herbipoliana* 5 (text): 1–859; 5 (Zeichnungen): 1–447.
- Comstock JA (1957) Notes on the early stages of two western North American moths. *Bulletin of the Southern California Academy of Sciences* 56: 42–47.
- Cook MA, Harwood LM, Scoble MJ, McGavin GC (1994) The chemistry and systematic importance of the green wing pigment in emerald moths (Lepidoptera: Geometridae, Geometrinae). *Biochemical Systematics and Ecology* 22: 43–51. doi: 10.1016/0305-1978(94)90113-9
- Crumb SE (1956) The larvae of the Phalaenidae. Technical Bulletin no. 1135, United States Department of Agriculture, Washington, 356 pp.
- Dyar HG (1899) Life history of *Diphthera fallax* H.-S. *Journal of the New York Entomological Society* 7: 67–68.
- Dyar HG (1902) A list of North American Lepidoptera and key to the literature of this order of insects. *Bulletin of the United States National Museum* 52: 1–723.
- Ferguson DC (1988 [1989]) New species and new nomenclature in the American Acronictinae (Lepidoptera: Noctuidae). *Journal of Research on the Lepidoptera* 26: 201–218.
- Fibiger M, Lafontaine JD (2005) A review of the higher classification of the Noctuoidea (Lepidoptera) with special reference to the Holarctic fauna. *Esperiana* 11: 7–92.
- Fibiger M, Ronkay L, Steiner A, Zilli A (2009) Noctuidae Europaeae. Vol. 11, Pantheinae, Dilobinae, Acronictinae, Eustrotiinae, Nolinae, Bagisarinae, Acontiinae, Metoponiinae, Heliethinae, and Bryophilinae. Entomological Press, Sorø, 504 pp.
- Forbes WTM (1954) Lepidoptera of New York and neighboring states. Part III. Noctuidae. Cornell University Agricultural Experiment Station, Memoir 329: 1–433.
- Franclemont JG, Todd EL (1983) Noctuidae. In: Hodges RW, Dominick T, Davis DR, Ferguson DC, Franclemont JG, Munroe EG, Powell JA (Eds) Check List of the Lepidoptera of America North of Mexico. EW Classey Ltd., London and The Wedge Entomological Research Foundation, Washington, 120–159.
- Goloboff P, Farris J, Nixon K (2003) TNT: tree analysis using new technology. Program and documentation. <http://www.zmuc.dk/public/phylogeny>

- Hampson GF (1908) Catalogue of the Lepidoptera Phalaenae in the British Museum 7: 1–709.
- Hampson GF (1909) Catalogue of the Lepidoptera Phalaenae in the British Museum 8: 1–583.
- Hebert PDN, Cywinska A, Balland SL, deWaard JR (2003) Biological identifications through DNA barcodes. *Proceedings of the Royal Society B* 270: 313–321. doi: 10.1098/rspb.2002.2218
- Hodges RW, Dominick T, Davis DR, Ferguson DC, Franclemont JG, Munroe EG, Powell JA (1983) Check List of the Lepidoptera of America North of Mexico. E. W. Classey Ltd., London and The Wedge Entomological Research Foundation Washington, 284 pp.
- Holloway JD (1989) The Moths of Borneo: Family Noctuidae, trifine subfamilies: Noctuinae, Heliiothinae, Handeninae, Acronictinae, Amphipyrynae, Agaristinae. *Malayan Nature Journal* 42: 57–226.
- Holloway JD (2011) The Moths of Borneo: Families Phauidae, Himantopteridae and Zygaenidae; revised and annotated checklist. *Malayan Nature Journal* 63: 1–548.
- Inoue H, Sugi S, Kuroko H, Moriuti S, Kawabe A (1982) Moths of Japan, Volume 2: Plates and synonymic catalogue. Kodansha, Tokyo, 552 pp.
- Kitching IJ, Rawlins JE (1998) The Noctuoidea. In: Kristensen NP (Ed) *Lepidoptera, Moths and Butterflies. Volume 1: Evolution, Systematics, and Biogeography. Handbook of Zoology, Volume IV, Arthropoda: Insecta*. Walter de Gruyter, Berlin, 355–401.
- Kononenko VS, Han HL (2007) Atlas Genitalia of Noctuidae in Korea (Lepidoptera). In: Park K-T (Ed) *Insects of Korea (Series 11)*. Junhaeng-Sa, Seoul, South Korea, 464 pp.
- Lafontaine JD (2004) Noctuoidea: Noctuidae (part) – Agrotini. In: Hodges RW (Ed) *The Moths of North America (Fascicle 27.1)*. The Wedge Entomological Research Foundation, Washington, 394 pp.
- Lafontaine JD, Fibiger M (2006) Revised higher classification of the Noctuoidea (Lepidoptera). *The Canadian Entomologist* 138: 610–635. doi: 10.4039/n06-012
- Lafontaine JD, Schmidt BC (2010) An annotated check list of the Noctuoidea (Insecta: Lepidoptera) of North America north of Mexico. *ZooKeys* 40: 1–239. doi: 10.3897/zookeys.40.414
- Lafontaine JD, Walsh JB, Holland RW (2010) A revision of the genus *Bryolymnia* Hampson in North America with descriptions of three new species (Lepidoptera: Noctuidae: Noctuinae: Elaphriini). *ZooKeys* 39: 187–204.
- McCabe TL (1991) Atlas of Adirondack Caterpillars with a Host List, Rearing Notes and a Selected Bibliography of Works Depicting Caterpillars. New York State Museum, Bulletin 470: 1–114.
- McDunnough JH (1938) Check list of the Lepidoptera of Canada and the United States of America, Part 1. Macrolepidoptera. *Memoirs of the Southern California Academy of Sciences* 1: 1–275.
- Poole RW (1989) *Lepidopterorum Catalogus (New Series)*. Fascicle 118 Noctuidae, Parts 1–3, EJ Brill, New York, 1314 pp.
- Powell JA, Opler PA (2009) *Moths of Western North America*. University of California Press, Berkeley, California, 369 pp.
- Ratnasingham S, Hebert PD (2007) BOLD: The barcode of life data system (www.barcodinglife.org). *Molecular Ecology Notes* 7: 355–364. doi: 10.1111/j.1471-8286.2007.01678.x

- Ronquist F, Huelsenbeck JP, van der Mark P (2005) MrBayes 3.1 Manual. Published online at: <http://mrbayes.csit.fsu.edu/manual.php>
- Sugi S (Ed) (1987) Larvae of the Larger Moths of Japan. Toppan Printing Co., Ltd., Tokyo, Japan.
- Tietz HM (1972) An index to the described life histories, early stages and hosts of the Macrolepidoptera of the continental United States and Canada. Volume 1. Allyn Museum of Entomology, Sarasota, FL, 536 pp.
- Wagner DL (2007a) The larva of *Cerma* Hübner and its enigmatic linkages to the Acronictinae (Lepidoptera: Noctuidae). Proceedings of the Entomological Society of Washington 109: 198–207.
- Wagner DL (2007b) Barking up a new tree: Ancient pupation behavior suggests *Cerma* Hübner is an acronictine noctuid (Lepidoptera). Systematic Entomology 32: 407–419. doi: 10.1111/j.1365-3113.2006.00378.x
- Wagner DL, McFarland N, Lafontaine JD, Connolly B (2008) Early stages of *Miracavira brillians* (Barnes) and reassignment of the genus to the Amphipyrrinae: Psaphidini: Feraliina (Noctuidae). Journal of the Lepidopterists' Society 62: 121–132.
- Wagner DL, Schweitzer DF, Sullivan JB, Reardon RC (2011) Owlet Caterpillars of Eastern North America. Princeton University Press, Princeton, 576 pp.
- Zahiri R, Kitching IJ, Lafontaine JD, Mutanen M, Kaila L, Holloway JD, Wahlberg N (2011) A new molecular phylogeny offers hope for a stable family-level classification of the Noctuoidea (Lepidoptera). Zoologica Scripta 40: 158–173.
- Zahiri R, Holloway JD, Kitching IJ, Lafontaine JD, Mutanen M, Wahlberg N (2012) Molecular phylogenetics of Erebiidae (Lepidoptera, Noctuoidea). Systematic Entomology 37: 102–124. doi: 10.1111/j.1365-3113.2011.00607.x
- Zahiri R, Lafontaine JD, Holloway JD, Kitching IJ, Schmidt BC, Kaila L, Wahlberg N (2013a) Major lineages of Nolidae (Lepidoptera, Noctuoidea) elucidated by molecular phylogenetics. Cladistics 1(2012): 1–23. doi: 10.1111/cla.12001
- Zahiri R, Lafontaine JD, Schmidt BC, Holloway JD, Kitching IJ, Mutanen M, Wahlberg N (2013b) Relationships of the basal lineages of Noctuidae (Lepidoptera, Noctuoidea) based on eight gene regions. Zoologica Scripta 42: 488–507. doi: 10.1111/zsc.12022

A revision of the genus *Protorthodes* McDunnough with descriptions of a new genus and four new species (Lepidoptera, Noctuidae, Noctuinae, Eriopygini)

J. Donald Lafontaine¹, J. Bruce Walsh², Clifford D. Ferris²

¹ Canadian National Collection of Insects, Arachnids, and Nematodes, Biodiversity Program, Agriculture and Agri-Food Canada, KW Neatby Bldg., C.E.F., Ottawa, Ontario, Canada K1A 0C6 ² Dept of Ecology and Evolutionary Biology, Biosciences West, University of Arizona Tucson, AZ USA 85721; Research Associate: McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA ³ 5405 Bill Nye Ave., R.R. 3, Laramie, Wyoming 82070, USA. Research Associate: McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA; C. P. Gillette Museum of Arthropod Diversity, Colorado State University, Fort Collins, Colorado, USA

Corresponding author: J. Donald Lafontaine (Don.Lafontaine@agr.gc.ca)

Academic editor: C. Schmidt | Received 21 November 2013 | Accepted 27 March 2014 | Published 27 June 2014

<http://zoobank.org/E09C5A85-664A-4305-B82B-45B960595BA1>

Citation: Lafontaine JD, Walsh JB, Ferris CD (2014) A revision of the genus *Protorthodes* McDunnough with descriptions of a new genus and four new species (Lepidoptera, Noctuidae, Noctuinae, Eriopygini). In: Schmidt BC, Lafontaine JD (Eds) Contributions to the systematics of New World macro-moths V. ZooKeys 421: 139–179. doi: 10.3897/zookeys.421.6664

Abstract

The genus *Protorthodes* McDunnough is revised to include 15 species including *P. ustulata* Lafontaine, Walsh & Ferris, **sp. n.**, from southwestern United States, *P. texicana* Lafontaine, **sp. n.**, from Texas and Mexico, and *P. mexicana* Lafontaine, **sp. n.**, from Mexico. A new genus, *Nudorthodes* Lafontaine, Walsh & Ferris, is proposed for two species formerly included in *Protorthodes*, *P. texana* (Smith, 1900), **comb. n.**, and *P. variabilis* (Barnes & McDunnough, 1912), **comb. n.**, and *N. molino* Lafontaine, Walsh & Ferris, **sp. n.**, described from southern Arizona. A key to species, descriptions, illustrations of adults and genitalia, and distribution maps are included.

Keywords

Taxonomy, Noctuinae, Eriopygini, *Protorthodes*, *Nudorthodes*, Arizona, California, Texas, Mexico

Introduction

The genus *Protorthodes* McDunnough was proposed in 1943 for a group of 17 species formerly included in *Orthodes* Guenée. The genus was later expanded to include 21 species (Franclemont and Todd 1983), and then reduced to 15 species by Lafontaine and Schmidt (2010) through new synonymies with *Protorthodes incincta* (Morrison). Here we illustrate and diagnose the 12 known species of *Protorthodes*, describe three new ones, and move two of them to a new genus, *Nudorthodes* Lafontaine, Walsh & Ferris, and we describe a new species of *Nudorthodes*.

Materials and methods

Repository abbreviations

Specimens were examined from the following collections:

| | |
|--------------|---|
| AMNH | American Museum of Natural History, New York, New York, USA |
| AWCC | Arizona Western College Collection, Yuma, Arizona, USA |
| BMNH | The Natural History Museum [statutorily, British Museum (Natural History)], London, UK |
| CDF | Personal collection of Clifford D. Ferris, Laramie, Wyoming, USA |
| CNC | Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Ontario, Canada |
| CUIC | Cornell University Insect Collection, Ithaca, New York, USA |
| FMNH | The Field Museum, Chicago, Illinois, USA |
| IAW | Personal collection of Ian A. Watkinson, Yuma, Arizona, USA |
| JBW | Personal collection of J. Bruce Walsh, Tucson, Arizona, USA |
| TLSRC | Texas Lepidoptera Survey Research Collection, Edward C. Knudson, Houston, Texas, USA |
| USNM | National Museum of Natural History (formerly, United States National Museum), Washington, District of Columbia, USA |

Dissecting methods and terminology. Dissection of genitalia and terms for genital structures and wing markings follow Lafontaine (2004).

Barcode sequences and analysis. Barcode sequences, 658 base-pair sequences of the mitochondrial cytochrome oxidase *c* subunit (CO1 barcodes), were obtained from the Barcode of Life Data (BOLD) System at the University of Guelph, Ontario, Canada, through collaboration with Paul D. N. Hebert. The barcode sequences were compared using neighbour-joining trees constructed using the Kimura-2-Parameter distance model as provided on the BOLD Systems website (www.boldsystems.org) (Ratnasingham and Hebert 2007).

Systematics

Protorthodes McDunnough, 1943

Type species. *Taeniocampa curtica* Smith, 1890, by original designation.

Diagnosis. Adults. Males and females of similar size (forewing length 11–17 mm). Vestiture of palpi, head, and thorax of long apically-forked or apically-serrated scales, sometimes with a slightly-raised central tuft near front of thorax. *Head* – Labial palpus porrect, apical segment about $\frac{1}{2}$ as long as second segment. Frons rounded, covered with strap-like scales projecting over it from sides and top. Eye covered with surface hair. Male antenna biserrate (like toothed edge of a saw) to bipectinate (lateral processes mainly parallel sided like a feather) with lateral processes 0.5–4.0 \times as long as central shaft. Female antenna filiform, setose ventrally. *Thorax* – *Wings*: Forewing ground color typically gray, brown, or orange; pattern variable, typically with reniform and orbicular spots with a pale or black outline, usually lower part or all of reniform spot filled with gray, which is darker than the ground color; postmedial line dentate or with inner element straight, outer element broken into series of dots on veins; subterminal line pale and sinuate in most species with dark wedges or shading along inner margin. Hindwing white to fuscous. *Legs*: Tibiae without spiniform setae. Tarsal segments 1–4 with three ventral rows of spiniform setae, and four ventral rows on tarsal segment 5. *Abdomen* – Base of abdomen without basal abdominal brushes. Eighth abdominal sternum of male with tuft of long setae on a short eversible coremata. *Male genitalia* – Uncus typically slender, slightly swollen mesially, tapered at apex to hook-like process. Valve broadest beyond middle, tapered to slight “neck” defining apical cucullus; sacculus more heavily sclerotized dorsally than ventrally with dorsal part crenulate and setose in some species; clasper a sclerotized plate in middle of valve distal to sacculus from which arises a long, heavily-sclerotized ampulla projecting posterodorsally, extending almost to, or beyond, dorsal margin of valve; ampulla centrally swollen in most species; digitus arising from large sclerotized plate in middle of valve, tapered posterolaterally into heavily-sclerotized pointed or blunt process projecting below ventral margin of valve at neck of cucullus; cucullus covered with long inward-projecting setae and with no defined apical corona. Vesica usually twisted or coiled above base with numerous pouches or diverticula basally and subbasally; a long, heavily-sclerotized basal or subbasal cornutus in most species; vesica 1–2 \times as long as aedeagus. *Female genitalia* – Corpus bursae thin and membranous, rounded or oval, without obvious signa. Appendix bursae typically with one or two short coils. Ductus bursae variably sclerotized, usually about as long as corpus bursae. Abdominal segment eight about 2 \times as long as wide; anterior apophyses 0.5–2.0 \times as long as abdominal segment eight; posterior apophyses folding near middle, about 2.5 \times as long as anterior apophyses. Ovipositor telescoping and projecting well beyond end of abdomen in most specimens. Anal papillae long and tapered, 0.5–1.0 \times as long as abdominal segment eight; anal papillae lightly sclerotized, setae mainly confined to apical area.

Note. Adults of *Protorthodes* are most likely to be confused with those of *Homorthodes* McDunnough and *Nudorthodes* (described below), but the male antennae in *Protorthodes* species are biserrate to bipectinate, whereas those of *Homorthodes* and *Nudorthodes* are filiform, without lateral processes.

Larva and habits. Most species are associated with relatively xeric habitats, but not open deserts, preferring open, dry shrubby or forested areas, especially with pines or fir. The larvae hide in the leaf litter during the day and feed at night on a variety of herbs and low-growing shrubs. The species overwinter as partly grown larvae and emerge as adults between spring and autumn. Adults are nocturnal. The larva can be associated with the tribe Eriopygini by the lack of teeth on the ridges on the inner surface of the mandible, in combination with the hypopharynx lacking a transverse groove that divides the hypopharynx in related tribes into anterior and posterior lobes. Within the Eriopygini, *Protorthodes* is unique in having a pale transverse area on the posterior part of the prothoracic shield, and in having a pair of sclerotized plates between the bases of the abdominal prolegs; the genus also is characterized by the pavement-granulose integument, setae arising from pinacula, head mainly dark with pale patches forming a reticulate pattern, spinneret $2 \times$ as long as the basal segment of the labial palpus, the apical seta of the labial palpus (Lp-2) is less than $\frac{1}{2}$ as long as the basal segment of the palpus (Lp-1), and the spines on the hypopharynx are similar throughout, without the proximal-lateral row of short stout spines found in many other genera. A key to species based on larvae is in Crumb (1956) and Godfrey (1972).

Key to species of *Protorthodes* and *Nudorthodes* (Adults)

- 1 Eye surface hairy (dissecting scope or strong magnifying lens needed); male antenna biserrate to bipectinate; vesica in male genitalia $1-2 \times$ as long as aedeagus; anal papillae mainly smooth, setose only apically (*Protorthodes*) **2**
- Eye surface smooth, hairless; male antenna filiform; vesica in male genitalia $4-5 \times$ as long as aedeagus; anal papillae setose throughout (*Nudorthodes*)... **30**
- 2 Male **3**
- Female..... **17**
- 3 Male antenna bipectinate; pectinations (at least on anterior side) longer than width of antennal shaft and parallel sided **4**
- Male antenna biserrate; serrations no longer than width of antennal shaft and tapered to a point **13**
- 4 Anterior antennal pectinations about $1.5 \times$ as long as shaft width **5**
- Anterior antennal pectinations $2-5 \times$ as long as shaft width..... **8**
- 5 Hindwing pearly white basally with increasing fuscous shading distally and on veins; forewing orbicular spot rounded, defined by black outline; vesica without a basal cornutus or diverticula; mainly southwestern (Texas to California and Mexico), and farther north in western US to southern Oregon ***P. alfkenii***
- Hindwing pale fuscous basally, darker fuscous distally, forewing orbicular spot usually obscure or absent; vesica with large basal cornutus and several diverticula..... **6**

- 6 Forewing dark gray brown with fine black streaks; maculation obscure except for black spot in lower part of reniform spot and a series of minute black wedges defining straight subterminal line; western Great Plains (Alberta to Colorado) and Great Basin (Idaho to Utah, Nevada, eastern California)*P. eureka*
- Forewing varying shades of gray, brown, and reddish brown; subterminal line pale, sometimes with diffuse dark wedges on inner margin of line7
- 7 Forewing gray brown, buffy brown, or reddish brown; subterminal line sinuate near middle; clasper of male with small swollen area immediately above base; widespread in open xeric habitats in Great Plains and southwestern US and locally in Great Basin and Great Lakes States *P. incincta*
- Forewing rusty brown; subterminal line straight or slightly curved; clasper of male with elongated swollen area centered on basal third; widespread in dry forested areas from British Columbia to southern California, extending eastward to western Montana and Ruby Mountains of Nevada *P. curtica*
- 8 Anterior pectinations (rami) of male antenna 4 × as long as central shaft; reniform spot on forewing inconspicuous except for three or four white spots on outer margin; digitus long and tapered; Arizona*P. antennata*
- Anterior pectinations of male antenna 2 × as long as central shaft; reniform spot on forewing darker than ground color and surrounded by pale outline; digitus short and swollen subapically9
- 9 Male hindwing white with some fuscous shading on wing margin and veins; basal part of vesica with swollen lobes projecting to each side; western Texas to southern Utah and California*P. melanopsis*
- Male hindwing fuscous; basal part of vesica cylindrical10
- 10 Dorsal margin of valve with elongated spine-covered process extending to base of clasper; Edwards Plateau of west-central Texas and Mexico.....11
- Dorsal margin of valve without spiny process12
- 11 Forewing brown or gray brown; hindwing fuscous on outer half; clasper with ventral process tapered to blunt point; Edwards Plateau of west-central Texas to southern Mexico (Chiapas).....*P. texicana*
- Forewing pale whitish gray; hindwing white; clasper with ventral process broad and spatulate apically; known only from Guadalajara, Mexico.....*P. mexicana*
- 12 Forewing reddish brown or purplish brown; reniform spot with rounded edges, kidney shaped; coil in vesica near base; occurring across Canada and northern United States southward in the East to northern Florida and in the West in the Rocky Mountain region to Colorado and Utah*P. oviduca*
- Forewing gray brown with dusting of white scales and white-lined maculation giving wing a frosted appearance; reniform spot parallel sided, rectangular; coil in vesica near middle; eastern Texas*P. orobia*
- 13 Forewing with black basal dash and black streak distal to reniform spot; hindwing white with dark terminal line; male genitalia with clasper swollen mesially; New Mexico, east-central Arizona*P. argentoppida*
- Forewing without a basal dash or dark streak distal to reniform spot; hindwing fuscous; male genitalia with clasper even in width14

- 14 Forewing orange with transverse lines prominent; reniform spot with lower half very large and filled with dark-gray shading; sacculus lightly sclerotized; western Texas to southeastern Arizona and southern Mexico ***P. mulina***
- Forewing variable; transverse lines usually obscure; reniform spot kidney shaped, lower part not larger; dorso-posterior part of sacculus heavily sclerotized and spiculate **15**
- 15 Forewing ground color burnt orange, darker on costa with fine white crosslines; valve long, narrow subapically; digitus lightly sclerotized and not extending ventral to lower margin of valve; Colorado, New Mexico, Arizona, western Texas ***P. ustulata***
- Forewing variable; costal area not particularly darker and without fine white crosslines on costa; valve broad, expanded subapically; digitus heavily sclerotized and extending below ventral margin of valve **16**
- 16 Forewing reddish brown, orange brown, or pale gray brown; digitus projecting posteroventrally below ventral margin of valve; Washington to south-western California ***P. rufula***
- Forewing pale gray brown; digitus projecting anteroventrally below ventral margin of valve; western Texas to south-central California and central Mexico ***P. perforata***
- 17 Forewing with black basal dash and black streak distal to reniform spot; New Mexico, eastern Arizona ***P. argentoppida***
- Forewing without a basal dash or dark streak distal to reniform spot **18**
- 18 Forewing orange with transverse lines prominent; reniform spot with lower half very large and filled with dark-gray shading; western Texas to southeastern Arizona and southern Mexico ***P. mulina***
- Forewing variable; transverse lines usually obscure; reniform spot kidney shaped, lower part not larger **19**
- 19 Ductus bursae with enlarged sclerotized area anterior to ostium **20**
- Ductus bursae cylindrical or tapered anteriorly from ostium **24**
- 20 Reniform and orbicular spots defined by pale outline **21**
- Outline of reniform and orbicular spots with dark and light elements **22**
- 21 Anterior 2/3 of ductus bursae with longitudinal sclerotized ridges; Washington to southwestern California ***P. rufula***
- Anterior part of ductus bursae membranous; western Texas to south-central California and central Mexico ***P. perforata***
- 22 Forewing dark gray brown with fine black streaks; maculation obscure except for black spot in lower part of reniform spot and a series of minute black wedges defining straight subterminal line; western Great Plains (Alberta to Colorado) and Great Basin (Idaho to Utah, Nevada, eastern California) ***P. eureka***
- Forewing varying shades of gray, brown, and reddish brown; subterminal line pale, sometimes with diffuse dark wedges on inner margin of line **23**
- 23 Forewing gray brown, buffy brown, or reddish brown; subterminal line sinuate near middle; widespread in open xeric habitats in Great Plains and south-western US and locally in Great Basin and Great Lakes States ***P. incincta***

- Forewing rusty brown; subterminal line straight or slightly curved; wide-spread in dry forested areas from British Columbia to southern California, extending eastward in northern US to western Montana and Ruby Mountains of Nevada..... ***P. curtica***
- 24 Ductus bursae with sclerotized plate on each side projecting posteriorly over ostium **25**
- Ductus bursae without specialized plates projecting posteriorly **28**
- 25 Sclerotized plates fused centrally to form a double-lobed plate over ventral part of ostium; west-central Texas to southern Mexico (Chiapas) [female of *P. mexicana* unknown; would probably key out here] ***P. texicana***
- Sclerotized plates on each side of ductus bursae with middle part of ductus membranous..... **26**
- 26 Forewing light gray brown; central part of ductus bursae with smooth heavily-sclerotized plate; western Texas to southern Utah and California ... ***P. melanopis***
- Forewing brown to reddish brown; central part of ductus bursae with lightly-sclerotized transversely-striated plate **27**
- 27 Forewing reddish brown or purplish brown; reniform spot with rounded edges, kidney shaped; eastern North America west to Texas, Utah, and British Columbia ***P. oviduca***
- Forewing gray brown with dusting of white scales and white-lined maculation giving wing a frosted appearance; reniform spot parallel sided, rectangular; Gulf Coast area of Texas ***P. orobia***
- 28 Ductus bursae mainly membranous with a sclerotized ring at posterior end; Arizona ***P. antennata***
- Posterior $\frac{3}{4}$ of ductus bursae heavily sclerotized **29**
- 29 Forewing with reniform and orbicular spots outlined in white; hindwing fuscous; Colorado, New Mexico, Arizona, western Texas ***P. ustulata***
- Forewing with reniform and orbicular spots outlined in black; hindwing white basally with increasing fuscous shading distally and on veins; mainly southwestern (Texas to California and northern Mexico), farther north in western US to southern Oregon..... ***P. alfkennii***
- 30 Forewing with medial line forming broad dark area from reniform spot to postmedial line; male genitalia with digitus broad and foot-like apically; southeastern Arizona..... ***N. molino***
- Forewing with medial line, if present, a thin line extending down from reniform spot; male genitalia with digitus narrow and tapered apically **31**
- 31 Forewing with orbicular spot pale and contrasting, outlined in black; male genitalia with dorsal process of sacculus almost square, so posterior margin of process straight or slightly curved; Texas to California northward to Oregon and Nevada..... ***N. texana***
- Forewing with transverse lines usually sharply defined in black against a dull-gray or gray-brown ground color; medial line present; male genitalia with posterior margin of dorsal process of sacculus with posteriorly-directed lobe toward top of process; southwestern California..... ***N. variabilis***

Species accounts

Protorthodes curtica (Smith, 1890)

Figs 1–3, 55, 73; Map 1

Taeniocampa curtica Smith, 1890: 122.

Taeniocampa bostura Smith, 1908b: 103.

Type material. *Taeniocampa curtica*: lectotype ♂, examined, AMNH. Type locality: USA, California, Sierra Nevada, designated by Todd (1982). *Taeniocampa bostura*: holotype ♂, examined, AMNH. Type locality: Canada, British Columbia, Kaslo.

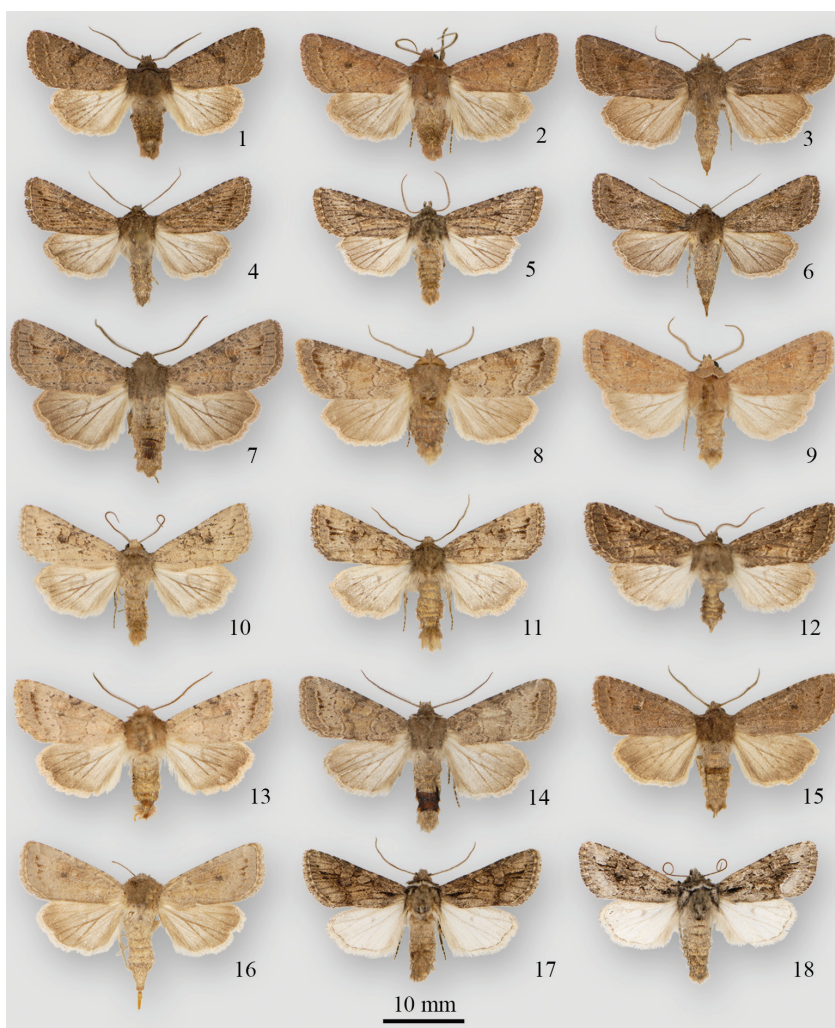
Diagnosis. *Protorthodes curtica* is the dominant species of *Protorthodes* in the Pacific Northwest, especially in the intermontane region between the Cascades and the Rocky Mountains. Superficially, adults usually can be identified by the dark-reddish tint on the forewing ground color, the pale, even-curved subterminal line that follows the wing margin, the even band of dark shading along the inner edge of the subterminal line, and the reniform is faintly outlined by a pale line. Forewing length varies from 12 to 16 mm. The male antenna of *P. curtica* is narrowly bipectinate, similar to those of *P. incincta*, the species with which *P. curtica* is most likely to be confused. The antenna of *P. curtica* is not as wide with the maximum width of the antenna being 2.6–2.9 × as wide as the central shaft, whereas it is 3.7–3.9 × as wide in *P. incincta*. The range of *P. curtica* is mainly to the west of the range of *P. incincta*. Populations of *P. incincta* where its range overlaps that of *P. curtica* usually have gray-brown or buffy-brown forewings with an irregular pale subterminal line that is margined on the inner side with dark shading that usually forms a series of larger wedges in the area distal to the reniform spot. The reniform spot of *P. curtica* is outlined with a dark line with a pale line inside this, and the forewing apex is not as acutely pointed as in *P. incincta*. The male and female genitalia of *P. curtica* and *P. incincta* are similar, but the digitus of *P. curtica* tends to be pointed where it projects beyond the ventral margin of the valve, whereas in *P. incincta* the apex of the digitus is tapered to a point.

Distribution and biology. *Protorthodes curtica* occurs from the interior of southern British Columbia southward in the West Coast states, mainly to the east of the Cascades and Coastal Ranges, to southern California. It occurs in the Rocky Mountains in Idaho and Montana and in the Ruby Mountains of Nevada. Adults occur from late June until mid-October, mainly in dry forested habitats. The larva was described by Crumb (1956) and Godfrey (1972).

Protorthodes eureka (Barnes & Benjamin, 1927)

Figs 4–6, 56, 74; Map 2

Eriopyga eureka Barnes & Benjamin, 1927: 6.



Figures 1–18. *Protorthodes* adults **1** *P. curtica* ♂, USA, California, San Diego Co., Palomar Mountain Rd, 4800' **2** *P. curtica* ♂, USA, Washington, Douglas Co., Pine Canyon 4 mi ENE Orono, 2200–2360' **3** *P. curtica* ♀, Canada, British Columbia, Seton Lake **4** *P. eureka* ♂, USA, Colorado, Moffat Co., Dinosaur National Monument, Harper's Corner Road Canyon Overlook, 7840' **5** *P. eureka* ♂, USA, Wyoming, 28 mi NW Riverton 5700' **6** *P. eureka* ♀, USA, Colorado, Moffat Co., Dinosaur National Monument, Harper's Corner Road Canyon Overlook, 7840' **7** *P. incincta* ♂, USA, Wyoming, Laramie 7500', 41°17'N, 105°31'W **8** *P. incincta* ♂, Canada, Alberta, Lethbridge **9** *P. incincta* ♂, Canada, Alberta, Manyberries, Dominion Range Station **10** *P. incincta* ♂, USA, Colorado, Moffat Co., Dinosaur National Monument, Poole Creek Canyon 5200' **11** *P. incincta* ♂, USA, Wyoming, 7498' (2287 m), 41°17.866'N, 105°31.519'W **12** *P. incincta* ♂, USA, Colorado, Chaffee Co., Buena Vista 7800' **13** *P. incincta* ♂, Canada, Alberta, Dinosaur Prov. Park 2100', 50°41'N, 111°30'W **14** *P. incincta* ♂, USA, New Mexico, Grant Co., 4360', 32°50.86'N, 108°35.56 W **15** *P. incincta* ♂, Canada, Ontario, Long Point, 42°34.82'N, 80°24.61 W **16** *P. incincta* ♀, USA, Nevada, 7 mi S Silver Springs, 4200' **17** *P. argentoppida* ♂, USA, New Mexico, Sandoval Co., La Jara Canyon, Jemez Mts, 7400' **18** *P. argentoppida* ♂, USA, New Mexico, Catron Co., 6200', 33°39.99'N, 108°52.34 W.



Maps 1–6. Distribution of examined material for *Protorthodes* species. **1** *P. curtica* **2** *P. eureka* **3** *P. incincta* **4** *P. argentoppoda* **5** *P. mulina* **6** *P. oviduca*.

Type material. *Eriopyga eureka*: holotype ♂, examined, USNM. Type locality: USA, Utah, Eureka.

Diagnosis. Adults of *Protorthodes eureka* can be recognized by relatively small size (forewing length: 11–13 mm), narrow forewings, and longitudinally-streaked pattern resulting from the dark-colored veins and lighter-brown color between the veins. A series of black sagittate spots is on the inner side of the almost straight subterminal line. The male antenna and male and female genitalia of *P. eureka* are similar to those of *P. curtica*, but the right clasper of *P. eureka* extends beyond the dorsal margin of the valve by about 1/3 of the length of the clasper, whereas in *P. curtica* it exceeds the dorsal margin of the valve by less than 1/5 of its length.

Distribution and biology. *Protorthodes eureka* occurs from southern Alberta southward in the western Great Plains to Colorado and in the Great Basin to east-central California and southwestern Colorado. Adults occur mainly in open xeric, especially sagebrush prairie and open pinyon-juniper woodlands. Adults occur from early August until late September. The larva was described by Crumb (1956) and Godfrey (1972).

***Protorthodes incincta* (Morrison, 1874)**

Figs 7–16, 57, 75; Map 3

Mamestra incincta Morrison, 1874: 156.

Taeniocampa utahensis Smith, [1888]: 473.

Orthodes akalus Strecker, 1899: 6.

Agrotis saturnus Strecker, 1900: 31.

Graphiphora communis race *smithii* Dyar, 1904: 868.

Taeniocampa indra Smith, 1906: 233.

Eriopyga melanopis var. *coloradensis* Strand, [1917]: 29, syn. rev.

Eriopyga daviesi Barnes & Benjamin, 1927: 5.

Type material. *Mamestra incincta*: 3 syntypes. No type material of this species was reported from MSU by Wilterding (1997), so the male syntype in USNM, examined, may be the only extant syntype. Type locality: Illinois. *Taeniocampa utahensis*: lectotype ♂, USNM, designated by Todd (1982), examined. Type locality: USA, Utah. *Orthodes akalus*: holotype ♀, FMNH, photograph examined. Type locality: USA, Colorado. *Agrotis saturnus*: holotype ♂ FMNH, photograph examined. Type locality: USA, southern Wisconsin. *Graphiphora communis* race *smithii*: holotype ♀, USNM, examined. Type locality: USA, Illinois. Note – the type locality for this taxon was given as “Canada, British Columbia, Kootnai District” by Poole (1989). However, the taxon was proposed for a singleton female from Illinois that Smith confused with the species Dyar described from British Columbia, therefore Dyar proposed the racial name *smithii* for this unique specimen. *Taeniocampa indra*: lectotype ♂, AMNH, designated by Todd (1982), examined. Type locality: USA, Arizona, Yavapai County, Minnehaha. *Eriopyga daviesi*: holotype ♂, USNM, ex-

aminated. Type locality: USA, New Mexico, Fort Wingate. *Orthodes melanopis* var. *coloradensis*: holotype ♂, BMNH, examined. Type locality: SW Colorado. Hampson (1905: 299) listed this specimen as “*Eriopyga melanopis* ab. 1.” Strand ([1917]: 29) proposed the name *Eriopyga melanopis* var. *coloradensis* for it. Poole (1989), assuming the name was proposed as an aberration, as Strand usually did, credited McDunnough (1938: 74) as validating the name by using it as a subspecies of *Orthodes melanopis*. However, the specimen is herein reidentified as *Protorthodes incincta*, not *P. melanopis*, so the name is hereby transferred to the synonymy of *Protorthodes incincta*.

Diagnosis. *Protorthodes incincta* is so variable in appearance that it is almost easier to identify it by eliminating the other species. The ground color varies from pale whitish gray, through various shades of brown, orange, and gray to blackish gray. Forewing length varies from 11–14 mm. The moths are most likely to be confused with those of *P. curtica* that mainly occurs farther to the west. *Protorthodes incincta* can be distinguished by the more irregular pale subterminal line, concentration of dark sagittate marks proximal to the subterminal line to the area distal to the reniform spot, and other characters of maculation, antenna, and male genitalia listed under *P. curtica*. The palest forms (e.g., Fig. 16) occur in xeric areas of Nevada, Arizona and New Mexico and previously were known as *P. indra*, and the most contrastingly marked forms (e.g., Figs 11, 12) are localized in southern Wyoming, Colorado, and northern New Mexico and previously were known as *P. daviesi*. However, both forms blend into more typical forms in these areas and do not differ in structural characters or barcodes from other populations.

Distribution and biology. *Protorthodes incincta* is mainly a species of the western Great Plains and dry open forests of the Rocky Mountain region, with range extensions into the Great Basin, the American Southwest, and eastward in relict prairie areas into the Great Lakes region. Adults occur from early June until early October. The larva was described by Crumb (1956) and Godfrey (1972).

***Protorthodes argentoppida* McDunnough, 1943**

Figs 17, 18, 58, 76; Map 4

Protorthodes argentoppida McDunnough, 1943: 52.

Type material. *Protorthodes argentoppida*: holotype ♂ CNC, examined. Type locality: USA, New Mexico, Silver City.

Diagnosis. The name of this species is derived from the silvery-gray ground color of the forewing. This, in combination with the prominent black basal dash on the forewing and the white somewhat translucent hindwing, make this the easiest species of *Protorthodes* to identify. In some males there is a narrow black terminal line and broken postmedial line on the hindwing and in the female the hindwing has a pale smoky tint to the white color. Forewing length varies from 13 to 16 mm. The male antenna

is biserrate, unlike other species in this group, with the maximum width of the antenna being $1.9\text{--}2.1 \times$ as wide as the central shaft. The male and female genitalia are similar to those of the other three species in the *P. incincta* group (*P. curtica*, *P. eureka*, *P. incincta*), surprising, because of the divergent external appearance of the moth. However, the cucullus is smaller, the two digiti apically truncated and more symmetrical, the subbasal diverticula in the vesica are smaller, and the basal cornutus larger than in the other three species in the group.

Distribution and biology. *Protorthodes argentoppida* has a very limited range, occurring in xeric forested areas of various mountain ranges in New Mexico and in the White Mountains in east-central Arizona. Adults occur from mid-May until early July. The immature stages are unknown.

***Protorthodes mulina* (Schaus, 1894)**

Figs 19, 20, 59, 77; Map 5

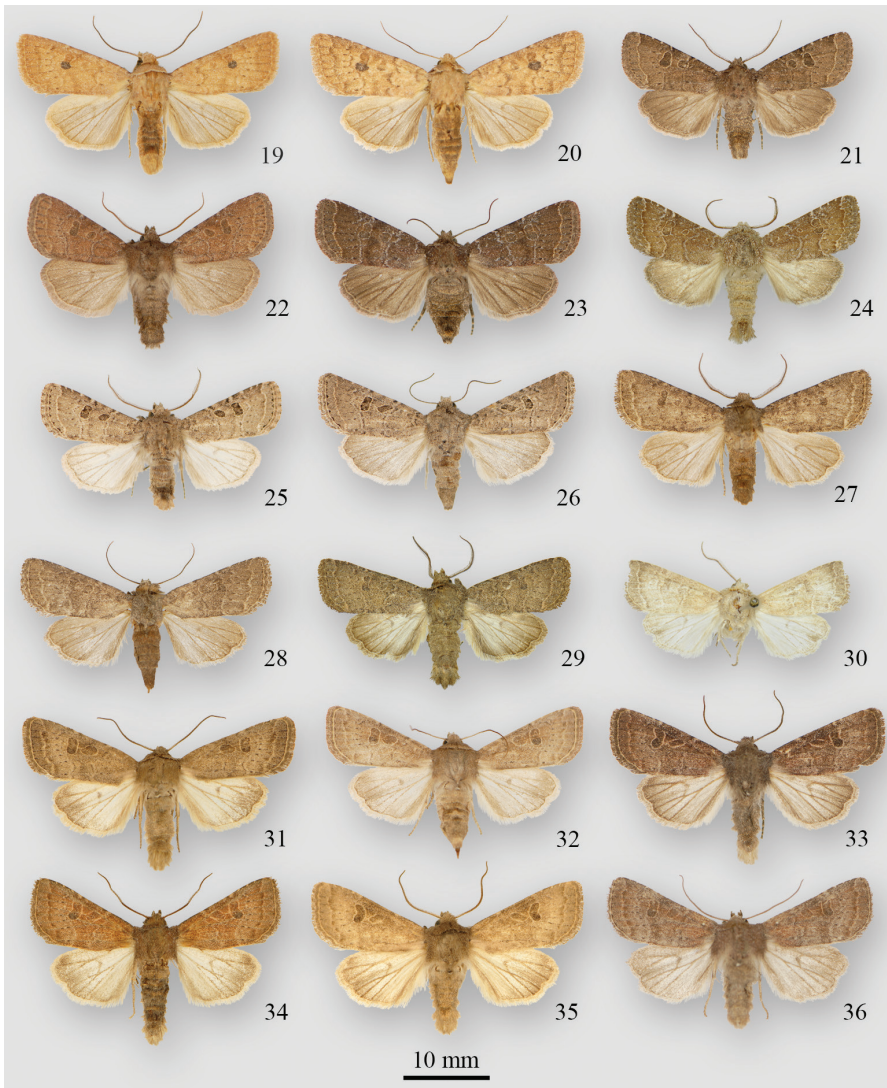
Taeniocampa mulina Schaus, 1894: 237.

Hyssia pseudochroma Dyar, 1913: 288.

Type material. *Taeniocampa mulina*: syntypes in USNM, examined. Type locality: Mexico, [Veracruz], Jalapa. *Hyssia pseudochroma*: holotype ♂, USNM, examined. Type locality: Mexico, [Veracruz], Zacualpan.

Diagnosis. *Protorthodes mulina* is easily recognized by the orange or yellow-orange ground color of the forewing with the maculation defined by darker orange-brown lines, and especially by the enlarged lower lobe of the reniform spot that is filled with a dark blue gray. Forewing length varying from 13 to 17 mm. The male and female genitalia are divergent from other species in the genus, although several features suggest a relationship to the *P. incincta* group; the vesica has a basal cornutus, the subbasal diverticula in the vesica are similar to those of species in the *P. incincta* group, but in *P. mulina* these structures are much larger than those of other species in the *P. incincta* group and the vesica is about twice as long. Unique features of the male genitalia are the enlarged, rounded cucullus, wider than the valve, unlike other species of *Protorthodes*, the clasper is almost straight with an abrupt 90° bend near the apex, and the digitus is reduced, lying entirely along the inner surface of the valve with the apex slightly expanded and forked. The female genitalia, like other species in the *P. incincta* group, has an amorphous sclerotized mass on the posterior part of the ductus bursae; the position and shape of the lobes of the corpus bursae are unique.

Distribution and biology. *Protorthodes mulina* undoubtedly has a wide range in Mexico, occurring as far south as the state of Chiapas, but is known from very few localities. In the United States it occurs from western Texas to southeastern Arizona. Adults are found in May and June and again from mid-August to early November, probably representing two generations. The larva was described by Crumb (1956) and Godfrey (1972).



Figures 19–36. *Protorthodes* adults **19** *P. mulina* ♂, USA, Arizona, Cochise Co., Huachuca Mts, Ash Canyon, 5100' **20** *P. mulina* ♀, USA, Arizona, Cochise Co., Huachuca Mts, Ash Canyon, 5100' **21** *P. oviduca* ♂, USA, Florida, Marion Co., W. Anthony Rd, 1.4 mi WSW Anthony **22** *P. oviduca* ♂, USA, Colorado, Grand Co., Hot Sulphur Springs, 7670' **23** *P. oviduca* ♀, USA, Florida, Marion Co., W. Anthony Rd, 1.4 mi WSW Anthony **24** *P. orobia* ♂, USA, Texas, San Patricio Co., Sinton **25** *P. melanopis* ♂, USA, New Mexico, Grant Co., Mangas Springs **26** *P. melanopis* ♀, USA, New Mexico, Eddy Co., Carlsbad Caverns National Park **27** *P. texicana* ♂ holotype, USA, Texas, Uvalde Co., Concan, 1300' **28** *P. texicana* ♀ paratype, USA, Texas, Uvalde Co., Concan **29** *P. texicana* ♂ paratype, Mexico, Chiapas, San Cristóbal de las Casas, 7200' **30** *P. mexicana* ♂ holotype, Mexico, Jalapa, Guadalajara **31** *P. perforata* ♂, USA, California, San Diego Co., Jacumba, 2850' **32** *P. perforata* ♀, USA, California, San Diego Co., Scissor's Crossing **33** *P. rufula* ♂, USA, Oregon, Josephine Co., Mi 6-13 Illinois River Road **34** *P. rufula* ♂, USA, California, San Diego Co., Torrey Pines State Reserve **35** *P. rufula* ♂, USA, California, Sonoma Co., Petaluma **36** *P. rufula* ♂, USA, California, San Diego Co., Mira Mesa at Penasquitos Canyon.

***Protorthodes oviduca* (Guenée, 1852)**

Figs 21–23, 60, 78; Map 6

Taeniocampa oviduca Guenée, 1852: 357.

Taeniocampa capsella Grote, 1874b: 201.

Protorthodes lindrothi Krogerus, 1954: 20.

Type material. *Taeniocampa oviduca*: type material lost. Type locality: North America. Note: no species is likely to be confused with *Taeniocampa oviduca* in the areas of eastern North America from where Guenée’s material originated, mainly the Southeast (Georgia and Florida), and the Northeast (mainly New York and eastern Canada), so no neotype is proposed. *Taeniocampa capsella*: syntype ♂, BMNH, examined. Type locality: New York, Albany. *Protorthodes lindrothi*: holotype ♂, CNC, examined. Type locality: Canada, Newfoundland, Badger.

Diagnosis. *Protorthodes oviduca* is mainly a boreal-zone species occurring in Canada from coast to coast. Because of its mainly northern and eastern distribution, its range overlaps that of only two other species, *P. curtica* in British Columbia and *P. incincta* in southern Canada and the Rocky Mountain region. Adults can be recognized by the reddish-brown coloration of the forewing and the contrastingly pale outline of the reniform and orbicular spots with the reniform spot usually entirely filled with dark shading. The male antenna is strongly bipectinate, 3.8 to 4.1 × as wide as the central shaft. The forewing length varies from 11 to 14 mm. This and the next two species (*P. orobia* and *P. melanopsis*) form a structurally similar species group in which the ampulla of the clasper is relatively short and teardrop shaped, and does not extend to the dorsal margin of the valve; the digitus is a broad triangular sclerotized plate extending from the costal margin of the valve and tapers ventrally into heavily-sclerotized process with the apex covered with short spines and minute setae and ends near the middle of the valve, not near the “neck” of the cucullus as in other species. The female genitalia of the group are characterized by the sclerotized area toward the posterior end of the ductus bursae, which is heavily sclerotized on each side of the ductus with the central area being only lightly sclerotized. *Protorthodes oviduca* can be distinguished from the other two species in the group by the characters given in the key.

Distribution and biology. *Protorthodes oviduca* occurs across boreal and temperate areas of Canada and northern United States with extensions in eastern US to central Florida and southern Alabama, and in the mountains in the West as far south as Colorado and Utah. In some areas (e.g., Ohio, Michigan) it is found only in sandy habitats (Eric Metzler, pers. comm.). Adults occur mainly from mid-May to early July with occasional records as late as mid-August. The larva was described by Crumb (1956) and Godfrey (1972).

***Protorthodes orobia* (Harvey, 1876)**

Figs 24, 61, 79; Map 7

Mamestra orobia Harvey, 1876: 154.

Type material. *Mamestra orobia*: syntype ♂, BMNH, examined. Type locality: Texas.

Diagnosis. *Protorthodes orobia* is closely related to *P. oviduca*, but can be recognized by the gray-brown color of the forewing with a dusting of white scales that gives the wing a hoary appearance; the maculation is defined by thin white lines with the transverse lines represented on the costa by seven wider white spots that immediately separate this species from *P. oviduca*. Unlike *P. oviduca*, the reniform and orbicular spots of *P. orobia* are concolorous with the rest of the forewing, being defined only by the white outline. The white subterminal line of *P. orobia* is white and contrasting, not yellow buff with red shading on its inner margin as in *P. oviduca*. Structurally, the two species differ by the characters of the vesica given in the key.

Distribution and biology. *Protorthodes orobia* is known only from eastern Texas with most records being on the Gulf Coast. All adults were collected in October. The immature stages are unknown.

***Protorthodes melanopis* (Hampson, 1905)**

Figs 25, 26, 62, 80; Map 7

Eriopyga melanopis Hampson, 1905: 299.

Type material. *Eriopyga melanopis*: syntypes 4 ♂, 1 ♀, BMNH, examined. Type locality: Arizona, Maricopa Co., Phoenix.

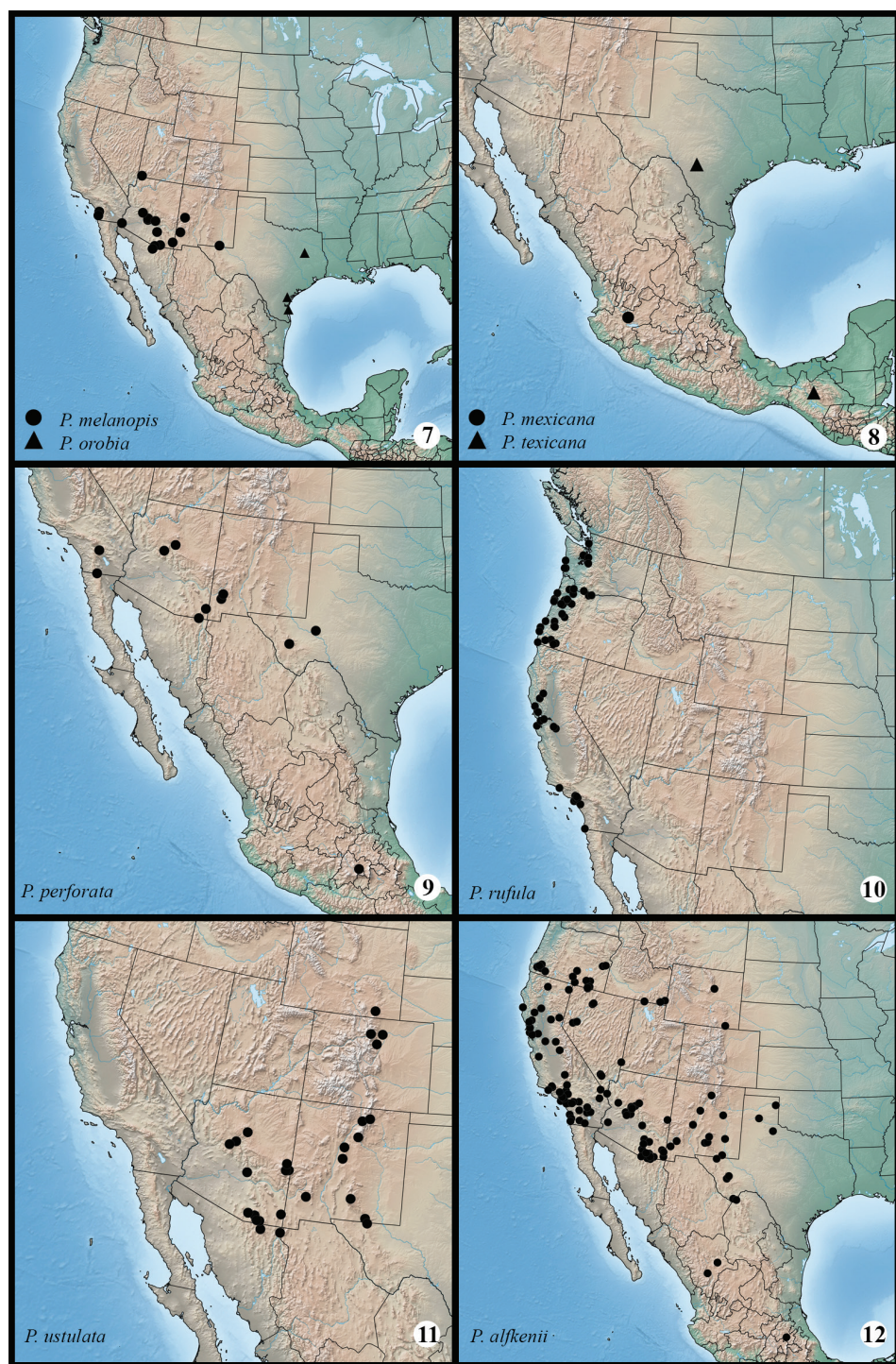
Diagnosis. *Protorthodes melanopis* is most easily recognized by the pale gray-brown forewing ground color, which emphasizes the contrast between the reniform spot, orbicular spot, and the ground color. The pale hindwings of the males contrast with the forewings. Forewing length varies from 11 to 14 mm. In males the hindwing is white and translucent, with some fuscous shading on the veins and wing margin; in females the hindwing is covered with a fuscous sheen, darker on the veins and wing margin. The antennal pectinations and wing size are the same as in *P. oviduca*. Structurally, the species differs from *P. oviduca* by the vesica character given in the key. The coil in the vesica in *P. melanopis* is mesial rather than basal, and the dorsal lobe on the sacculus tapers to a pointed process, whereas the dorsal lobe of the sacculus is rounded in *P. oviduca* and *P. orobia*.

Distribution and biology. *Protorthodes melanopis* occurs across the southern United States from western Texas to southern California. Its range extends as far north as southern Utah and as far south as northern Mexico. Adults were collected from late February to early May and again from mid-August to late September. The larva was described by Godfrey (1972).

***Protorthodes texicana* Lafontaine, sp. n.**

<http://zoobank.org/AB0E914C-193A-483D-9561-170B352D9062>

Figs 27–29, 63, 81; Map 8



Maps 7–12. Distribution of examined material for *Protorthodes* species. **7** *P. orobia* and *P. melanopis* **8** *P. texicana* and *P. mexicana* **9** *P. perforata* **10** *P. rufula* **11** *P. ustulata* **12** *P. alfenii*.

Type material. Holotype ♂. USA, Texas, Uvalde Co., Concan, Neals Lodges, 1300', at uv, 3 April 1990, Noel McFarland. CNC. **Paratypes:** 22 ♂, 23 ♀. Same locality and collector as for holotype, 23 March 1990 (1 ♀); USA, Texas, Uvalde Co., Concan, 3 Oct. 1992, E. Knudson (1 ♂). Mexico, Chiapas, San Cristóbal de las Casas, 7200', 4–29 May 1969, J.E.H. Martin (21 ♂, 22 ♀). Paratypes deposited in CNC, TLSRC, USNM.

Etymology. This species is both Texan and Mexican, thus the name *texicana*.

Diagnosis. *Protorthodes texicana* can be recognized by the brown forewings with the transverse lines defined by pale buff and dark-brown lines, and the reniform and orbicular spots darker brown than the ground color with a pale buff outline. *Protorthodes texicana* is most likely to be confused with *P. oviduca* or *P. orobia*, however, *P. texicana* but does not have the reddish tints to the forewing of *P. oviduca*, and has by the less contrasting white lines on the forewing than *P. orobia*. The male genitalia of *P. texicana* are characterized by large, heavily-sclerotized, spinulose hood-like structure that projects posteriorly from the dorsal margin of the sacculus, and the clasper-digitus combination that creates a structure with three processes; the homologies of this assemblage are best interpreted by comparison with the more rudimentary form found in *P. oviduca*. The female genitalia are characterized by the large, heavily-sclerotized, double-lobed plate covering the ostium bursae ventrally.

Description. Adult. Male and female similar in size, color, and maculation. Forewing length: 12–14 mm. **Head** – Male antenna with individual segments bipectinate, 3.8–4.0 × as wide as the central shaft (anterior rami 1.9–2.1 × as wide, posterior rami 1.4–1.5 × as wide). Female antenna filiform, minutely setose ventrally. Palpi and head clothed with spatulate apically-forked setae, pale buff or gray basally, dark-brown patch subapically, with pale-gray and pale buff tips creating a brown color with a hoary overlay. **Thorax** – Covered with similar scales to those of head; with slightly raised prothoracic and metathoracic tufts. **Legs:** Appearing speckled with mixture of buff and darker gray-brown scales. Tibiae without spiniform setae. Tarsi with three ventral rows of spiniform setae. **Wings:** Dorsal forewing pale brown with dusting of darker-brown scales; subbasal, antemedial, postmedial, and subterminal lines buff, partially bordered by darker-brown scales; reniform spot gray-brown, darker than forewing and with pale-buff outline, with slight constriction on anterior and posterior margin, giving it a figure 8 shape; orbicular spot similar in color, rounded or obliquely oval; fringe with two irregular rows of spatulate scales, pale-brown at base, darker toward tips. Dorsal hindwing pale fuscous basally with darker fuscous on discal spot, wing veins, and marginal area of wing; fringe pale fuscous white with irregular darker fuscous medial line. **Male genitalia** – Uncus mainly evenly tapered from base to apex except slightly swollen laterally subbasally, sparsely covered with long hair-like setae, apex compressed and flattened. Valve gradually tapered from base, abruptly constricted subapically to define a rounded cucullus; sacculus sclerotized, about 0.4 × length of valve, dorsal margin extended into elongated, hollow, hood-like process with outer surface covered by spines, its apex extending to base of ampulla of clasper; ventral base of clasper extending from sacculus ending in rounded lobe from which arises a heavily-sclerotized, partially articulated, tear-drop-shaped process projecting

posteriorly; dorsal base of clasper articulates with long heavily-sclerotized ampulla of clasper with apex spatulate, extending posterodorsally beyond costal margin of valve; digitus appearing to be a heavily-sclerotized extension from editum; apex of digitus a stout apically blunt process with short conical setae-tipped spines at apex; cucullus densely covered with long, stiff setae projecting anterodorsally, and no apical corona; central part of transtilla densely spinulose; juxta a long narrow plate, broad basally, tapered posteriorly with subapical constriction. Aedeagus extended ventrally into short spine-like tip free of vesica. Vesica about $2 \times$ as long as aedeagus; vesica with submedial coil and $\frac{1}{2}$ postmedial coil, the latter with short diverticulum on posterior side; vesica without spines or cornuti. **Female genitalia** – Corpus bursae membranous, rounded, without signa. Appendix bursae with two short coils, arising from posterior dorsal surface of corpus bursae. Ductus bursae $1.5 \times$ as long as corpus bursae, anterior $\frac{2}{3}$ membranous, posterior $\frac{1}{3}$ covered with thin, longitudinal sclerotized striations; a heavily sclerotized, double-lobed plate covering ostial part of ductus bursae and anterior-ventral part of abdominal segment eight; abdominal segment eight $1.5 \times$ as long as wide, lightly sclerotized; anterior apophyses $0.5 \times$ as long as abdominal segment eight; posterior apophyses folding near middle, about $2.5 \times$ longer than anterior apophyses. Anal papillae long and tapered, $0.5 \times$ as long as abdominal segment eight; anal papillae lightly sclerotized, long setae sparsely scattered over surface, short setae abundant near apex of papillae.

Distribution and biology. The immature stages are unknown. *Protorthodes texicana* is known from two areas, west-central Texas and southern Mexico. Adults were collected between late March and late May and in early October. The immature stages are unknown.

***Protorthodes mexicana* Lafontaine, sp. n.**

<http://zoobank.org/C80FBEEF-2BA2-4C96-966C-7517C3CD38EA>

Figs 30, 64; Map 8

Type material. **Holotype** ♂. Mexico, Jalapa, Guadalajara, 28–30 April 1961, Howden & Martin, CNC.

Etymology. This species is known only from Mexico, thus the species name *mexicana*.

Diagnosis. *Protorthodes mexicana* is closely related to *P. texicana*. *Protorthodes mexicana* can be recognized by the pale whitish-buff color of the forewing, the white translucent hindwing. In the male genitalia the ventral process of the clasper assemblage is apically spatulate in *P. mexicana* (apically tapered in *P. texicana*), and the vesica has two full coils ($1\frac{1}{2}$ in *P. texicana*).

Description. Adult male. (Female unknown). Forewing length: 12 mm. **Head** – Male antenna with individual segments bipectinate, $3.8 \times$ as wide as the central shaft (anterior rami $1.9 \times$ as wide, posterior rami $1.4 \times$ as wide). Palpi and head clothed with spatulate apically-forked setae, pale whitish, some with pale-brown patch subapically, with whitish-buff tips. **Thorax** – Covered with similar scales to those of

head; with slightly raised prothoracic and metathoracic tufts. *Legs*: Appearing speckled with mixture of whitish-buff and gray-buff. Tibiae without spiniform setae. Tarsi with three ventral rows of spiniform setae. *Wings*: Dorsal forewing pale whitish buff brown with dusting of pale-brown scales; subbasal, antemedial and postmedial lines very faint, indicated by paler lines bordered on each side by scattered pale-brown scales; subterminal line more distinct because of darker shading in terminal area and outer part of subterminal area adjacent to it; reniform and orbicular spots slightly darker than ground color, outlined in white; terminal area darker than remainder of forewing because of more numerous gray-brown scales; fringe similar in color to subterminal area with base of fringe whitish-buff. Dorsal hindwing white, translucent, with trace of darker scaling on veins and wing margin; fringe white with scattered pale fuscous scales. **Male genitalia** – Similar to those of *P. texicana* with following exceptions: lower process of clasper apically flattened and enlarged, spatulate (apically tapered and tear-drop shaped in *P. texicana*); spine-covered dorsal process of sacculus acutely tapered to point (posterior apex blunt and rounded in *P. texicana*); vesica with two coils (1½ coils in *P. texicana*).

Distribution and biology. The female and immature stages are unknown. The species is known only from the type locality where the holotype was collected in late April.

Protorthodes perforata (Grote, 1883)

Figs 31, 32, 65, 82; Map 9

Taeniocampa perforata Grote, 1883: 73.

Eriopyga constans Dyar, 1918: 344, **syn. n.**

Type material. *Taeniocampa perforata*: syntypes, USNM, examined. Type locality: Arizona. *Eriopyga constans*: holotype ♂, USNM, examined. Type locality: Mexico.

Diagnosis. *Protorthodes perforata* can be recognized by the pale whitish gray to buffy gray color of the forewings with the reniform and orbicular spots darker gray than the ground color and each is outlined by a contrastingly pale line. Forewing length varies from 12 to 14 mm. The hindwing is dirty white with fuscous shading on the wing margins and veins in both sexes. This species is most likely to be confused with *P. rufula* in southern California where their ranges overlap. The forewing in *P. rufula* is darker and more mottled than that of *P. perforata*, and *P. rufula* usually has shades of red in the ground color. Males of *P. perforata* can readily be distinguished from those of *P. rufula* by brushing the scales away from the apices of the valves; in *P. perforata* the apices of the digitus on each valve are similar, barely extend beyond the ventral margins of the valve, and the apices curl to project anteroventrally. In *P. rufula*, by contrast, the left digitus projects posteroventrally, whereas the right digitus is much longer and projects posteriorly and extends beyond the apex of the right valve (Fig. 66). On dissection, the valves of *P. perforata* are very wide postmedially with both the dorsal and ventral margins rounded and

convex; the ampulla of the clasper is almost straight, bending posteriorly only near the apex; the heavily-sclerotized dorsal lobe of the sacculus is much larger and more convex than in *P. rufula*; and the large cornutus in the vesica is near the middle, whereas in *P. rufula* it is much closer to the base of the vesica; also the cornutus projects at a right angle to the axis of the vesica and parallel to the aedeagus. In the female genitalia of *P. perforata* the sclerotized mass of the ostium bursae covers almost the entire ductus bursae and is rounded anteriorly.

Distribution and biology. *Protorthodes perforata* occurs across the southern United States from western Texas to southern California and southward to central Mexico. According to material examined, the range of *P. perforata* lies to the east of that of *P. rufula* with the westernmost records of *P. perforata* being from the desert areas in interior southern California. Adults were collected from early April to early July and again from mid-August to late October. The immature stages are unknown.

***Protorthodes rufula* (Grote, 1874)**

Figs 33–38, 66, 83; Map 10

Dianthoecia rufula Grote, 1874a: 64.

Type material. *Dianthoecia rufula*: holotype ♀, BMNH, examined. Type locality: California, Oakland.

Diagnosis. *Protorthodes rufula* is much more varied in color than *P. perforata* with the forewing varying from pale whitish buff, through various shades of red and orange, to brown. Unlike in *P. perforata*, almost all specimens show some areas or patches of rufous shading and the ground color is much more mottled in *P. rufula*. Forewing length ranges from 13 to 16 mm, averaging larger than in *P. perforata*. In the male genitalia, the right digitus projects posteriorly beyond the end of the valve, whereas on the left valve it is shorter and projects posteroventrally below the valve; the ampulla of the clasper is evenly curved in a rounded arc on both valves; the dorsal lobe of the sacculus is elongated and narrow with the dorsal margin slightly concave and extending into a rounded densely setose lobe anteriorly. The vesica has a long cornutus about 1/3 from the base that projects along the axis of the vesica toward the end of the aedeagus. In the female genitalia the ostium bursae is covered by a heavily-sclerotized ventral plate that is lobed and convex posteriorly and concave where it meets the ductus bursae anteriorly; the ductus bursae is elongated, about 2 × as long as the ostial plate, and is sclerotized with elongated ridges and folds.

Distribution and biology. *Protorthodes rufula* is a species of the far west with most records being from the Pacific Coast, and the coastal mountain ranges from northern Washington to southern California – to the west of the known range of *P. perforata* in southern California. Adults were collected from mid-April to mid-June in the North (from mid-February in southern California) and again from early August to late October. The larva was described by Crumb (1956) and Godfrey (1972).

***Protorthodes ustulata* Lafontaine, Walsh & Ferris, sp. n.**

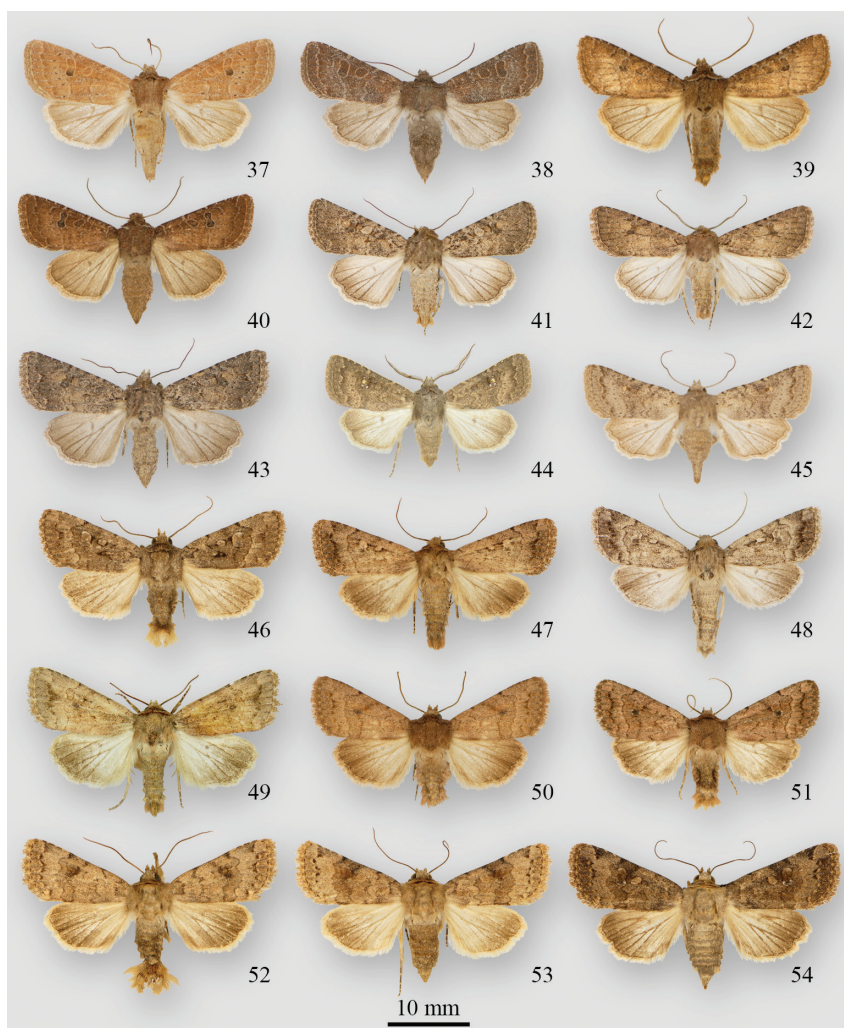
<http://zoobank.org/49452489-03F9-4654-8799-C900EE7692C2>

Figs 39, 40, 67, 84; Map 11

Type material. Holotype ♂. USA, Arizona, Cochise Co., [Chiricahua Mts], Pinery Canyon, 7000', 31°55.99'N, 109°16.33'W, 22 April 2007, C.D. Ferris. CNC. **Paratypes:** 29 ♂, 29 ♀. Type series restricted to specimens from Arizona. Same data as for holotype (1 ♂, 2 ♀); Arizona, Cochise Co., [Chiricahua Mts], Pinery Canyon, 6000', 31°56.89'N, 109°18.40'W, 13 April 2005, C.D. Ferris (3 ♀); Arizona, Cochise Co., Chiricahua Mts, Southwestern Research Station, 8–25 April 1962 (14 ♂, 7 ♀), 18 Sept. 1962 (1 ♀), Carl Kirkwood; Arizona, Cochise Co., [Huachuca Mts], Carr Canyon, 5600', 31°26.38'N, 110°15.87'W, 11 Oct. 2006 (1 ♀), Barcode of Life sample ID # CNCNoctuioidea12245; Arizona, Cochise Co., [Huachuca Mts], Carr Canyon, 5600', 31°26.38'N, 110°17.35'W, 2 Oct. 2004, 10 April 2005, C.D. Ferris (2 ♂); Arizona, Cochise Co., Huachuca Mts, Garden Canyon, 4 Aug. 1966 (1 ♂), 17 Sept. 1967 (1 ♂), R.F. Sternitzky; Arizona, [Cochise Co.], Huachuca Mts, Ramsey Canyon, 24 April 1965 (1 ♀), 17 Sept. 1967 (1 ♂), R.F. Sternitzky; Arizona, [Cochise Co.], Huachuca Mts, Ramsey Canyon, 6000', 15 mi SW Sierra Vista, 5100', 13 May 1967 (2 ♀), R.F. Sternitzky; Arizona, [Cochise Co.], Sierra Vista, 20 Aug. 1966 (1 ♂), 20 Sept. 1967 (1 ♂), R.F. Sternitzky; Arizona, Cochise Co., Huachuca Mts, 5354 Ash Canyon Rd, 0.5 mi W Hwy 92, 15 Sept. 1999, Noel McFarland (1 ♀); Arizona, Pima Co., Madera Canyon, 4600', 23 Sept. 1986, D.F. Hardwick (1 ♀); Arizona, Pima Co., Santa Catalina Mts, Bear Canyon, 4800', [NE of] Tucson, 7 Oct. 2006, Ian A. Watkinson (1 ♀); Arizona, Yavapai Co., 4 mi N Prescott, 31 Aug. 1970 (1 ♂), 8 Sept. 1970 (1 ♂), 25 Aug. 1972 (2 ♀), 9 Sept. 1972 (1 ♀), Lloyd M. Martin; Arizona, [Yavapai Co.], Jerome, 4 mi SSW, 7000', 20 Sept. 1970, D.F. Hardwick (2 ♀); Arizona, Flagstaff, [Coconino Co.], 6850', 31 Aug. 2007, Ian A. Watkinson (1 ♀); Arizona, Apache Co., White Mts, Diamond Rock, 5–6 Sept. 1947, G.H. & J.L. Sperry (4 ♂, 1 ♀); Arizona, Apache Co., 3 mi W Eagar, 7100', 11 Aug. 1962, E. & I. Munroe (1 ♀); Arizona, Apache Co., Alpine, 8117', 31 Aug. 2003, Ian A. Watkinson (1 ♂, 1 ♀); Paratypes deposited in CDE, CNC, IAW, JBW, USNM.

Etymology. The name *ustulata* is Latin and refers to the burnt-orange color of with body and forewings of the species.

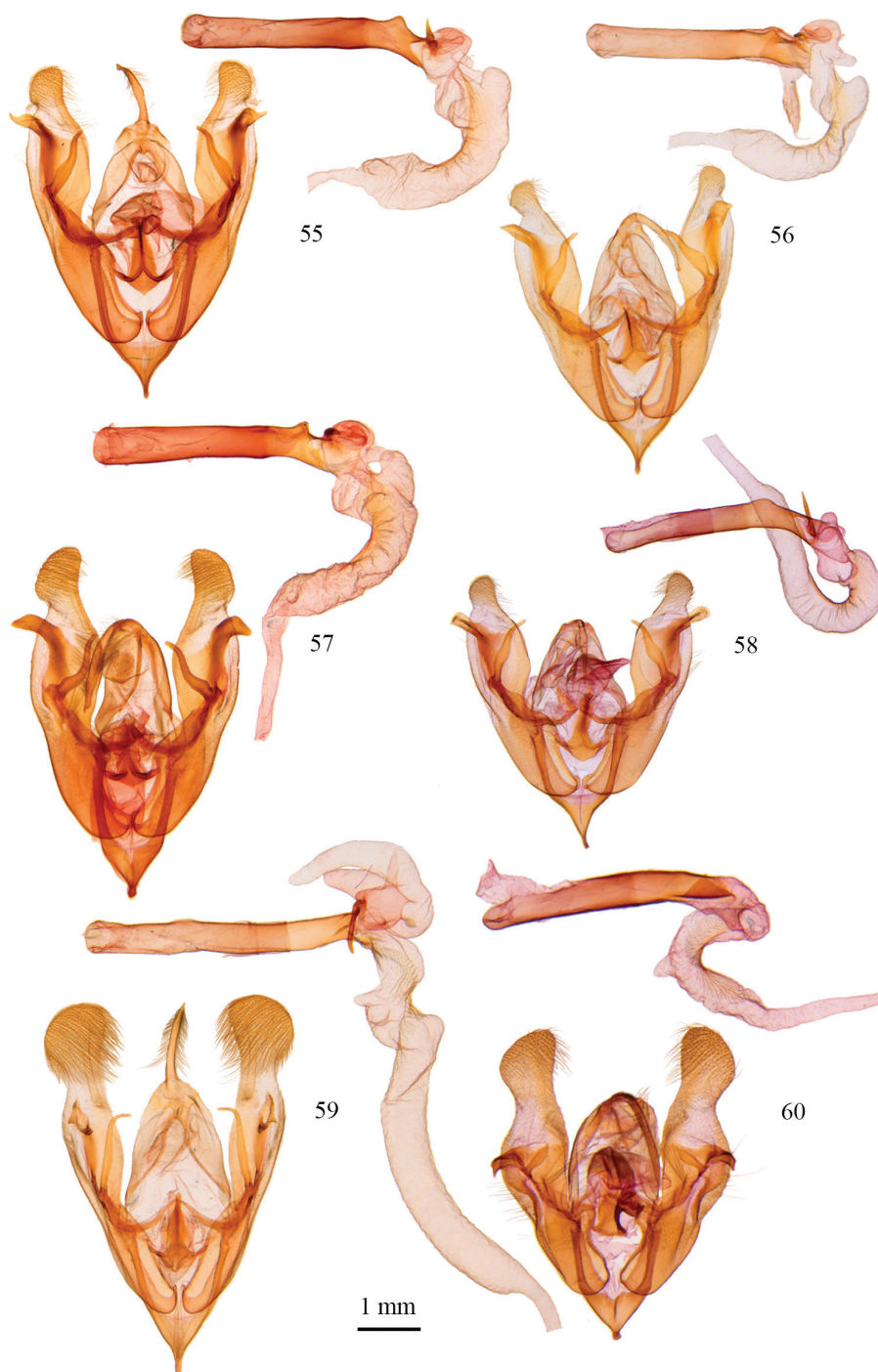
Diagnosis. *Protorthodes ustulata* looks like a dark burnt-orange form of *P. perforata* and was usually identified as either *P. perforata* or as *P. oviduca* in collections because of the orange in the ground color and the contrasting pale outlines around the reniform and orbicular spots. The species appears to be most closely related to *P. perforata* and *P. rufula*, not just because of the superficial similarity, but because of the heavily-sclerotized spiculate lobe on the dorsal part of the sacculus, a structure restricted to these three species. Beyond that, however, *Protorthodes ustulata* is unique within the genus in several features: in the male genitalia the valves are very long and slender and the apices easily broken in brushing or dissection; the digitus is vestigial, ending



Figures 37–54. *Protorthodes* and *Nudorthodes* adults **37** *Protorthodes rufula* ♀, USA, California, Sonoma Co., Petaluma **38** *P. rufula* ♀, USA, California, San Diego Co., Mira Mesa at Penasquitos Canyon **39** *P. ustulata* ♂ paratype, USA, Colorado, Larimer Co., Viestenz-Smith Mtn Park W of Loveland, 5700' **40** *P. ustulata* ♀, USA, New Mexico, Grant Co., Signal Peak, 8020', 32°55.62'N, 108°09.91' W **41** *P. alfenii* ♀, USA, California, San Bernardino Co., San Bernardino Mts, Cactus Flats, 6100' **42** *P. alfenii* ♂, USA, Arizona, Cochise Co., Huachuca Mts, Carr Canyon, 5600' **43** *P. alfenii* ♀, USA, California, Ventura Co., Cuyama Valley, Apache Canyon **44** *P. antennata* ♂, USA, Arizona, Pima Co., Madera Canyon, 4600' **45** *P. antennata* ♀, USA, Arizona, Pima Co., Baboquivari Mts **46** *Nudorthodes texana* ♂, USA, Texas, San Patricio Co., Sinton **47** *N. texana* ♂, USA, Utah, Grand Co., Segoe Canyon, 5900', 39°03.00'N, 109°43.42'W **48** *N. texana* ♂, USA, Nevada, Humboldt Co., Winnemucca Mts, 5600' **49** *N. texana* ♂, USA, California, Yuma Co., Yuma **50** *N. variabilis* ♂, USA, California, Los Angeles Co., La Tuna Canyon **51** *N. variabilis* ♂, USA, California, San Diego Co., Mira Mesa **52** *N. molino* holotype ♂, USA, Arizona, Pima Co., Santa Catalina Mts, mi 5.5 Mt. Lemon Hwy, 4400' **53** *N. molino* paratype ♀, USA, Arizona, Pima Co., Baboquivari Mts, Brown Canyon, 4100' **54** *N. molino* paratype ♀, USA, Arizona, Santa Catalina Mts, mi 5.7 Mt. Lemon Hwy, 4400'.

in small lobe free of surface of valve at ventral margin of valve; the spine-covered dorsal lobe on the sacculus is oblique to the longitudinal axis of the valve. In the female genitalia, the ostium bursae and posterior part of the ductus bursae form an elongated, narrow, heavily-sclerotized tube, and the appendix bursae has two coils, both features otherwise found only in *Protorthodes alfkenii*.

Description. Adult. Male and female similar in size, color, and maculation. Forewing length: 12–15 mm. **Head** – Male antenna biserrate with projections (rami) tapered, anterior rami about as long as width of central shaft, posterior rami half as long. Female antenna filiform, minutely setose ventrally. Palpi and head clothed with spatulate apically-forked setae, dark orange or brown, some with white tips giving head a hoary look, white tips more frequent on margin of prothoracic collar (patagia). **Thorax** – Covered with similar scales to those of head; with slightly raised prothoracic and metathoracic tufts. **Legs:** Appearing speckled with mixture of dark-orange, brown scales, some white tipped. Tibiae without spiniform setae. Tarsi with three ventral rows of spiniform setae. **Wings:** Dorsal forewing a burnt-orange color, tending to be darker toward costal and outer edge of forewing; subbasal, antemedial, postmedial, and subterminal lines whitish gray, partially bordered by dark-brown scales; reniform spot kidney shaped, to markedly constricted mesially, so almost figure 8 shaped, upper part gray brown, lower part blackish gray, overall darker than forewing and with contrasting whitish-gray outline; orbicular spot obliquely oval, slightly darker than ground color, outlined in whitish gray; terminal line dark brown; fringe similar in color to forewing except base yellow with fine yellow streak at end of each wing vein. Dorsal hindwing pale fuscous basally with darker fuscous on discal spot, wing veins, and marginal area of wing; fringe buff white with fuscous medial line. **Male genitalia** – Uncus slender, evenly tapered from base to apex, sparsely covered with long hair-like setae, apex tapered to point. Valve elongated and narrow, about $5 \times$ as long as width at base of clasper, gradually narrowing to long “neck” before rounded cucullus densely covered with long, stiff setae projecting anterodorsally, with no apical corona; sacculus sclerotized, about $0.4 \times$ length of valve, ending posteriorly in spine-covered oblique lobe, somewhat mushroom shaped, with sides extending posteroventrally almost to ventral margin of valve and anterodorsally over dorsal margin of valve; clasper about $1/3$ length of valve, curved in slight arc to project posterodorsally over dorsal margin of valve; digitus vestigial, a slightly raised, lightly sclerotized rod extending to base of “neck” of cucullus and ending in slightly raised lobe projecting posteroventrally to ventral margin of valve; juxta a long posteriorly-tapered plate with middle cleft and lightly sclerotized almost to anterior end, posterior apices on each side of cleft pointed and heavily sclerotized. Aedeagus long and cylindrical, $12 \times$ as long as medial width, mainly lightly sclerotized except for posterior half of ventral margin, which ends in slightly-sclerotized lobe. Vesica about $1.5 \times$ as long as aedeagus; vesica with slight basal coil from which arises a curved, tapered diverticulum, and a medial coil with a minute diverticulum; apex of vesica swollen; vesica without spines or cornuti. **Female genitalia** – Corpus bursae membranous, rounded,



Figures 55–60. *Protorthodes* male genitalia. **55** *P. curtica*; CNC slide 15555 **56** *P. eureka*; CNC slide 10889 **57** *P. incincta*; CNC slide 15327 **58** *P. argentoppida*; CNC slide 15237 **59** *P. mulina*; CNC slide 15576 **60** *P. oviduca*; CNC slide 15238.

without signa. Appendix bursae with two short coils, arising from posterior dorsal surface of corpus bursae. Ductus bursae $0.6 \times$ as long as corpus bursae, anterior $1/3$ membranous, posterior $2/3$ covered with smooth heavily-sclerotized plate, slightly wider anteriorly than posteriorly; ostium not differentiated from ductus bursae; abdominal segment eight slightly longer than wide, more lightly sclerotized posteriorly; anterior apophyses slightly longer than abdominal segment eight; posterior apophyses folding near middle, about $2 \times$ as long as anterior apophyses. Anal papillae long and tapered, $0.75 \times$ as long as abdominal segment eight; anal papillae lightly sclerotized, long setae sparsely scattered over surface, short setae abundant near apex of papillae.

Distribution and biology. *Protorthodes ustulata* occurs from southeastern Wyoming southward to the Guadalupe Mountains in western Texas and westward to central and southeastern Arizona and northern Mexico. Adults were collected from early April to mid-May and again from early August to early October. The immature stages are unknown.

***Protorthodes alfkenii* (Grote, 1895)**

Figs 41–43, 68, 85; Map 12

Perigea alfkenii Grote, 1895: 79.

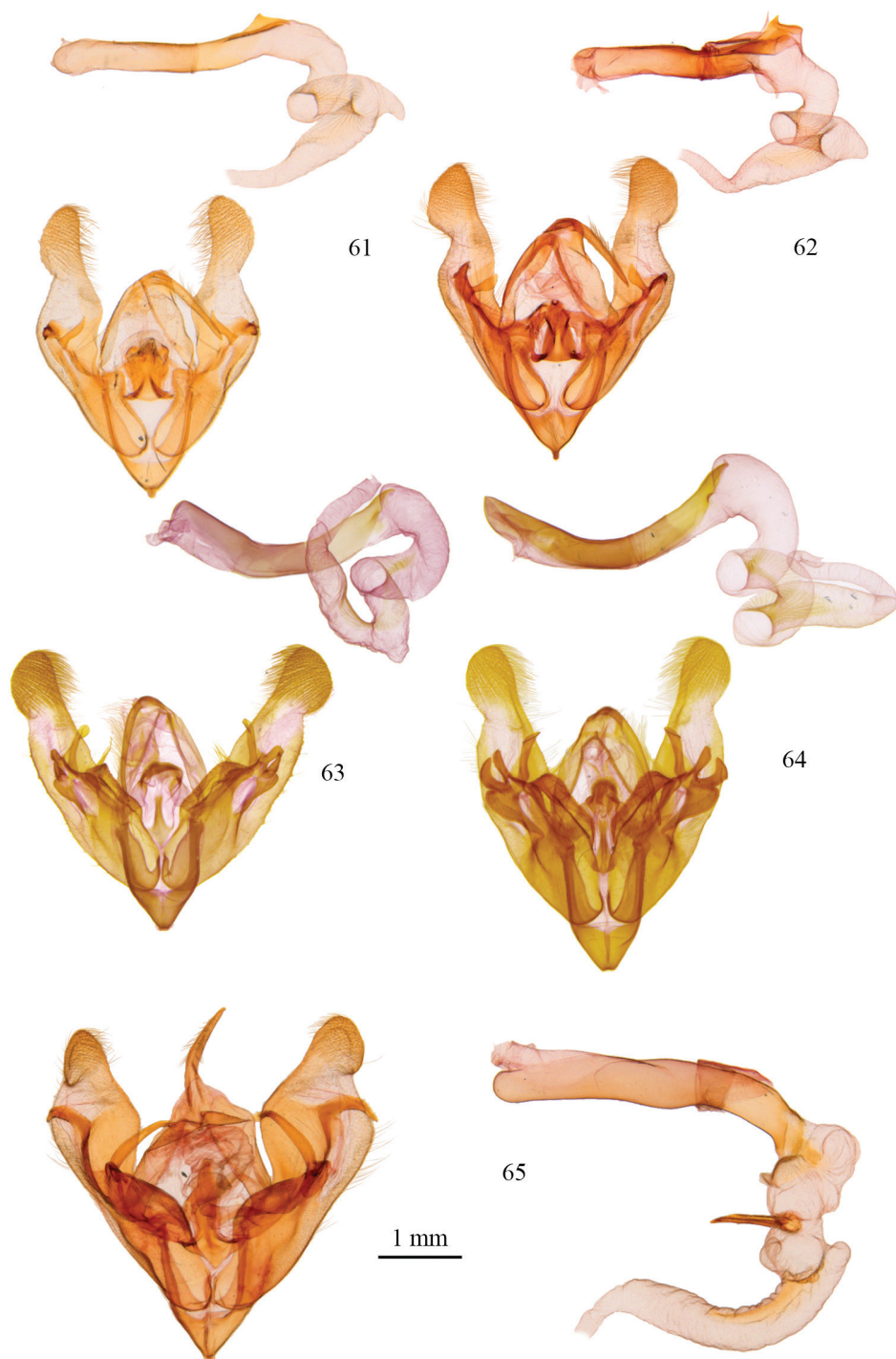
Perigea latens Smith, 1908a: 92.

Taeniocampa occluna Smith, 1909: 64.

Type material. *Perigea alfkenii*: syntypes, 1 ♂ male, 2 ♀ females, USNM, examined. Type locality: [southwestern USA]. *Perigea latens*: lectotype ♂, USNM, examined. Type locality: California, San Diego. *Taeniocampa occluna*: holotype ♂, USNM, examined. Type locality: New Mexico, Mesilla Park.

Note. The name *Perigea perplexa* was listed without description by Smith (1893) and credited to Grote by virtue of Grote distributing the name through his check lists, which lacked any description. Grote described *Perigea alfkenii* in 1895 and lists *Perigea perplexa* as his check list manuscript name for it. Hampson (1909) lists *Perigea perplexa* as an unavailable senior synonym of *Perigea alfkenii* and credits the name to Smith. Franclemont and Todd (1983) simply list *Protorthodes* [*Perigea*] *perplexa* (Grote, 1895) as a synonym of *Protorthodes alfkenii*. The name, neither validated, nor made available, should be deleted from the synonymy.

Diagnosis. *Protorthodes alfkenii* is an extremely variable species in terms of size, ground color, and pattern, yet with practice it usually is easily identified by a combination of features. The orbicular spot usually is rounded, surrounded by a thin black line, and the spot itself usually is paler than the ground color, often contrasting so; the reniform spot is oblique, unlike other species in the genus, with the lower part of the spot projecting toward the anal angle of the wing; the light and dark marks on the forewing, and the tendency for longitudinal streaks on the wing, give the forewing a busy appearance instead of



Figures 61–65. *Protorthodes* male genitalia. **61** *P. orobia*; CNC slide 15580 **62** *P. melanopis*; CNC slide 11603 **63** *P. texicana*; CNC slide 15658 **64** *P. mexicana*; CNC slide 11593 **65** *P. perforata*; CNC slide 11478.

the softer, more even ground pattern of most other species. The hindwing in males, and many females, is white, often with a slight pearly sheen, with fuscous shading confined to the veins and outer part of the wing. Some females have more extensive fuscous shading on the hindwings, but usually a pearly sheen is still evident. Forewing length varies from 11 to 14 mm. The male genitalia differ from those of other species of *Protorthodes* in that the digitus is long and pointed, projecting below the ventral margin of the valve at a right angle, the ampulla of the clasper is almost straight, projecting dorsoposteriorly toward the upper part of the cucullus, then bending abruptly through 90° near its apex to project ventrally. The vesica has 2½ medial coils and projects anterolaterally to the right from the end of the aedeagus. In the female genitalia the appendix bursae has two full coils and is at the posterior end of the corpus bursae on the left side. The ductus bursae is long and cylindrical, about 7 × as long as wide with the posterior 4/5th lightly sclerotized.

Distribution and biology. *Protorthodes alfkenii* is the most abundantly collected species in the American Southwest, including southern California. It occurs from central Oregon, southern Idaho, central Wyoming, and northwestern Texas southward to southern Mexico. It occurs mainly in open arid woodlands and although its range surrounds the Great Basin, it is largely absent from the Basin. Adults were collected in the South from April until late June and again from early September to early November. In the Pacific Northwest they fly mid-July to late September. The larva was described by Crumb (1956) and Godfrey (1972).

***Protorthodes antennata* (Barnes & McDunnough, 1912)**

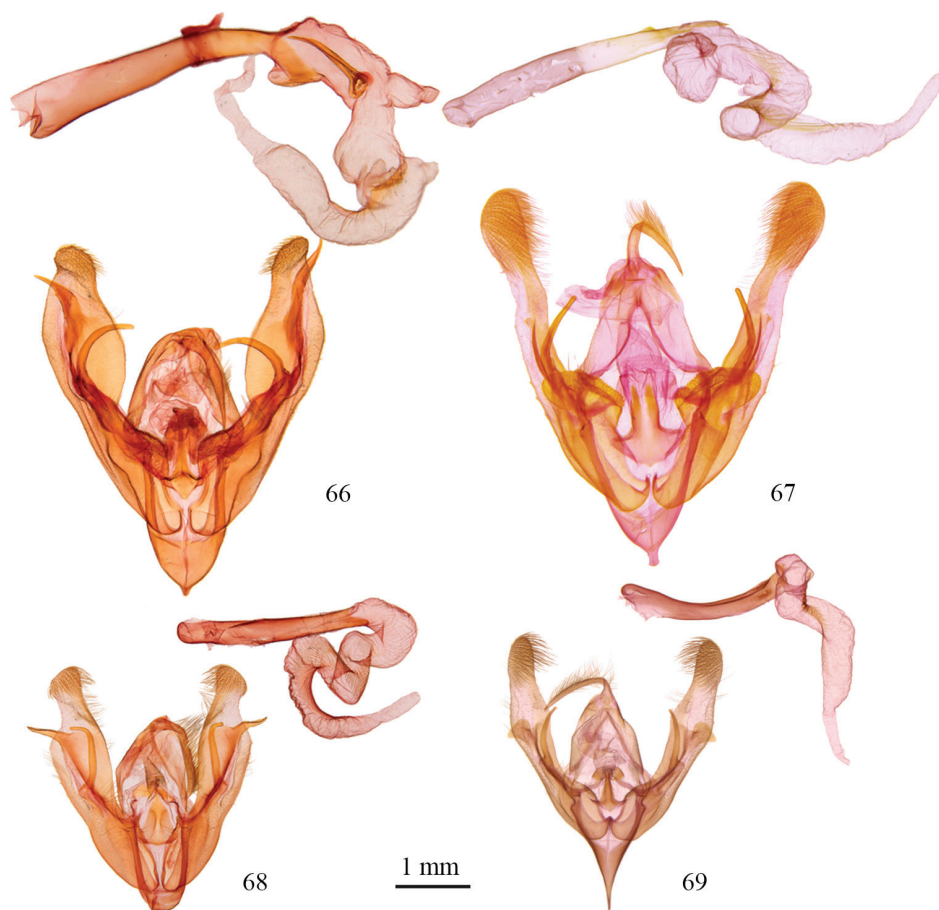
Figs 44, 45, 69, 86. Map 13

Eriopyga antennata Barnes & McDunnough, 1912a: 21.

Type material. Syntypes 4 ♂, 3 ♀, USNM, examined. Type locality: Arizona, Redington.

Diagnosis. Males of *Protorthodes antennata* can easily be identified by the very long pectinations of the antennae, which gives them a feathery appearance. The other diagnostic feature, which applies to females as well, is the form of the reniform spot. In *P. antennata* the reniform spot is not outlined like in other species of *Protorthodes*; there is a series of tiny white dots that partially define the reniform spot, and a series of tiny yellow dots that form a partial outer border of the spot. Forewing length varies from 10 to 14 mm with females tending to be larger than males. The male genitalia are characterized by the short, broad, apically-truncated digitus, and the very narrow, posteriorly tapered juxta. The apex of the aedeagus has a double field of flattened scale-like sclerites that create a lizard-skin appearance. In the female genitalia, the ductus bursae is inflated mesially and covered with minute sclerotized spicules; the ductus is mainly membranous except for a narrow sclerotized “collar” at the posterior end.

Distribution and biology. *Protorthodes antennata* is rarely collected but can occasionally be locally common. It has a small distribution extending from central Arizona to northernmost Mexico. Adults seem to have an abbreviated flight period between mid-May and mid-June, and in October. The immature stages are unknown.



Figures 66–69. *Protorthodes* male genitalia. **66** *P. rufula*; CNC slide 11476 **67** *P. ustulata*; CNC slide 16599 **68** *P. alfenii*; CNC slide 11788 **69** *P. antennata*; CNC slide 16608.

***Nudorthodes* Lafontaine, Walsh & Ferris, gen. n.**

<http://zoobank.org/81DE3680-4B3E-456B-B7E9-D2FA578487CA>

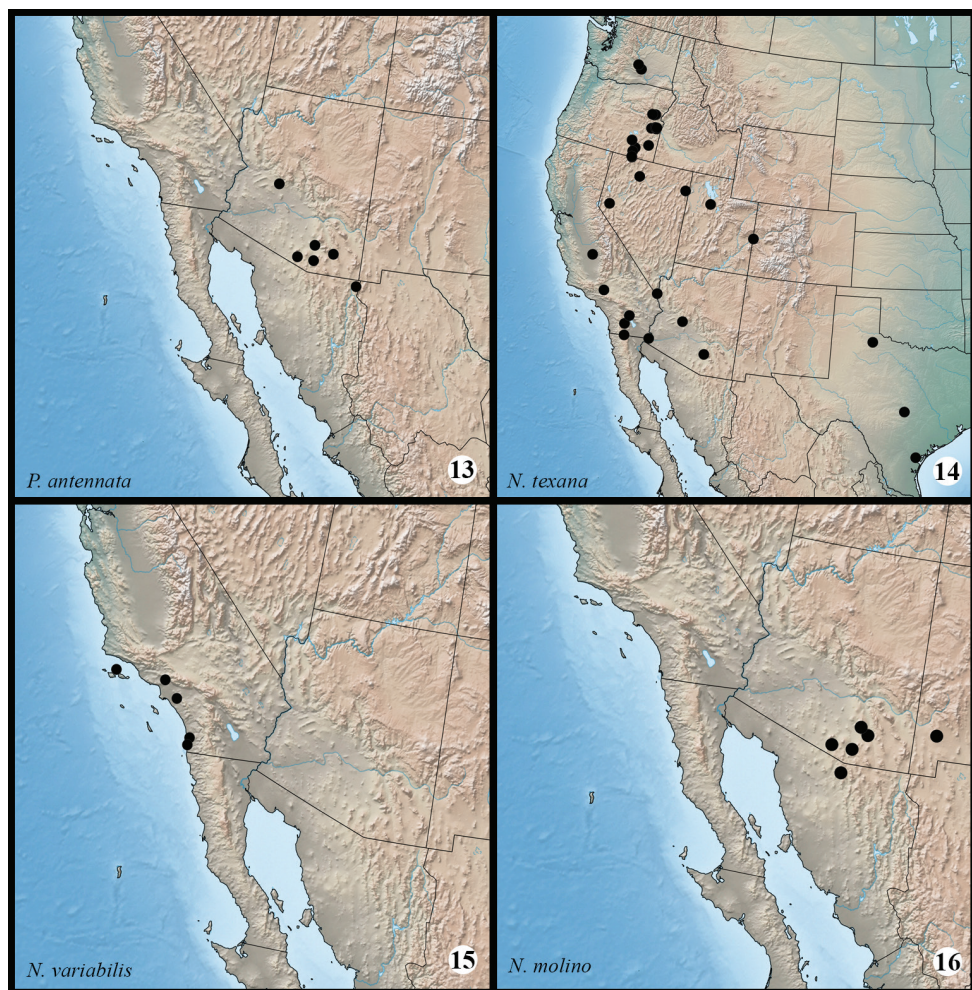
Type species. *Perigea texana* Smith, 1900: 476.

Etymology. The generic name *Nudorthodes* is a reference to this species being removed from the other members of the *Orthodes* group of genera by the lack of hairs on the surface of the eye. From the Latin *Nudus* [bare] + *Orthodes*.

Diagnosis. The genus *Nudorthodes* differs from other genera in the Hadenini: Eriopygina in lacking visible hair-like setae on the surface of the eye, and by the very long vesica in males and appendix bursae in females. Males can be distinguished from those of most other eriopygine genera by the filiform antennae. The genus includes three species: *N. texana* (Smith, 1900), *N. variabilis* (Barnes & McDunnough, 1912), and *N. molino* Lafontaine, Walsh, & Ferris, sp. n.

Description. Adult: Head – Frons rounded; labial with apical segment about 1/4 as long as second segment; male antenna filiform, or very slightly constricted between segments (*N. variabilis*), setose ventrally; female antenna filiform, setose ventrally; eye rounded, without surface hairs; ocellus present. **Thorax** – Thorax clothed with narrow, spatulate, apically serrated scales that form a slightly raised tuft on the prothorax, and a partially divided tuft on the metathorax. **Legs**: middle and hind tibiae without spiniform setae and with three ventral rows of spiniform setae on tarsi. **Wings**: forewing venation typically quadrifine, cubital vein appearing four branched; hindwing with typical triline venation (i.e., M2 reduced, about 2/3 down cell and parallel to M3). **Abdomen** – basal abdominal brushes and pockets absent; eighth abdominal sternite of male with a slightly eversible coremata with a transverse tuft of long setae. **Male genitalia** – *Valva*: symmetrical, basal 3/4 of valve mainly parallel-sided except for dorsal lobe of sacculus (basal half of valve, mainly sacculus, massive compared to narrow apical half in *N. molino*); valve slightly constricted at 3/4 from base to define a tapered densely setose cucullus with much stouter setae on apical and ventro-apical part of cucullus forming an irregular corona; digitus projecting posteriorly along middle of valve, bending ventro-posteriorly near base of cucullus and flattened into elongated plate extending beyond ventral margin of valve (apical part of digitus slightly s-curved and flattened into a foot-shaped structure in *N. molino*); clasper arising as a sclerotized rod at apex of sacculus projecting posteriorly with ampulla bending abruptly through 45° angle to project posterodorsally beyond costal margin of valve; sacculus heavily sclerotized, with a large dorsal process (lobe somewhat quadrangular in two species, and produced posteriorly in *N. molino*), without membranous flap; *Uncus*: decurved, cylindrical, tapered apically to a down-curved sharply pointed apex. *Aedeagus*: long and slender, about 7 × as long as wide, dorsal surface mostly membranous, lateral margins extended on to base of vesica; everted vesica tubular, about 4–5 × as long as aedeagus, basal area angled and with several diverticula, main part gently curved through 5 or 6 coils, vesica expanded and covered with short sclerotized spine-tipped granules toward apex. **Female genitalia** – Corpus bursae rounded, membranous, without signa and with inner surface covered with minute spicules. Appendix bursae arising from left posterior part of corpus bursae and extending anteriorly through several open coils; appendix bursae about 2 × as long as corpus bursae. Ductus bursae about as long as corpus bursae, mainly membranous, with a sclerotized collar-like ring at posterior end forming a slightly wider ostium bursae. Abdominal segment eight sclerotized, covered posteriorly with numerous long, heavily-sclerotized setae, many half as long as segment. Anterior apophyses rod-like, 1.2–1.4 × as long as abdominal segment eight. Posterior apophyses 1.6–1.9 × longer than anterior apophyses. Anal papillae lightly sclerotized, bullet shaped, gradually tapered to rounded apex; surface covered with long hair-like setae, especially toward apex.

Larva and habits. The only species of *Nudorthodes* known as a larva is *Nudorthodes texana*. Like *Protorthodes* the species are generally associated with xeric habitats. The



Maps 13–16. Distribution of examined material for *Protorthodes* and *Nudorthodes* species. **13** *Protorthodes antennata* **14** *Nudorthodes texana* **15** *N. variabilis* **16** *N. molino*.

larvae were described by Crumb (1956) and Godfrey (1972), and were separated from *Protorthodes* by both authors and described as being more similar to larvae of *Homothodes* McDunnough. The larva of *Nudorthodes texana* differs from those of *Protorthodes* species in that the larval skin is smooth, not granulose, the setae arise from sclerotized rings, not pinacula, the posterior part of the prothoracic shield is not contrastingly pale, sclerotized plates between the bases of the abdominal prolegs are lacking, and the apical seta of the labial palpus (Lp-2) is similar in length to the basal segment of the palpus (Lps-1).

Distribution. USA (Arizona, California, Nevada, Oregon, Texas, Utah, Washington).

***Nudorthodes texana* (Smith, 1900), comb. n.**

Figs 46–49, 70, 87; Map 14

Perigea texana Smith, 1900: 476.

Perigea consors Smith, 1900: 477.

Type material. *Perigea texana*: lectotype ♂, USNM, designated by Todd (1982), examined. Type locality: USA, Texas, Round Mountain. *Perigea consors*: lectotype ♂, USNM, designated by Todd (1982), examined. Type locality: USA, Phoenix, Arizona.

Diagnosis. *Nudorthodes texana* is the most widely distributed and common species in the genus. In most of its range adults can be recognized by the pale buffy-brown or gray-brown color of the forewings with darker shading around the reniform and orbicular spots and in the outer part of the subterminal area. The male and female genitalia of *N. texana* form the basis for the description of the genus *Nudorthodes*; it and *N. variabilis* are structurally very similar, differing mainly in the shape of the costal process of the sacculus and the relative lengths of the ampulla of the clasper in the male genitalia. The barcode of *N. texana* is most similar to that of *N. variabilis*, the two differing by 3.67–3.98 %.

Distribution and biology. *Nudorthodes texana* occurs from the intermontane region of Washington, Oregon, Nevada, and Utah southward to southern California and Arizona and southeastward to the Gulf Coast of Texas. Adults were collected rarely in the spring, mostly in March; the second generation occurs from mid-August to mid-November with the flight earlier in the North than in the extreme South. The larva was described by Crumb (1956) and Godfrey (1972).

Notes. A peculiar form of *Nudorthodes texana* (Fig. 49) occurs in southwestern Arizona in the vicinity of Yuma. The forewing is a mottled pale orange brown or reddish brown, without the dark shading between the reniform and orbicular spots characteristic of *N. texana*. The barcodes of this population differ from those of *N. variabilis* by 3.36–3.67 % and from those of *N. texana* by 4.43–5.05 %. However, many specimens from the Yuma area are intermediate in appearance between the mottled-orange form and the normal form of *N. texana* and these barcode with either haplotype clade, suggesting adults of the two haplotype groups are interbreeding, or did so in the past. For this reason we do not describe the Yuma form as a distinct species, but suggest more research on the two haplotype groups in this area is needed. Only five specimens of the deviant haplotype are known.

***Nudorthodes variabilis* (Barnes & McDunnough, 1912), comb. n.**

Figs 50, 51, 71, 88; Map 15

Namangana variabilis Barnes & McDunnough, 1912b: 21.

Type material. *Namangana variabilis*: syntypes, USNM, examined. Type locality: USA, California, San Diego.



Figures 70–72. *Nudorthodes* male genitalia. **70** *N. texana*; CNC slide 15581 **71** *N. variabilis*; CNC slide 15583 **72** *N. molino*; CNC slide 14211.

Diagnosis. *Nudorthodes variabilis* is a rarely collected species confined to coastal southern California. Adults are most likely to be confused with those of *N. texana*, but average larger (forewing length: 13 to 14 mm). In *Nudorthodes variabilis*, the medial line usually is prominent, extending obliquely from the costa to the reniform spot and as a straight line from there to the hind margin of the forewing, and the lower third of the reniform spot is filled with a well-defined dark blue-gray patch. In *N. texana* the medial line is absent or barely traceable, and the lower third of the reniform spot

has diffuse dark shading. In southern California where the ranges of the two species overlap, the forewing ground color in *N. variabilis* is an even gray brown, sometimes with a slight reddish tint; whereas in *N. texana* the ground color is pale buff and powdery in appearance. In the male genitalia the dorsal lobe on the sacculus of *N. variabilis* is produced posteriorly towards the top, giving it a slight mushroom shape, whereas the posterior margin of the lobe in *N. texana* is straight and perpendicular to the longitudinal axis of the sacculus. The female genitalia of the two species appear to be indistinguishable.

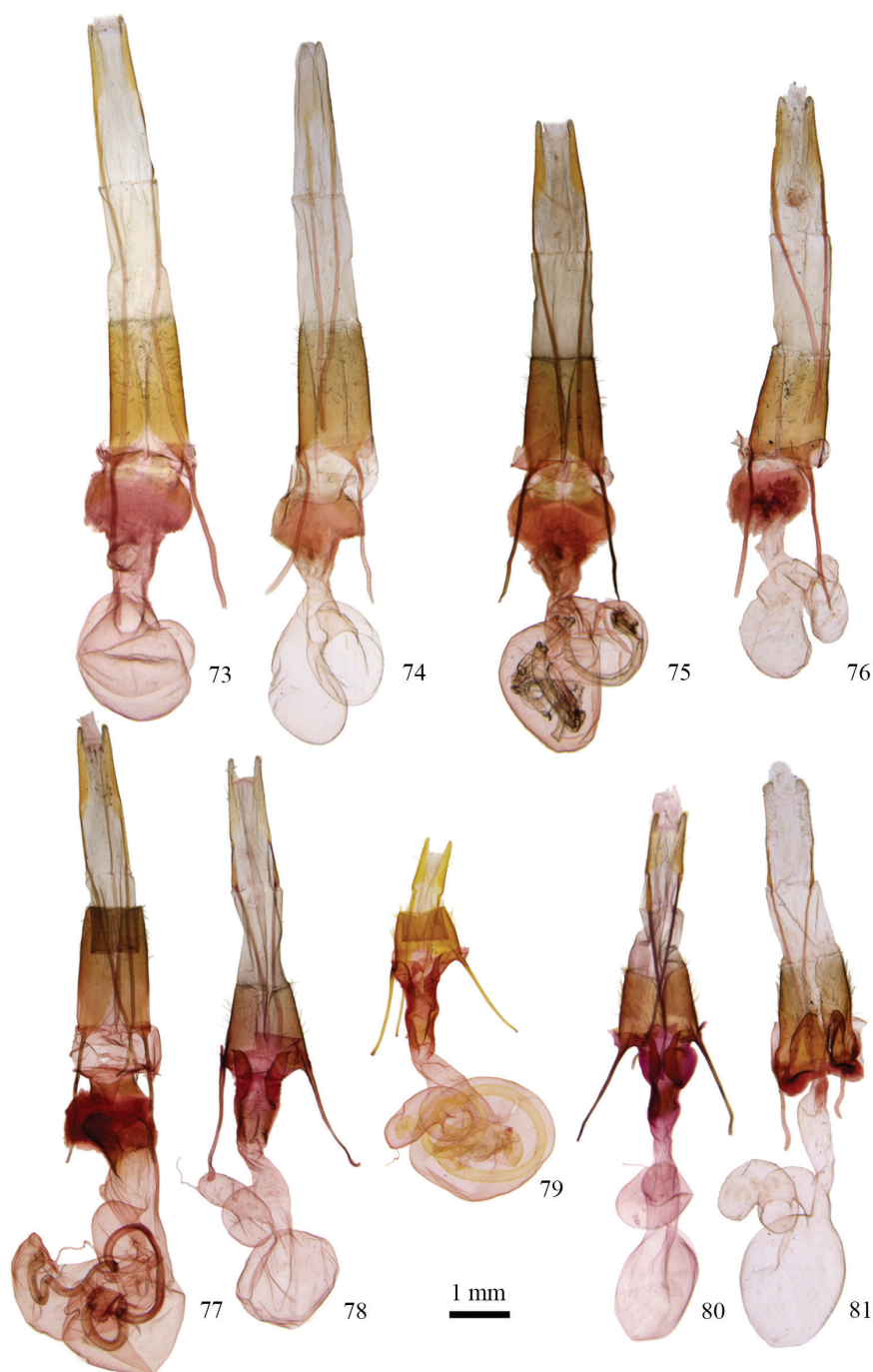
Distribution and biology. *Nudorthodes variabilis* occurs along the coast of southern California from Santa Barbara County to San Diego County. Adults were been collected from late August until mid-September. The immature stages are unknown.

***Nudorthodes molino* Lafontaine, Walsh & Ferris, sp. n.**

<http://zoobank.org/B5727D96-128D-44B4-A95A-93D7704CBFE9>

Figs 52–54, 72, 89; Map 16

Type material. **Holotype** ♂. USA, Arizona, Pima Co., Santa Catalina Mts., mi 5.5 Mt Lemmon Hwy., 4400', riparian blue oak woodland, uv light trap, 27 October 2007, B. Walsh. CNC. **Paratypes:** 59 ♂, 34 ♀. USA, Arizona, Pima Co., Baboquivari Mts., Brown Canyon Nature Center, , 4200', oak woodland/ocotillo forest, mv/uv light trap, 11 June 2004, B. Walsh (1 ♂, 2 ♀, 1 ♀ Barcode of Life sample ID # CNCNoctuoidea13977); USA, Arizona, Pima Co., Baboquivari Mts., Brown Canyon Nature Center, 4200', 11 June, 2004, CD Ferris (1 ♂); USA, Arizona, Pima Co., Baboquivari Mts., Brown Canyon Nature Center, 4100', oak/ocotillo forest, mv/uv light trap, 22 & 28 June 2005 & 10 Sept. 2004, B. Walsh (2 ♂, 3 ♀); USA, Arizona, Pima Co., Baboquivari Mts., Brown Canyon Nature Center, 4300–4400', 28 June, 2005 (1 ♂), 18 June, 2008 (36 ♂, 1 ♀), CD Ferris; USA, Arizona, Pima Co., Santa Catalina Mts., mi 5.7 Mt Lemmon Hwy., 4400', riparian/oak woodland, uv light trap, 18 Sept. 2003, 4 October 2003, 13 June 2005, B. Walsh (3 ♂, 2 ♀, 1 ♀ Barcode of Life sample ID # CNCNoctuoidea12245); USA, Arizona, Pima Co., Santa Catalina Mts., Molino Basin, mi 5.5 Mt Lemmon Hwy., 4400', riparian blue oak woodland, uv light trap, 3 June 2004, B. Walsh (1 ♀); USA, Arizona Pima Co., Santa Catalina Mts., Molino Basin, mi 5.5 Mt Lemmon Hwy., 4400', 26 September, 2003 (1 ♀); 24 May, 2004 (2 ♂); 3 June, 2004 (1 ♂), JB Walsh; USA, Arizona, Pima Co., Santa Catalina Mts., mi 5.5 Mt Lemmon Hwy., 4400', riparian blue oak woodland, uv light trap, 29 May 2008, 27 October 2004, 8 November 2004 (Barcode of Life sample ID # CNCNoctuoidea12246), B. Walsh (1 ♂, 2 ♀); USA, Arizona, Pima Co., Rincon Mts., Happy Valley, Mescal Road 9 miles N Jct. Interstate 10, oak/riparian, 9 June 2005, B. Walsh (1 ♀); USA, Arizona, Pima Co., Santa Rita Mts., Madera Canyon, 4400', 7 Sept. 1960 (1 ♂) and 4800', 31 August 1959 (1 ♀), J. G. Franclemont; USA, Arizona, Santa Cruz Co., Peña Blanca Cyn., 3940', 31°23.87'N,



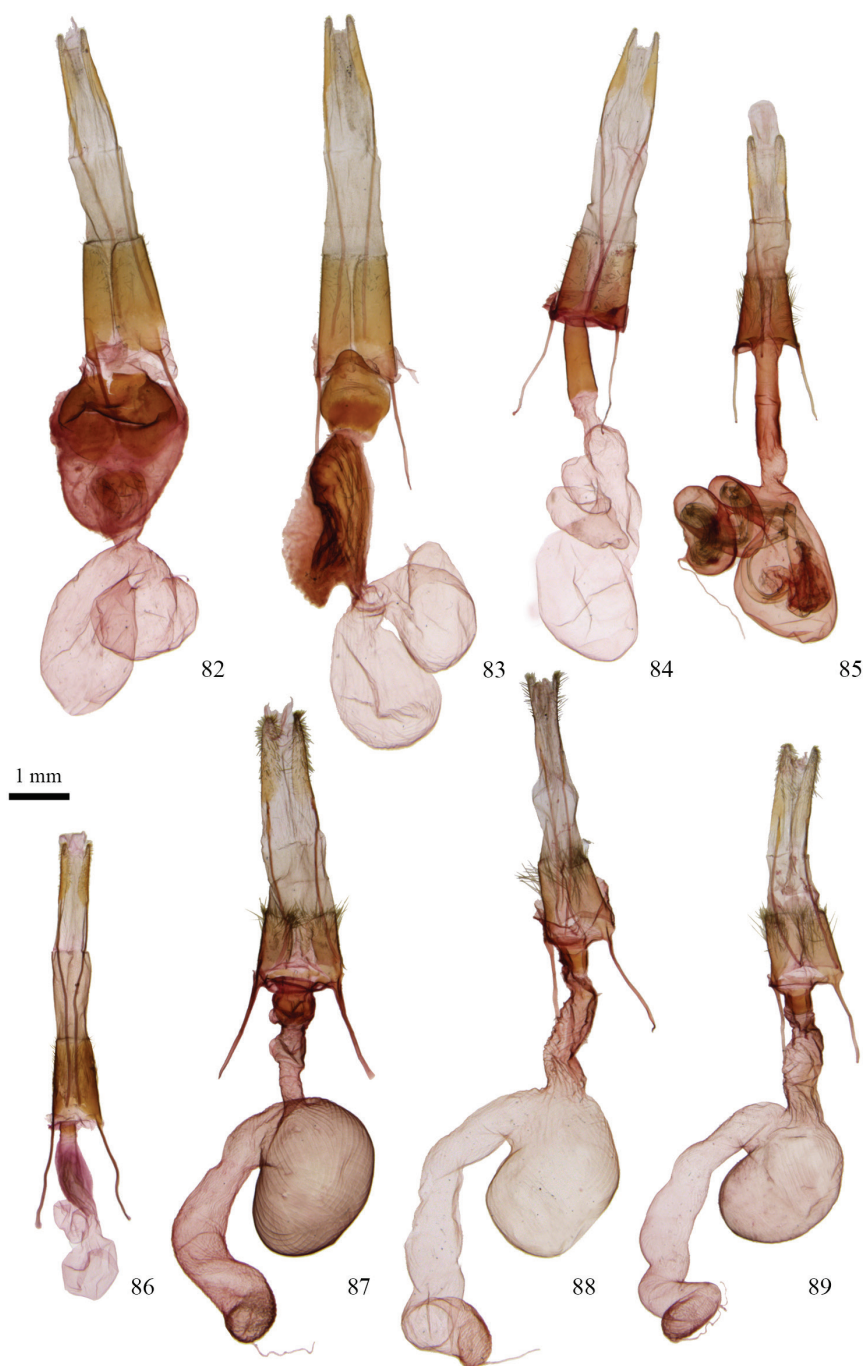
Figures 73–81. *Protorthodes* female genitalia. **73** *P. curtica*; CNC slide 16552 **74** *P. eureka*; CNC slide 15255 **75** *P. incincta*; CNC slide 15562 **76** *P. argentoppida*; CNC slide 15253 **77** *P. mulina*; CNC slide 15577 **78** *P. oviduca*; CNC slide 15245 **79** *P. orobia*; CNC slide 11604 **80** *P. melanopis*; CNC slide 16004 **81** *P. texicana*; CNC slide 15254.

111°05.61'W, 8 Sept. 2010, C.D. Ferris (5 ♂, 9 ♀); USA, Arizona, Santa Cruz Co., Walker Canyon E. of Peña Blanca Lake, 3885', 12 June 2009, C.D. Ferris (1 ♀); Arizona, Santa Cruz Co., Peña Blanca Cyn., 4000', 3 September, 2010, JB Walsh (1 ♀); USA, Arizona, Santa Cruz Co., Patagonia, 4040', 13 June 2009, C.D. Ferris (1 ♀); USA, Arizona, Santa Cruz Co., Harshaw Rd., 4310', 14 June 2008 (1 ♂), 12 June 2013 (1 ♂), CD Ferris; USA, Arizona, Cochise Co., Dragoon Mts., 4950', 4 June, 2009, C.D. Ferris (1 ♂); USA, Arizona, Cochise Co., Huachuca Mts., Ash Canyon, 5170', 16 June, 2008 (1 ♂), 20 June, 2008 (1 ♀), 7 June, 2009 (2 ♀), 6 June, 2010 (1 ♀), 9 June, 2010 (1 ♀), CD Ferris; USA, Arizona, Cochise Co., Mule Mts., Banning Creek, 5700', 12 June, 2010 (1 ♀), CD Ferris; USA, New Mexico, Grant Co., Patterson Cyn., 5270', 26 May, 2012, CD Ferris (1 ♂). Paratypes deposited in CDF, CNC, CUIC, JBW, USNM.

Etymology. This species is named after the Molino Basin on Mt Lemmon where most of the type series was collected. The name is a noun in apposition.

Diagnosis. *Nudorthodes molino* can be recognized by the diffuse dark-brown band across the outer third of the forewing between the medial line and the subterminal line, and the dark-brown shading of the medial line that fills most of the reniform spot. The male genitalia are characterized by the large triangular sacculus, the elongated oval cucullus, and the S-curved, foot-shaped digitus. The female genitalia are similar to those of *N. texana* and *N. variabilis*, but in *N. molino* the ostium bursae is more rounded with the sides convex, whereas in *N. texana* and *N. variabilis* the ostium bursae is quadrangular with the sides parallel. The barcode of *N. molino* is the most deviant of the species in the genus *Nudorthodes*, differing from the other species by as little as 5.05% (*N. variabilis*) to as much as 5.81% (*N. texana*).

Description. Adult. Male and female similar in size, color, and maculation. Forewing length: 13–15 mm. **Head** – Male antenna filiform, setose ventrally. Female antenna filiform, ventral setae visible only under high magnification. Palpi and head clothed with spatulate apically-forked setae, pale buffy brown or gray brown. **Thorax** – Covered with similar scales to those of head; with slightly raised prothoracic and metathoracic tufts. **Legs:** Appearing speckled with mixture of buff and darker brown scales. Tibiae without spiniform setae. Tarsi with three ventral rows of spiniform setae. **Wings:** Dorsal forewing pale brown with dusting of darker-brown scales, especially in outer part of medial area, outer part of subterminal area, and usually in terminal area; subbasal, antemedial, postmedial lines dark brown, subterminal line a series of pale-buff dots with dark brown shading proximally that highlights line; reniform spot kidney shaped, infuscated with dark-brown shading from medial line; orbicular spot rounded, generally paler than ground color and outlined by thin dark-brown line; medial line variably expressed, usually forming a broad diffuse brown shading between it and postmedial line and filling most of reniform spot with dark shading; terminal line dark brown, sinuate; fringe with two irregular rows of spatulate scales, pale-brown at base, darker toward tips. Dorsal hindwing pale fuscous basally with darker fuscous toward wing margin without a well-defined discal spot; fringe mainly whitish buff with fuscous medial line. **Male**



Figures 82–89. *Protorthodes* and *Nudorthodes* female genitalia. **82** *P. perforata*; CNC slide 15244 **83** *P. rufula*; CNC slide 15241 **84** *P. ustulata*; CNC slide 15246 **85** *P. alfkenii*; CNC slide 10927 **86** *Protorthodes antennata*; CNC slide 16605 **87** *Nudorthodes texana*; CNC slide 15239 **88** *N. variabilis*; CNC slide 15251 **89** *N. molino*; CNC slide 15240.

genitalia – Similar to generic description except as noted. Valves mainly symmetrical except dorsal process of sacculus, and ampulla of clasper larger on right valve than on left valve. Valve widest at $1/3$ from base, abruptly tapered near middle, then gradually tapered to $3/4$ from base to “neck” of cucullus; cucullus densely covered with posterodorsally-directed hairlike setae on anterior half of cucullus with stout setae curving to project anterodorsally on posterior half of cucullus; digitus abruptly-angled ventrally near neck of cucullus with apical part curved, ventrally flattened and foot shaped; ampulla of clasper expanded and lobed at base, then gradually tapered to apex, abruptly curved through 90° angle at $3/4$ to project dorsally, right clasper about 15% larger than left one; dorsal process of sacculus elongated and lobed posteriorly, process larger on right valve than on left valve; juxta an elongated flattened plate extending into series of oblique sclerotized ridges in membrane directed toward midline. Aedeagus and vesica similar to those of *N. texana* and other species but apical part of vesica more inflated. **Female genitalia** – Corpus bursae membranous, rounded, without signa; appendix bursae arising from posterior dorsal surface of corpus bursae, $1.5 \times$ as long as corpus bursae and slightly coiled toward anterior end; ductus bursae about as long as corpus bursae, with expanded sclerotized ostium bursae on posterior $1/4$; abdominal segment eight as long as wide, lightly sclerotized; anterior apophyses $1.5 \times$ as long as abdominal segment eight; posterior apophyses folding near middle, about $2 \times$ as long as anterior apophyses. Anal papillae long and tapered, about as long as abdominal segment eight; anal papillae lightly sclerotized, long setae sparsely scattered over surface, short setae abundant near apex of papillae.

Distribution and biology. *Nudorthodes molino* is known from southeastern Arizona and southwestern New Mexico. Adults were collected from late May until late June and from late August until early November. The immature stages are unknown.

Acknowledgments

We thank David Grimaldi (American Museum of Natural History, New York, NY), Martin Honey (Natural History Museum, London, UK), Michael Pogue (Systematic Entomology Laboratory, National Museum of Natural History, Washington, DC), for the loan of specimens. We also thank James Boone (FMNH, Chicago, Illinois) for providing photographs of the type material of *Protorthodes akalus* and *P. saturnus*, and Jocelyn Gill (CNC, Ottawa, Canada) for preparing genitalia slides, photography and the color plates. Lars Crabo, Terhune Dickel, Tom Dimock, Chris Grinter, Richard Holland (deceased), Eric Metzler, Tomas Mustelin, and Jim Troubridge contributed material for the project. Eric Metzler reviewed the manuscript and provided many useful suggestions. Paul Hebert and the staff at the Canadian Centre for DNA Barcoding (Biodiversity Institute of Ontario, University of Guelph, Guelph, Canada) provided data and information from the Barcode of Life Data (BOLD) system.

References

- Barnes W, Benjamin (1927) Notes and new species (Lepid.). Canadian Entomologist 59: 4–10. doi: 10.4039/Ent594-1
- Barnes W, McDunnough (1912a) New species and genera of North American Lepidoptera. Canadian Entomologist 44: 17–22. doi: 10.4039/Ent4417-1
- Barnes W, McDunnough (1912b) Fifty new species; notes on the genus *Alpheias*. Contributions to the Natural History of the Lepidoptera of North America 1(5): 1–44.
- Crumb SE (1956) The larvae of the Phalaenidae. United States Department of Agriculture, Technical Bulletin 1135: 1–356.
- Dyar HG (1904) The Lepidoptera of the Kootnai District of British Columbia. Proceedings of the United States National Museum 27: 779–938. doi: 10.5479/si.00963801.27-1376.779
- Dyar HG (1913) Descriptions of new Lepidoptera chiefly from Mexico. Proceedings of the United States National Museum 44: 279–324. doi: 10.5479/si.00963801.44-1951.279
- Dyar HG (1918) Descriptions of new Lepidoptera from Mexico. Proceedings of the United States National Museum 54: 335–372. doi: 10.5479/si.00963801.54-2239.335
- Franclemont JG, Todd EL (1983) Noctuidae. In: Hodges RW, Dominick T, Davis DR, Ferguson DC, Franclemont JG, Munroe EG, Powell JA (Eds) Check List of the Lepidoptera of America North of Mexico. EW Classey Ltd., London and The Wedge Entomological Research Foundation, Washington, 120–159.
- Godfrey GL (1972) A review and reclassification of larvae of the subfamily Hadeninae (Lepidoptera, Noctuidae) of America north of Mexico. United States Department of Agriculture, Technical Bulletin 1450: 1–265.
- Grote AR (1874a) List of the Noctuidae of North America. Bulletin of the Buffalo Society of the Natural Sciences 2: 1–77.
- Grote AR (1874b) New species of North American Noctuidae. Proceedings of the Academy of Natural Sciences of Philadelphia 1874: 197–214.
- Grote AR (1883) Notes on species in Mr. Neumoegen's collection. Papilio 3: 73–80.
- Grote AR (1895) List of North American Eupterotidae, Ptilodontidae, Thyratiridae, Apatelidae, and Agrotidae. Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen 14: 43–128.
- Guenée A (1852) Vol. 5, Noctuérites. Tome 1. In: de Boisduval JBAD, Guenée A (Eds) Histoire Naturelle des Insectes. Species Général des Lépidoptères. Roret, Paris, 407 pp.
- Hampson GF (1905) Hadeninae. Catalogue of the Phalaenae Lepidoptera in the British Museum Volume 5. Taylor and Francis, London, 634 pp.
- Hampson GF (1909) Acronyctinae. Catalogue of the Phalaenae Lepidoptera in the British Museum Volume 8. Taylor and Francis, London, 583 pp.
- Harvey LF (1876) New Noctuidae. Canadian Entomologist 8: 154–156. doi: 10.4039/Ent8154-8
- Krogerus H (1954) Investigations on the Lepidoptera of Newfoundland. 1. Macrolepidoptera. Acta Zoologica Fennica 82: 1–80.
- Lafontaine JD (2004) Noctuoidea, Noctuidae (part), Noctuinae (part – Agrotini). In: Hodges RW (Ed) The Moths of America North of Mexico fasc. 27.1. The Wedge Entomological Research Foundation, Washington, 385 pp.

- Lafontaine JD, Schmidt BC (2010) Annotated check list of the Noctuoidea (Insecta, Lepidoptera) of North America north of Mexico. *ZooKeys* 40: 1–239. doi: 10.3897/zookeys.40.414
- McDunnough JH (1938) Check list of the Lepidoptera of Canada and the United States of America. Part 1. Macrolepidoptera. *Memoirs of the Southern California Academy of Sciences*, 275 pp.
- McDunnough JH (1943) Hadenine notes and description (Phalaenidae, Lepidoptera). *The Canadian Entomologist* 75: 43–57. doi: 10.4039/Ent7543-3
- Morrison HK (1874) Descriptions of new Noctuidae. *Proceedings of the Boston Society of Natural History* 17: 131–166.
- Poole RW (1989) *Lepidopterorum Catalogus* (New Series). Fascicle 118 Noctuidae, Parts 1–3. E.J. Brill, New York, 1314 pp.
- Ratnasingham S, Hebert PDN (2007) BOLD: The barcode of life data system. *Molecular Ecology Notes* 7: 355–364. doi: 10.1111/j.1471-8286.2007.01678.x [www.barcodinglife.org]
- Schaus (1894) New species of Noctuidae from tropical America. *Transactions of the American Entomological Society* 21: 223–244.
- Smith JB ([1888]) New genera and species of North American Noctuidae. *Proceedings of the United States National Museum* 10: 450–479. doi: 10.5479/si.00963801.647.450
- Smith JB (1890) New species of Taeniocampini. *Entomologica Americana* 6: 121–125.
- Smith JB (1893) A catalogue bibliographical and synonymical of the species of moths of the lepidopterous superfamily Noctuidae found in boreal America. *Bulletin of the United States National Museum* 44: 1–424. doi: 10.5479/si.03629236.44
- Smith JB (1900) A hundred new moths of the family Noctuidae. *Proceedings of the United States National Museum* 22: 413–495. doi: 10.5479/si.00963801.1203.413
- Smith JB (1906) New species of Noctuidae for 1906. No. 2. *Canadian Entomologist* 38: 225–238. doi: 10.4039/Ent38225-7
- Smith JB (1908a) New species of Noctuidae for 1908. 1. With notes on *Charadra*, *Raphia* and *Pseudanarta*. *Journal of the New York Entomological Society* 16: 79–98.
- Smith JB (1908b) New species and genera of the Lepidopterous family Noctuidae for 1907 (Part II). *Annals of the New York Academy of Sciences* 18: 91–127. doi: 10.1111/j.1749-6632.1908.tb55098.x
- Smith JB (1909) New species of Noctuidae for 1909. *Journal of the New York Entomological Society* 17: 57–71.
- Strand E ([1917]) Neue aberrationen der Noctuiden - subfamilien Hadeninae, Erastriinae, Catocalinae, Mominae und Phytometrinae. *Archiv für Naturgeschichte* 82A2: 28–50.
- Strecker H (1899) Lepidoptera, Rhopaloceres and Heteroceres, indigenous and exotic. Supplement 2, 11 pp. [published privately]
- Strecker H (1900) Lepidoptera, Rhopaloceres and Heteroceres, indigenous and exotic. Supplement 3, 37 pp. [published privately]
- Todd EL (1982) The noctuid type material of John B. Smith (Lepidoptera). United States Department of Agriculture, Technical Bulletin 1645, 228 pp.
- Wilterding JH (1997) Type specimens of Lepidoptera in the Tepper Collection at Michigan State University. *Journal of the New York Entomological Society* 105: 65–104.

Check list of *Protorthodes* and *Nudorthodes*

- 933103* *Protorthodes curtica* (Smith, 1890)
syn. *P. bostura* (Smith, 1908)
- 933104 *Protorthodes eureka* (Barnes & Benjamin, 1927)
- 933105 *Protorthodes incincta* (Morrison, 1874)
syn. *P. utahensis* (Smith, a [1888])
syn. *P. akalus* (Strecker, 1899)
syn. *P. saturnus* (Strecker, 1900)
syn. *P. smithii* (Dyar, 1904)
syn. *P. indra* (Smith, 1906)
syn. *P. coloradensis* (Strand, [1917])
syn. *P. daviesi* (Barnes & Benjamin, 1927)
- 933107 *Protorthodes argentopida* McDunnough, 1943
- 933112 *Protorthodes mulina* (Schaus, 1894)
syn. *P. pseudochroma* (Dyar, 1913)
- 933113 *Protorthodes oviduca* (Guenée, 1852)
syn. *P. capsella* (Grote, 1874)
syn. *P. lindrothi* Krogerus, 1954
- 933114 *Protorthodes orobia* (Harvey, 1876)
- 933115 *Protorthodes melanopis* (Hampson, 1905)
- 933115.1 *Protorthodes texicana* Lafontaine, 2014
** *Protorthodes mexicana* Lafontaine, 2014
- 933115.2 *Protorthodes perforata* (Grote, 1883)
syn. *P. constans* (Dyar, 1918)
- 933115.3 *Protorthodes rufula* (Grote, 1874)
- 933115.4 *Protorthodes ustulata* Lafontaine, Walsh & Ferris, 2014
- 933115.5 *Protorthodes alfkenii* (Grote, 1895)
syn. *P. latens* (Smith, 1908)
syn. *P. occluna* (Smith, 1909)
- 933115.6 *Protorthodes antennata* (Barnes & McDunnough, 1912)
- 933116 *Nudorthodes texana* (Smith, 1900)
syn. *N. consors* (Smith, 1900)
- 933117 *Nudorthodes variabilis* (Barnes & McDunnough, 1912)
- 933117.1 *Nudorthodes molino* Lafontaine, Walsh & Ferris, 2014
* Numbers adapted from Lafontaine & Schmidt (2010) check list
** Mexico only

A new apameine genus and species from the southern Appalachian Mountains, USA (Lepidoptera, Noctuidae, Noctuinae)

Eric L. Quinter¹, J. Bolling Sullivan²

1 P.O. Box 74, Willimantic, Connecticut, 06226, USA **2** 200 Craven Street, Beaufort, North Carolina, 28516, USA

Corresponding author: Eric L. Quinter (protapamea@yahoo.com); J. Bolling Sullivan (sullivan14@earthlink.net)

Academic editor: C. Schmidt | Received 15 April 2014 | Accepted 15 May 2014 | Published 27 June 2014

<http://zoobank.org/C935D050-0B82-4396-8B93-40305586F683>

Citation: Quinter EL, Sullivan JB (2014) A new apameine genus and species from the southern Appalachian Mountains, USA (Lepidoptera, Noctuidae, Noctuinae). In: Schmidt BC, Lafontaine JD (Eds) Contributions to the systematics of New World macro-moths V. ZooKeys 421: 181–191. doi: 10.3897/zookeys.421.7727

Abstract

Cherokeea **gen. n.** is proposed for a rarely collected apameine moth species from the southern Appalachian Mountains, *C. attakullakulla* **sp. n.** It is recorded from foothills and lower montane habitats of North Carolina and Georgia where hill cane, *Arundinaria appalachiana* Triplett, Weakley & L.G. Clark is found. Adults and their genitalia are figured and a mtDNA barcode sequence is given.

Keywords

Apameini, *Arundinaria*, bamboo, barcode, biogeography, endophagy, evolution, Noctuoidea

Introduction

Most of the species formerly placed in the “*Oligia*” *semicana* (Walker) group were resolved by Troubridge and Lafontaine (2002) and placed in the new genus *Neoligia* Troubridge & Lafontaine. Omitted from that revision was a rarely-seen species from

the southern Appalachian Mountains. First collected by John G. Franclemont in 1958 during his studies of the fauna at Highlands Biological Station in Macon County, North Carolina, the species remained uncollected until faunal studies began in the Great Smoky Mountain National Park in the late 1990's. While conducting various lepidopteran surveys in Swain County, the species was rediscovered at numerous localities. Although it superficially resembles *Neoligia semicana* (Walker), an uncommonly collected species of the northeastern United States, genitalic dissections and DNA sequences at the CO1 locus reveal it is distinct at the generic level.

This paper describes the second of a number of new genera of apameine moths that are highly restricted to the limited occurrences of their known or presumed host plants, *Arundinaria* Michx. (Poaceae: Bambusoideae) that occur in the southeastern United States. The first new genus, *Protapamea* Quinter (Quinter 2009), and several additional new genera (Quinter, in prep.) share a suite of characters unique among the Nearctic and western Palearctic Apameini, suggesting an ancient lineage involving a common ancestor. With no obvious close relatives known in these regions, it seems likely that the closest relatives of this particular group of apameine genera will be found elsewhere. Given the unique occurrence of the single genus of bamboo native to North America, and with most of the closest relatives of *Arundinaria* confined to temperate and subtemperate montane regions of the eastern Palearctic and Oriental Regions (Judziewicz et al. 1999), we suggest that the closest relatives of these apameine moth genera will be found there as well. Whether these seemingly unique morphological features are shared with as yet undiscovered species in Asia, and whether they are synapomorphic or symplesiomorphic relative to the rest of the Apameini remains to be determined. Such speculation might seem inappropriate, were it not provided with the hope that workers in the eastern Palearctic and Oriental Regions might pay special attention to any of the subtribe Arundinariinae Benthani, and any evidence of either endophagous or external feeding by noctuid larvae upon the culms of the various monopodial bamboo species occurring there. The montane regions of southern China west at least as far as Assam would appear particularly inviting. It is interesting to note that two of the three species of the genus *Enodia* Hübner (Lepidoptera: Nymphalidae: Satyrinae: Satyrini) occurring in the United States are also known specialists upon *Arundinaria*, and that their closest relatives within the Satyrini (Wahlberg 2014) occur in southeastern Asia (e.g., Leech 1892-93). It should be pointed out that, aside from their sedentary nature, many of the apameine moths associated with *Arundinaria* in North America do not respond well to UV lights or traps, even when such are deployed directly within the canebrakes where the adult moths are actively breeding. Quinter has repeatedly observed mating and oviposition behavior of numerous individuals by searching these habitats with a flashlight at night, yet traps placed in or near these same sites yielded few or no specimens the following day. By far the most productive method for detecting the presence of some of these species is daytime searching for evidence of larval feeding, whether endophagous or external, and nocturnal searching for externally feeding climbing cutworms which rest in detritus lodged on the culms of the host plants, or on the forest floor, by day. For these reasons, almost all of these recently discovered species were previously unknown.

Materials and methods

Photographic methods used herein are described in Sullivan and Adams (2009). Procedures for dissecting and preparing genitalia follow that of Lafontaine (2004). Terminology for genital structures and wing markings follows that of Lafontaine (1987, 2004). DNA sequencing of the barcode fragment of the CO1 gene was carried out at the Canadian Center for DNA Barcoding in Guelph, Ontario. Barcode sequences were compared by nearest neighbor analyses as implemented on the Barcode of Life Data systems website (Ratnasingham and Hebert 2007).

Repository abbreviations

| | |
|-------------|--|
| BMNH | The Natural History Museum, London, UK |
| ELQ | Eric L. Quinter, Willimantic, Connecticut, USA |
| CNC | Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada |
| JBS | J. Bolling Sullivan, Beaufort, North Carolina, USA |
| USNM | National Museum of Natural History, Washington, District of Columbia, USA |

Systematics

Cherokeea Quinter & Sullivan, gen. n.

<http://zoobank.org/DF48154A-49CD-4C62-A82A-3490032DD253>

Gender. Masculine.

Type species. *Cherokeea attackullakulla* Sullivan & Quinter, 2014

Etymology. *Cherokeea* is derived from Cherokee, a Nation of Native American people who occupied the southern Appalachians and were exemplary stewards of the habitats and resources of the region.

Diagnosis. This genus exhibits most but not all of the primary characteristics of the tribe Apameini, i.e., ovipositor heavily sclerotized and dorsoventrally flattened, rugose sclerotized appendix bursae, and medially corrugated ductus bursae in the female; pleural sclerite a double helix in the male. It is distinguished from all known Nearctic and western Palearctic apameine genera by the conspicuous asymmetry of the saccular lobes of the male genitalia. This condition appears to be a uniquely derived synapomorphy shared with other as yet undescribed apameine genera restricted to southeastern United States. A sclerotized medial protrusion arising caudally from the basal margin of the male juxta appears to be autapomorphic. Additionally, the left valve bears a minute setose projection at the base of the sacculus, resembling a miniature clavus, which may be autapomorphic. The sole included species, *C. attackullakulla*, is a small, dull-colored moth bearing a superficial resemblance to some species of *Neoligia*.

Cherokeea is immediately distinguishable from *Neoligia*, *Oligia* Hübner, *Mesoligia* Boursin, and *Mesapamea* Heinicke by quite different genitalic morphology given in the description below. Troubridge and Lafontaine (2002) characterized the genera related to *Neoligia*. *Oligia* is differentiated by an elongated pollex (spatulate and setose) that projects from the base of the cucullus, a prominent digitus, a uniquely bent uncus and unarmed vesica in the aedeagus. *Mesapamea* has a paddle-like cucullus, no pollex, and an embedded digitus; the vesica has a basal cornutus. *Mesoligia* combines characters of the first two genera by lacking a distinct pollex, the digitus is embedded but more sclerotized, the uncus is similar to that of *Oligia* and the vesica contains a field of cornuti near the apex. *Neoligia* has a smooth pollex, a plate-like digitus fused to the inner surface of the valve but not projecting over the anal edge, and the vesica has both a basal cornutus and an apical field of small cornuti. None of these characters aptly fits the rarely-collected apameine of the southern Appalachians, described herein.

Description. Head. Male and female antennae simple, setose-ciliate; 54 segments. Eye smooth, round. Labial palpus of both sexes laterally flattened, upcurved; first segment swollen basally, arching slightly upward and somewhat more than half as long as second segment, which is straight; second segment about as long as eye width, broadly scaled; third segment $1/3 \times$ length of second, narrowly scaled, and projecting slightly anteriorly. Frons convex, unmodified; with a central dense tuft of converging spatulate hairs. **Thorax.** Vestiture a mixture of coarse spatulate scales, spatulate hairs and simple hairs; mesoscutellar crest prominent, metascutellar tuft, less so. **Wings.** Forewings elongated and acutely rounded at apex. Venation typical apameine, as figured in Mikkola et al. (2009) except that R3 and R4 are stalked for half the distance from the areole to the margin. **Legs.** Normal apameine; tibia devoid of spiniform setae, but with the usual pair of spurs on the mesothoracic leg and two pairs on the metathoracic leg. Epiphysis on prothoracic leg $0.5 \times$ length of tibia; prothoracic tibia $1.3 \times$ length of first tarsomere. Tarsus with three rows of spiniform setae on first two proximal tarsomeres; four irregular rows on distal three tarsomeres. **Abdomen.** First segment lacking paired, lateral coremata; eighth sternite with deciduous, non-eversible brush. A prominent mid-dorsal tuft on A1; no tufts on remaining segments. **Male genitalia** (Figs 5, 6). Uncus long, slender and downcurved to sharp apex; fine, long setae on outer half of dorsal surface. Tegumen broad at base of uncus, then flaring laterally, forming broad peniculi before narrowing sharply at pleural sclerite to meet U-shaped vinculum; distal edges of peniculi covered with fine setae. Saccus short, blunt, broadly V-shaped. Juxta an elongated trapezoidal shield, $2 \times$ as long as basal width; a medial protrusion with a keyhole-like center extending caudally from the basal margin. Anellar arms not fused. Valve with subapical “neck” defining cucullus; ventral margin of valve slightly convex to $3/4$ from base, then abruptly angled dorsally into deep notch at anteroventral edge of cucullus; dorsal margin of valve evenly concave to $3/4$ from base, then abruptly angled dorsally to form rounded process at anterodorsal edge of cucullus. Cucullus triangular, apically slightly spatulate, with corona reduced to one or two apical setae; outer margin of cucullus bearing several larger spines, including two prominent anal spines; inner face of cucullus with a patch of fine hairs, denser

apically. Valves bilaterally asymmetrical with respect to shape of sacculus. Left valve bearing a minute setose projection at base of sacculus, resembling a miniature clavus, which appears autapomorphic; otherwise, costal lobe of left sacculus normal, rounded; costal lobe of right sacculus greatly expanded dorsally into a free, flattened process that extends distally half length of entire valve; saccular lobe attached at its distal base to more heavily sclerotized basal sclerite of clasper. Basal sclerite of clasper a narrow, sclerotized bar subparallel to ventral margin of valve, terminating in a point that fuses indistinguishably with digitus. A slender, setose ampulla projects posterodorsally from dorsal arm of clasper; ampulla 7–10 × as long as wide. Costal margin of valve heavily sclerotized, becoming free from surface of valve toward cucullus to form digitus. Digitus abruptly angled near neck of cucullus to project posteroventrally along anteroventral margin of cucullus, dorsal arm shorter, projecting in opposition; dorsal arm fused with rounded process at anterodorsal edge of cucullus; free, curved, ventral arm extended length of cucullus. Aedeagus (1.6 mm; $n = 7$, 1.5–1.8 mm) curved ventrally, 5–6 × as long as wide, with sclerotized band extending onto basal 1/4 of vesica on left. Vesica (3.5 mm; $n = 6$, 3.4–3.7 mm) kidney shaped, about 2 × as long as aedeagus, curving to right through 180° to project anteriorly; without basal or subbasal cornuti, but with two basal sclerotized straps projecting on to base of vesica, and a single spine-like bundle of smaller subparallel spines projecting distally near apex of vesica.

Female genitalia (Fig. 7). Posterior tip of papillae anales to anterior end of corpus bursae 7.2 mm; $n = 2$, 6.6–7.8 mm. Corpus bursae membranous, elongate, 2 × as long as wide, ovoid, slightly constricted posterior to middle, without signa. Appendix bursae corrugated, arising posteriorly on left, more heavily sclerotized distally, 0.8 × length corpus bursae. Ductus bursae long, narrow, 12 × as long as wide, 0.8 × length corpus bursae, heavily sclerotized in longitudinal ridges, wider anteriorly than posteriorly, entering at their junction on right side 1/3 distance from posterior end of appendix bursae to anterior end corpus bursae. Lamella antevaginalis quadrate with W-shaped outline, sclerotized, strongly indented anteriorly at juncture with ostium, somewhat concave posteriorly; dorsal wall of ostium membranous, lacking any discernible lamella. Anterior and posterior apophyses 1.5 × length A8, slender with paddle-like terminations. Papillae anales dorsoventrally flattened, evenly tapered, acutely pointed cones with dorsal surface densely spinulose, ventral surface minutely setose. The two sclerotized rods between the anal papillae characteristic of Apameini apparently secondarily lost in the very small adults.

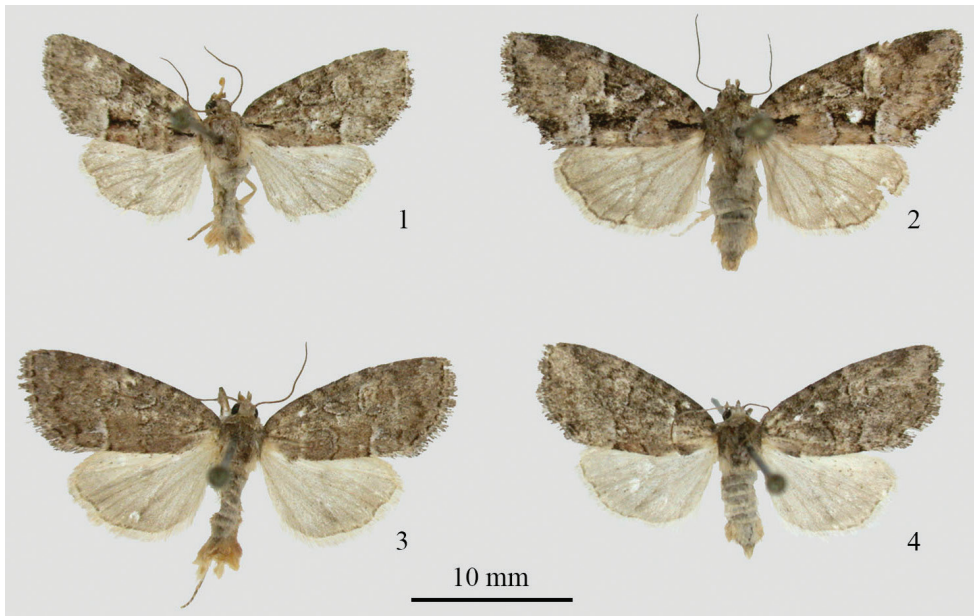
***Cherokeea attakullakulla* Sullivan & Quinter, sp. n.**

<http://zoobank.org/F8CF625C-480D-4BE2-9354-13CAEA2C388A>

Figs 1–7

Type locality. Fontana View Estates on Lake Fontana, Swain County, North Carolina.

Type material. Holotype male: USA, North Carolina: Swain County, 2000', Fontana Lake Estates (35°38.44'N; 83°55.79'W), mesic mixed pine/hardwoods June 10,



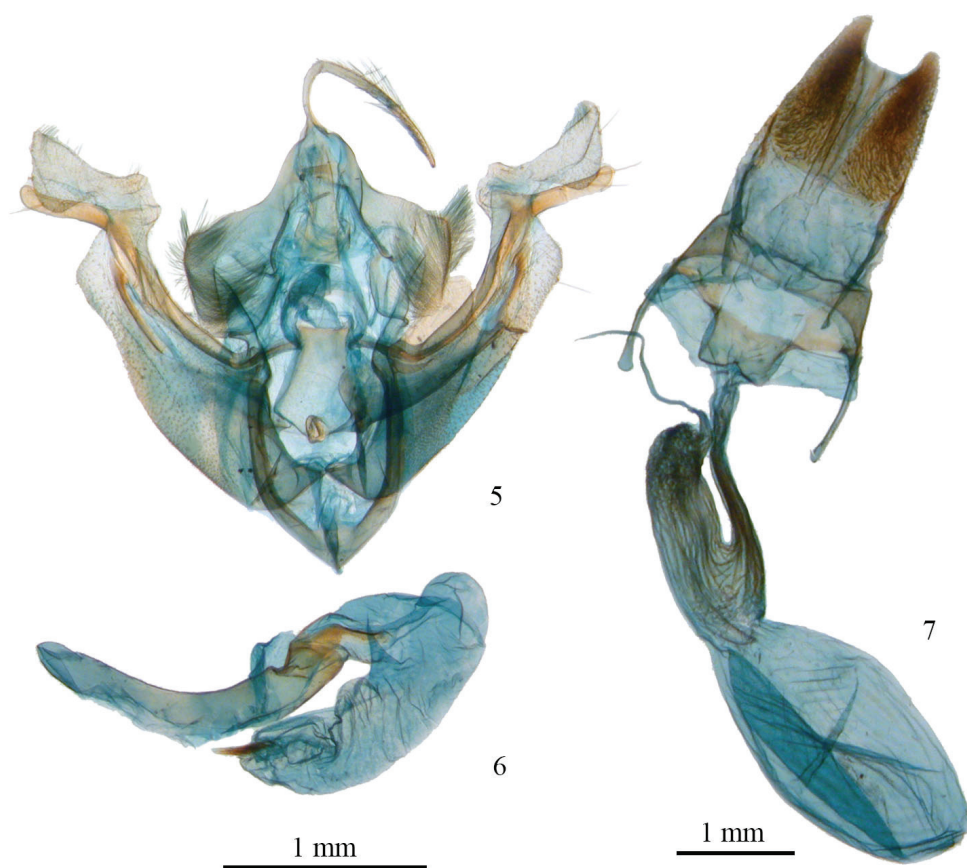
Figures 1–4. *Cherokeea attakullakulla* adults. **1** male holotype **2** female paratype, mottled form **3** male paratype, plain form **4** female paratype, plain form.

2002. J. Bolling Sullivan (USNM). **Paratypes:** (9♂ 12♀) same data as holotype, 8 and 10 June, 2002 (BMNH, USNM, CNC, ELQ, JBS). **Other material examined:** over 100 of both sexes collected from June 8–24 from: Great Smoky Mountains National Park, Swain County, North Carolina (Wiggins-Watson Cemetery, Deep Creek, 2215' (35°28.0'N; 83°26.2'W); Forney Creek, 1840' (35°28.1'N; 83°34.0'W); Big Cove Road, 2054' (35°51.6'N; 83°29.4'W); Welch Ridge, 1840' (35°26.9'N; 83°44.6'W); Rutherford County, North Carolina, Box Creek Preserve, 1100–1500' (35°54.8'N; 81°53.9'W).

Etymology. The name Attakullakulla, herein treated as a noun in apposition, refers to the Supreme Cherokee Leader (from 1761–1775) who represented his people in London in 1730 and at home in the Carolinas while negotiating various peace treaties.

Diagnosis. The very limited distribution of this species to moderate altitudes in the southern Appalachian Mountains and foothills is unlikely to coincide with any species of *Neoligia*. It is possible the moth might be confused with worn specimens of the common, widely distributed eustrotiine moth *Protodeltote muscosula* (Guenée), but adults of that species are slightly larger, with an olivaceous cast to the forewings, a prominent, subquadrate dark patch between the orbicular and reniform spots, and lack the characteristic genitalic features of Apameini. Otherwise, the genitalic characters described under the genus will serve to distinguish this species from anything of similar appearance occurring in North America.

Description. **Head.** Dorsum of antenna with alternating brown and gray rings of scales, underside tan; scape white. Labial palpus with gray and brown rough



Figures 5–7. Genitalia structure of *Cherokeea attakullakulla*. **5** male genitalia (aedeagus removed) (JBS5761) **6** male aedeagus and vesica (JBS5761) **7** female genitalia (JBS5757).

scaling. Frons with a mixture of white and brown erect scales, vertex and collar similar but with more dominant brown scaling. **Thorax.** Vestiture a mixture of coarse, brownish, spatulate scales, spatulate hairs and simple hairs; mesoscutellar crest prominent, metascutellar tuft, less so. **Legs.** As detailed in generic description. **Wings** (Figs 1–4). Forewings elongated and acutely rounded at apex. Forewing base to wing tip, 10.7 mm; N=20, (9.8–11.7 mm). Appearance variable, ranging from nearly uniform dull gray to much more contrasting and mottled, especially in females. Both phenotypes occur in both sexes, however. Antemedial line excurved, doubled, with pale gray to nearly white filling; slightly scalloped and comprised of black scales. Medial line or shade obscure. Postmedial line sinuous, excurved around reniform, most distinct at posterior margin, becoming obscure toward costa; slightly scalloped and doubled, with pale gray to nearly white filling; inner element of pm line much darker than the outer, which is defined by black points

on veins. Subterminal line a merged series of brownish-black indistinct chevrons. Terminal line a series of sharp, tiny black chevrons between veins. Fringe pale gray, with unbroken dark gray basal line. Basal, medial and terminal areas predominantly uniform gray, but with some reddish-brown scaling in the medial and basal areas in some individuals, especially toward posterior margin. Subterminal area usually paler gray, with quadrate, subapical dark patch on costa. Basal dash usually clearly visible, black, often highlighted below with whitish scales; medial dash variable, from completely obscure to a prominent bar, which may be the most distinct marking of the forewing; anal dash obscure or, at most, represented by an indistinct, dark, triangular patch of scales. Reniform spot auriculate, pale gray, of same shade as subterminal area. Orbicular spot similarly colored, ovoid, with an outline of black scales. Suborbicular and claviform spots not visible on worn material studied. Dorsal hindwing pale gray, plain, unmarked except for faint discal spot; fringe pale gray with darker gray basal line. **Abdomen.** Dorsal abdominal scaling white basally then brownish to tip; a prominent mid-dorsal tuft on first segment; ventral abdominal scaling brownish, becoming more yellow on ventral brush on eighth segment. **Genitalia.** As detailed for both sexes in generic description.

Molecular results. Barcodes were obtained for seven specimens from both Swain and Rutherford Counties. There were five haplotypes which differed by as much as 0.6%. The most common haplotype was:

```
AACATTATATTTTATTTTGGGAATTTGAGCAGGTATAGTTGGAAC
CTCTTTAAGATTACTAATTCGAGCTGAATTAGGAAACCCCGGATCTT
TAATTGGTGACGATCAAATTTATAATACTATTGTTACAGCTCAT
GCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAG
GATTTGGAAATTGACTTGTTACCTTTAATATTAGGAGCTCCAGATATAG
CATTTCCACGAATAAATAATATAAGTTTTTGGTTACTTCCCCCATCTT
TAACTTTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCTGGAA
CAGGATGAACAGTGTACCCCCCACTTTCATCTAATATTGCTCACG
GAGGAAGTTCTGTAGATTTAGCCATTTTTTCTCTTCATTTAGCTG
GTATTTCTTCTATTTTAGGAGCTATTAATTTTATTACTACAATTAT
TAATATACGATTAAATAATTTATCTTTTGATCAAATACCTTTATT
TATTTGAGCGGTAGGAATTACTGCATTTTTATTATTATTATCACTACC
CGTTTTAGCGGGAGCTATCACAATATTATTAACAGATCGAAATTTAAA
TACATCTTTTTTTGATCCTGCAGGAGGAGGAGATCCAATTTTATAT
CAACATTTATTT
```

Barcode sequences for *C. attakullakulla* did not associate with *Neoligia* or other related genera when nearest neighbor similarity searches were conducted.

Two patterns of maculation are seen (Figs 1–4), which we are calling mottled and plain. Intermediates are seen as well. These phenotypes did not segregate by location or by barcodes. Females are usually more heavily marked than males.

Immature stages

We have not yet had the opportunity to investigate the bionomics of this species fully, so the early stages remain unknown. Based upon habitat association, unequivocal placement within the Apameini, and especially details of genitalic morphology clearly linking this species to other taxa known to be specialists upon *Arundinaria*, it appears virtually certain that its larva will be found to be an endophagous feeder upon *Arundinaria appalachiana* Triplett, Weakley & L.G. Clark (Triplett et al. 2006), the native grass occurring at the locations and altitudes where the adult moths were collected.

Distribution and habitat

In North Carolina the species is known from Swain and Macon Counties in the mountains and from Rutherford County in the foothills. The only record for Georgia is Rabun Co., slopes of Rabun Bald, 0.7 road mi. past Kelsey Mtn. Road parking lot, 4000', June 21, 2001, James Adams (Adams, personal communication). The species is univoltine and flies from the 8th through the 24th of June. It is always found in association with hill cane (*Arundinaria appalachiana*), which grows on well-drained forested slopes. Two other species of *Arundinaria* occur in North Carolina but are associated with wet habitats, are often over 6' in height, and grow in dense colonies. Hill cane grows singularly or in poorly defined clumps and is less than four feet in height and can be found on rocky knobs, hillsides, and throughout mesic oak-hickory forests in the foothills and lower mountains (up to about 3000').

Discussion

Despite well-developed flight musculature, most adult apameine moths are highly sedentary and non-vagile. As a result, many of the species occur only in small, extremely localized populations and thus are infrequently collected, creating a false impression of rarity, when in fact they can be extremely abundant within their respective niches. Hence the availability of suitably fresh study material for molecular analysis represents a major challenge. Some of the earlier molecular analyses were based on a very limited subset of the species occurring in a region, and of relatively little value as a consequence. More recent work in North America and Europe has a high degree of species-level coverage in the 94% range (J.D. Lafontaine, pers. com.). Issues of generic non-monophyly are thus revealed. Phylogenetic studies based on morphology have one advantage in that comprehensive representation is more readily achievable.

Morphological studies of Lepidoptera in general and Noctuoidea in particular (e.g., Forbes 1948, 1954, 1960) traditionally have relied heavily upon genitalic structure, es-

pecially of adult males. Female genitalic characters were too often ignored. What has become most apparent in the broad overview of such studies is that the genitalic characters so emphasized range from practically useless even as diagnostic for species-level taxa, much less indicators of phylogenetic relationships among them, to moderately useful in other instances, to extremely so in certain groups, notably the Apameini. This in large part likely reflects the various evolutionary mechanisms operating in different groups. In those lepidopteran groups where diurnal behavior or temporal isolation mechanisms function, or where pheromone-driven selection mechanisms prevail, there may be little need for adaptive modifications of the genitalia. Where genitalia have evolved into so-called “lock-and-key” type of function, as apparent in the Apameini (Mikkola 1992), genitalic character states may be extraordinarily promising indicators of phylogenetic relationships. The Apameini have evolved extremely complex genitalic morphology, the most complex within the Noctuoidea, and perhaps even of all Lepidoptera. The long history of debate over whether these morphological adaptations truly function as reproductive isolation mechanisms has been revisited recently and summarized Masly (2012). Many such claims have been rejected in the past as untestable, but Masly suggests the future may be brighter in this regard. Mikkola (1992) left little doubt that apameines remain ideal subjects for such study. These moths are clearly well suited for phylogenetic analyses involving combined morphological and molecular data. The inclusion of data regarding the immature stages will render such analyses even more robust. The bionomics of western Palearctic taxa are relatively better known than those of North America, but much progress is being made here as well.

Even with regard solely to morphology, global treatments have thus far been quite uneven. The apameine fauna of the western Palearctic recently have been comprehensively studied and documented (Zilli et al. 2005). That work now serves as a model of what is needed elsewhere. More recent work (Mikkola et al. 2009) has made significant progress toward elucidating certain Nearctic apameine taxa and unifying the nomenclature across the Holarctic Region. Much work remains to be done in North America, however. The present paper represents one small step in that direction, with related studies in progress. It is hoped that a global review incorporating molecular data will ultimately result in a clearer understanding of the phylogenetic relationships of these fascinating insects.

Acknowledgements

We thank the staff of the Great Smoky Mountains National Park, the Cherokee Nation, and Tim Sweeney, Chris Wilson and Kevin Caldwell with Box Creek Preserve in Rutherford County for collecting permits and access to habitats as well as financial support. James Adams provided additional collecting records for Georgia. Jocelyn Gill assisted with the preparation of the figures and Paul Hebert and Barcode of Life Data systems technicians obtained barcode sequences. Don Lafontaine and Jane O'Donnell provided helpful reviews of the manuscript.

References

- Forbes WTM (1948) Lepidoptera of New York and neighboring states. Part 2 Geometridae, Sphingidae, Notodontidae, Lymantriidae. Cornell University Agriculture Experiment Station, Memoir 274, 263 pp.
- Forbes WTM (1954) Lepidoptera of New York and neighboring states. Part 3 Noctuidae. Cornell University Agriculture Experiment Station, Memoir 329, 433 pp.
- Forbes WTM (1960) Lepidoptera of New York and neighboring states. Part 4 Agaristidae through Nymphalidae. Cornell University Agriculture Experiment Station, Memoir 371, 188 pp.
- Judziewicz EJ, Clark LG, Londono X, Stern MJ (1999) American Bamboos. Smithsonian Institution Press, Washington DC, 392 pp.
- Lafontaine JD (1987) Noctuoidea: Noctuidae (part). In: Dominick RB et al. (Eds) The Moths of America North of Mexico fasc. 27.2. The Wedge Entomological Research Foundation, Washington, 237 pp.
- Lafontaine JD (2004) Noctuoidea, Noctuidae (part), Noctuinae, Agrotini. In: Hodges RW (Ed) The Moths of North America fasc. 27.1. The Wedge Entomological Research Foundation, Washington, 385 pp.
- Leech JH (1892–93) Butterflies from China, Japan and Corea. Part 1. Nymphalidae and Lemoniidae. London, 297 pp.
- Masly JP (2012) 170 Years of “Lock-and-Key”: Genital Morphology and Reproductive Isolation. International Journal of Evolution and Biology 2012: 1–10. [ID 247352]
- Mikkola K (1992) Evidence for lock-and-key mechanisms in the internal genitalia of the *Apamea* moths (Lepidoptera, Noctuidae). Systematic Entomology 17: 145–153. doi: 10.1111/j.1365-3113.1992.tb00327.x
- Mikkola K, Lafontaine JD, Gill JD (2009) Noctuoidea, Noctuidae (part): Xyleninae (part): Apameini (part – *Apamea* group of genera). In: Hodges RW et al. (Eds) The Moths of North America, fasc. 26.9. The Wedge Entomological Research Foundation, Washington, 192 pp.
- Quinter EL (2009) Noctuoidea, Noctuidae (part): Xyleninae (part): Apameini (part – *Apamea* group of genera). In: Hodges RW et al. (Eds) The Moths of North America, fasc. 26.9. The Wedge Entomological Research Foundation, Washington, 192 pp.
- Ratnasingham S, Hebert PD (2007) Bold: The barcode of life data system. Molecular Ecology Notes 7: 355–364. doi: 10.1111/j.1471-8286.2007.01678.x
- Sullivan JB, Adams JK (2009) A new species of *Morrisonia* (Noctuidae) from southeastern North America. Journal Lepidopterists’ Society 63: 21–26.
- Triplett JK, Weakley AS, Clark LG (2006) Hill cane (*Arundinaria appalachiana*) a new species of bamboo (Poaceae: Bambusoideae) from the southern Appalachian Mountains. SIDA 22(1): 79–95.
- Troubridge JT, Lafontaine JD (2002) Revision of species of the “*Oligia*” *semicana* group (Lepidoptera: Noctuidae) with descriptions of a new genus and 12 new species. Canadian Entomologist 134: 157–191. doi: 10.4039/Ent134157-2
- Wahlberg N (2014) <http://www.nymphalidae.net/Phylogeny/Phylogeny.htm> [accessed April 30, 2014]
- Zilli A, Ronkay L, Fibiger M (2005) Noctuidae Europaeae Vol. 8, Apameini. Entomological Press, Soró, 323 pp.

