

A new Brazilian *Passiflora* leafminer: *Spinivalva gaucha*, gen. n., sp. n. (Lepidoptera, Gracillariidae, Gracillariinae), the first gracillariid without a sap-feeding instar

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Abstract

Male, female, pupa, larva and egg of a new genus and species of Gracillariidae (Gracillariinae), *Spinivalva gaucha* Moreira and Vargas from southern Brazil are described and illustrated with the aid of optical and scanning electron microscopy. A preliminary analysis of mitochondrial DNA sequences including members of related lineages is also provided. The immature stages are associated with *Passiflora actinia*, *P. misera* and *P. suberosa* (Passifloraceae), and build mines on the adaxial leaf surface. Initially the mines are serpentine in shape, but later in larval ontogeny become a blotch type. Although the larvae are hyper-metamorphic as in other Gracillariidae, there is no sap-feeding instar in *S. gaucha*; the larva feeds on the palisade parenchyma, thus producing granular frass during all instars. Pupation occurs outside the mine;

prior to pupating, the larva excretes numerous bubbles that are placed in rows on the lateral margins of the cocoon external surface. This is the second genus of gracillariid moth described for the Atlantic Rain Forest, and the second gracillariid species known to be associated with Passifloraceae.

Keywords

Atlantic Rain Forest, gracillariids, leaf-mining moths, Neotropical region, passion vines, Passifloraceae

Introduction

Gracillariidae is a diverse lineage of leaf-mining Lepidoptera, with a total of 102 recognized genera and 1,880 species, distributed worldwide except for Antarctica; 24 of the genera (181 species) have been recorded in the Neotropical region (De Prins and De Prins 2013). Only four genera are recognized as endemic to South America; one occurs in the Atlantic Rain Forest of Brazil (*Leurocephala* Davis & McKay, 2011) and three in Chile: one in the southern Valdivian forests (*Prophylllocnistis* Davis, 1994) and two in the northern coastal valleys of the Atacama Desert (*Angelabella* Vargas & Parra, 2005; *Chileoptilia* Vargas & Landry, 2005) (Davis 1994, Vargas and Landry 2005, Vargas and Parra 2005, Davis et al. 2011). Only 29 gracillariid species have been recorded up to now for the Amazon and Atlantic rain forests of Brazil. This small number likely results from low collecting effort, since microlepidopterans in general have been undercollected in these biomes. Recent surveys conducted in a relatively small area of Central America suggested that a single gracillariid genus (*Phyllocnistis* Zeller, 1848) may include hundreds of species (Davis and Wagner 2011).

Almost all of what is known about the diversity of Brazilian gracillariids is concerned with the adult stage, in general associated with the original species descriptions, which were provided primarily by the pioneer work of Meyrick (1921, 1928, 1932). Several recent studies have suggested that the most informative characters for distinguishing species of some leaf-mining moths including gracillariids might be found in the pupal morphology (e.g., Patočka 1989, Fujihara et al. 2001, Kawahara et al. 2009, Kobayashi et al. 2011). However, studies that include the description of immatures are still in their infancy for microlepidopterans in general, in both the Amazon and Atlantic regions of Brazil (e.g., Brown et al. 2004, Becker and Adamski 2008, Brito et al. 2012, Moreira et al. 2012), and thus should be taken as a priority in research on this group.

The Atlantic Rain Forest, where only six species of gracillariids have been recorded up to now (Davis and Miller 1984, Davis et al. 2011, Brito et al. 2012), originally extended for more than 3,300 km along the eastern Brazilian coast and covered more than 1.1 million km² (for a general description, see Morellato and Haddad 2000, Oliveira-Filho and Fontes 2000). Although now restricted to less than 8% of its earlier range, this biome is still among the areas with the greatest diversity of plants and animals on earth, and has long been recognized as extremely rich in endemics (Myers et al. 2000, Carnaval et al. 2009), including Lepidoptera (Freitas et al. 2011). For example,

Stehmann et al. (2009) listed 14,552 species of vascular plants for the entire Atlantic Rain Forest, of which 6,933 (49%) are endemic. Considering the wide range of host plants used and the high level of host specificity usually found for the leaf-mining gracillariids in general (Davis 1987), it seems reasonable to predict that hundreds of gracillariid species await description in this understudied, species-rich biome, to which probably most of them are also endemic.

In the course of an ongoing survey on the diversity of microlepidopterans in the Atlantic Rain Forest in southern Brazil, we recently found a leaf-mining gracillariid associated with Passifloraceae. A search of the literature indicated that this taxon is distinct from other described genera of Gracillariidae, and therefore a new genus is proposed herein. We describe and illustrate all the life stages of this new species, and provide a preliminary characterization of its life history, including histological aspects of the leaf mine. We also present a preliminary analysis of mitochondrial DNA sequences, including members of related genera.

Materials and methods

Specimens used in the study were reared in small plastic vials under controlled abiotic conditions (14 h light / 10 h dark; 25 ± 2 °C) in the Laboratório de Morfologia e Comportamento de Insetos, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre city, Rio Grande do Sul State (RS), Brazil, from May 2011 through December 2012. They came from field-collected leaves with eggs, mines with feeding larvae inside, and pupae on plant shoots of *Passiflora actinia* Hook. (São Francisco de Paula municipality, RS), *P. misera* Kunth and *P. suberosa* L. (Porto Alegre municipality, RS).

Immature stages were fixed in Dietrich's fluid and preserved in 75% ethanol. For descriptions of the gross morphology, the specimens were cleared in a 10% potassium hydroxide (KOH) solution and slide-mounted in either glycerin jelly or Canada balsam. Observations were performed with the aid of a Leica® M125 stereomicroscope. Measurements were performed with the aid of an ocular micrometer (precision = 0.01mm). Structures selected to be drawn were previously photographed with a Sony Cyber-shot DSC-H10 digital camera mounted on the stereomicroscope. Vectorized line drawings were then made with the software Corel Photo-Paint® X3, using the corresponding digitalized images as a guide. At least five specimens were used for the descriptions of each life stage or instar.

For scanning electron microscope analyses, additional specimens were dehydrated in a Bal-tec® CPD030 critical-point dryer, mounted with double-sided tape on metal stubs, and coated with gold in a Bal-tec® SCD050 sputter coater. They were examined and photographed in a JEOL® JSM5800 scanning electron microscope at the Centro de Microscopia Eletrônica (CME) of UFRGS.

Descriptions of plant anatomy were based on diaphanized, field-collected leaf-mines (n = 5) from *P. actinia* shoots that were fixed in FAA (37% formaldehyde, glacial

acetic acid, and 50% ethanol, 1:1:18, v/v), stained with rose bengal (aqueous solution: 200 mg/1) and mounted either whole or in freehand section in glycerin on slides, following a procedure described in detail by Brito et al. (2012).

Molecular analysis

High-quality DNA was purified from larval tissue using the organic method of Cetyl Trimethyl Ammonium Bromide (CTAB) to investigate (i) levels of genetic variation within *Spinivalva* specimens collected in different localities and from different host plants (*Passiflora misera*, *P. suberosa* and *P. actinia*) and (ii) reconstruct phylogenetic relationships of this new genus among and within the *Parectopa* group of gracillariids. A total of nine field-collected specimens from three populations: 1) Porto Alegre, RS, from *P. suberosa* and *P. misera* (Pop. 1); 2) São Francisco de Paula, RS, from *P. actinia* (Pop. 2) and 3) Curitiba, PR, also from *P. actinia* (Pop. 3). They were used to amplify 1.5 kb of mitochondrial genes cytochrome *c* oxidase subunit I (CO-I), transfer RNA (tRNA-Leu), and cytochrome *c* oxidase subunit II (CO-II). For the PCR amplification we used the primer pairs Jerry + Pat II for the first segment (700 bp), and Patrick + Eva for the second (800 bp), following the procedure described by Caterino and Sperling (1999). Additionally, we amplified genetic material from three specimens of *Spinivalva*, using the universal barcode primers LCO1490 (5'-gggtcaacaatcataaa-gatatgg-3') and HCO2198 (5'-taaacttcagggtgacaaaaaatca-3'), following the procedure of Folmer et al. (1994). We obtained variants that exactly matched the region previously sequenced in 6 representative taxa of the *Parectopa* group of gracillariids, downloaded from GenBank and incorporated into our analysis (Table 1). The remaining PCR products were treated with exonuclease I and shrimp alkaline phosphatase (ExoSAP) (Fermentas Inc.), sequenced using the BigDye sequencing kit and analyzed in an ABI 3730XL DNA Analyzer (Applied Biosystems Inc.). Sequences were aligned and visually inspected using the algorithm Clustal X in MEGA 5 (Tamura et al. 2011) running in full mode with no manual adjustment. The dataset of 1.5 kb generated for specimens of *Spinivalva* from three different localities was deposited in GenBank and BOLD, under the accession numbers KC512114 to 512123 and GRABR001-13 to 010-13, respectively. The phylogenetic tree was reconstructed based on Bayesian inference and implemented in BEAST 2.0 (Drummond et al. 2012) to recover (i) the evolutionary distance within *Spinivalva* taxa from different localities and host plants, and (ii) relationships of *Spinivalva* among the lineages of gracillariids surveyed in this study. In both trees, the HKY85 model of sequence evolution (Hasegawa et al. 1985) was used with empirical base frequencies and 4 gamma categories. A relaxed uncorrelated log-normal clock was used, with no fixed mean substitution rate and a Yule prior on branching rates. We used four independent runs of 10 million generations, with the first 500,000 of each run discarded as burn-in. Posterior probabilities were used as an estimate of branch support. The species-level tree was unrooted, while the genus-level was rooted with a species of Bucculatricidae (*Bucculatrix ulmella* Zeller, 1848).

Table 1. Specimens used to investigate phylogenetic relationships of *Spinivalva* within the *Parectopa* group of gracillariids (following Kawahara et al. 2011). See Material and Methods for a detailed description of *Spinivalva* specimens.

Taxa	Voucher	GenBank Accession Number
Ingroup		
GRACILLARIIDAE		
<i>Conopomorpha sinensis</i> Bradley, 1986	-	HQ824810
<i>Epicephala mirivalvata</i> Li, Wang & Zhang, 2012	-	JX231168
<i>Leurocephala schinusae</i> Davis & McKay, 2011	RDOPO385-10	HM382093
<i>Liocrobyla desmodiella</i> Kuroko, 1982	G95AK	GU816416
<i>Parectopa</i> sp.	10-JDWBC-0213	HM863870
<i>Spinivalva gaucha</i> sp. n.	LMCI 186-12	KC512112
	LMCI 164-15	KC512113
<i>Spinivalva</i> sp.1	LMCI 169-A1	KC512114
<i>Stomphastis</i> sp.	USNM:ENT 00455002	JF415895
Outgroup		
BUCCULATRICIDAE		
<i>Bucculatrix ulmella</i> Zeller, 1848	RMNH.INS.18466	JX215365

Museum collections

Abbreviations of the institutions from which specimens were examined are:

- DZUP** Coll. Padre Jesus S. Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil.
- LMCI** Laboratório de Morfologia e Comportamento de Insetos, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil.
- MCNZ** Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil.
- MCTP** Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil.

Results

Spinivalva Moreira & Vargas, gen. n.

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<http://species-id.net/wiki/Spinivalva>

Figs 1–11

Type species. *Spinivalva gaucha* Moreira and Vargas, sp. n. by present designation.

Diagnosis. *Spinivalva* males show several abdominal and genital features that in conjunction differentiate this taxon from all known gracillariid genera: 1) saccular

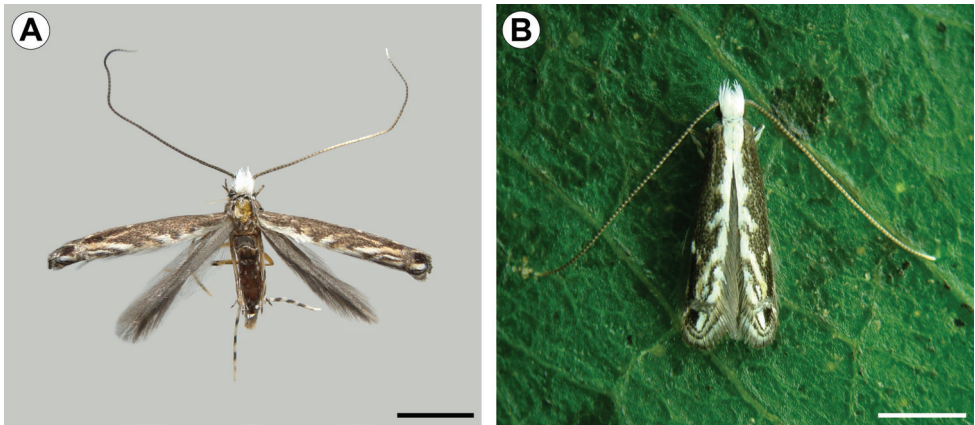


Figure 1. *Spinivalva gaucha* adult, dorsal view: **A** wings spread, pinned, dorsal view **B** wings folded, on *Passiflora actinia* leaf. Scale bars = 1.0 mm.

extension of valva abruptly narrowing distally, forming a single, medially bent process bearing a stout sensillum at the apex; 2) aedeagus tubular, slender, straight and long, ending as a sharply pointed spine; 3) saccus with anterior process long and tubular; 4) two pairs of coremata, each with two unit types that are formed by an external hair pencil and a tubular, membranous, corrugated pouch. In the female genitalia, the circular ostium bursae is located near the anterior margin of sternum VII, having a membranous corpus bursae associated with an accessory bursa, with no signum. The larvae construct mines on the adaxial surface of passion-vine leaves; initially the mines are serpentine in shape but later in ontogeny become a blotch type. Unlike all known stages of other leaf-miner gracillariids, *S. gaucha* has no larval sap-feeding instars; all instars of its larvae have a conspicuous spinneret and mandibles of the chewing type, and feed on the palisade parenchyma after hatching. Pupation occurs outside the mine; the larva excretes numerous bubbles that are aligned on the lateral margins of the cocoon surface prior to pupation.

Description. Adult (Figs 1–4). Male and female similar in size and color. Small moth, forewing length 2.78–3.61 mm ($n = 5$). *Head* (Fig. 2A): Vestiture moderately smooth, with a large, light-gray dorsal scale tuft that curves forward to the frons; scales slender, with apices slightly rounded. Eye relatively large, rounded, with dorsal margin slightly concave; vertical diameter \sim double minimum interocular distance across frons ($n = 6$). Antenna filiform, long, exceeding length of forewing; scape slightly elongate, $\sim 2.4\times$ length of pedicel; flagellomeres completely encircled by single, dense row of slender scales. Labrum trilobed, pilifers well developed, triangular. Mandible absent. Haustellum naked, elongate, $\sim 2.0\times$ length of labial palpus. Maxillary palpus short, smoothly scaled, 4-segmented; ratios of segments from base: $\sim 1.0 : 2.2 : 3.6 : 3.5$. Labial palpus smoothly scaled, moderately long, bent anteriorly and upward; ratio of segments from base: $\sim 1.0 : 4.6 : 0.3$. *Thorax*: Forewing (Fig. 2B) lanceolate, with 12 veins, all arising separately from the cell and reaching the margin;

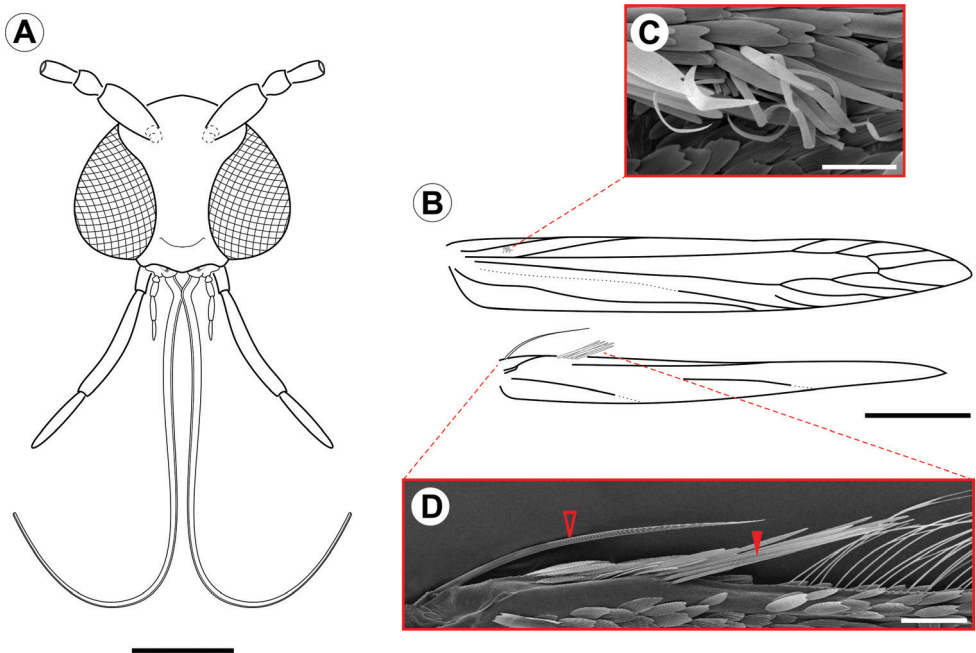


Figure 2. *Spinivalva gaucha* adult morphology: **A** head, anterior view **B** fore- and hind-wing venation **C** detail of retinaculum **D** detail of basal frenulum (open arrow) and more distal pseudofrenulum (closed arrow). Scale bars = 0.2, 0.5 mm; 50, 100 μ m, respectively.

L/W index ~ 7.3 ; retinaculum consisting of few subcostal, narrow, flat, longer, loosely coiled scales (Fig. 2C); discal cell $\sim 0.8 \times$ length of forewing ($n = 4$) ending near distal fifth of wing margin; R5-branched; R1 ending near proximal third of wing margin; M3-branched, CuA not branched, and faded basally; CuP weak proximally and not stalked, with 1A+2A that is well developed, extending past midlength of posterior margin. Hindwing (Fig. 2B) extremely lanceolate, L/W index ~ 9.6 , $\sim 1/8$ forewing in length; male frenulum (Fig. 2D) a single stout bristle; female with frenulum divided at base, then fused for nearly its entire length and appearing as a single stout bristle; pseudofrenulum consisting of ~ 8 modified scales arising in two to three irregular rows near $Sc+R_1$ ending at circa $1/5$ anterior margin; Rs faded proximally, ending at circa $1/3$ anterior margin; M and CuA unbranched, both faded proximally and weak distally, ending at circa $1/3$ and $2/3$ of posterior margin. Legs with tibial spur pattern 0-2-4; epiphysis present. Tibial length ratios (anterior / middle / posterior legs) $\sim 0.55/0.85/1.0$. *Abdomen*: Male with segments VII-VIII complex and reduced, except for enlarged tergum VIII; segment VII reduced to narrow, almost completely sclerotized ring; tergum VIII elongate, hoodlike, partly covering tegumen; sternum VII bearing two pairs of coremata, arising from distal apex of rodlike sclerites that protrude from intersegmentary membrane VII-VIII; each coremata (Fig. 3D) bearing two types of units – an external hair pencil (\sim valva in length) and a tubular, membranous, corrugated pouch; pouches of anterior pair $\sim 1/2$ hair pencil in length; those

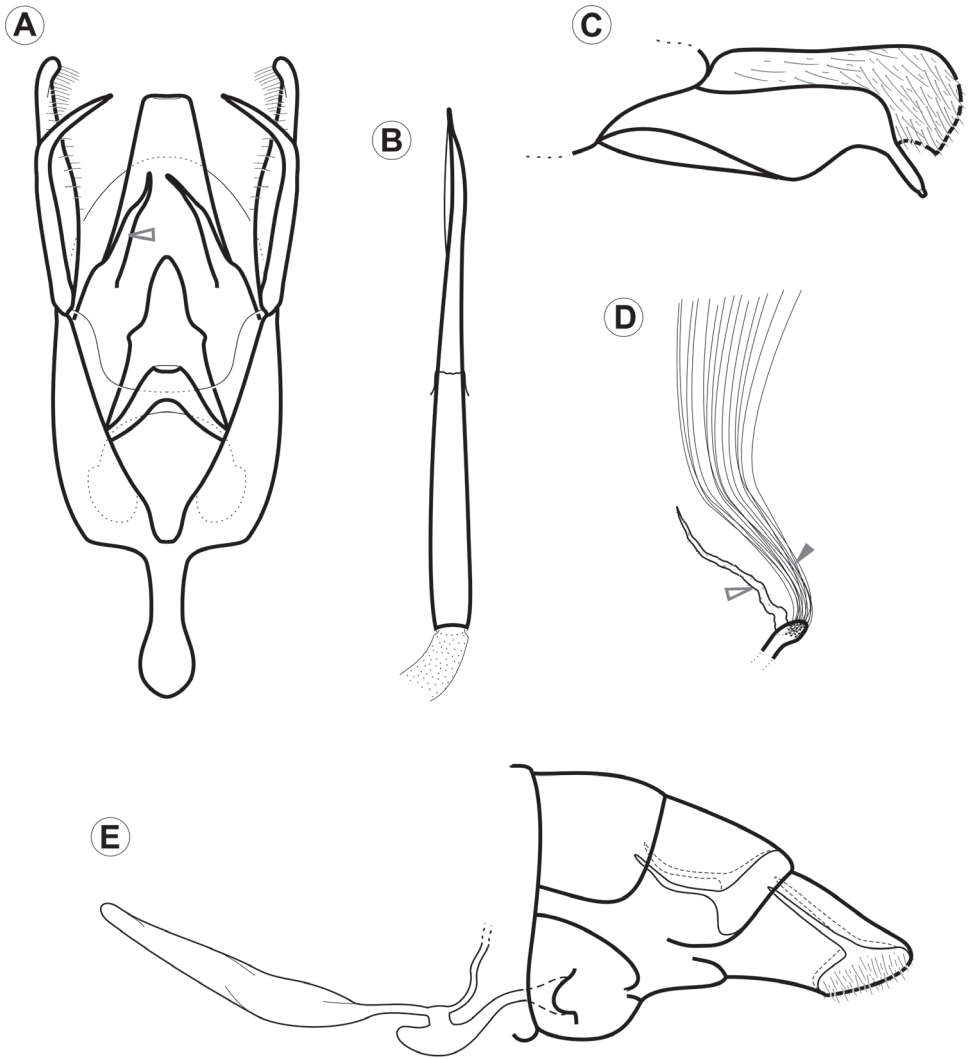


Figure 3. Genital morphology of *Spinivalva gaucha* under light microscopy: **A** male genitalia, ventral view (aedeagus omitted; open arrow indicates gnathal lobe) **B** aedeagus, lateral view **C** male right valve, median view **D** units of the coremata anterior pair, ventral view (open and closed arrows indicate tubular pouch and hair pencil, respectively) **E** female genitalia, lateral view. Scale bar = 0.2 mm.

of caudal pair double in size (near to hair pencil in length). Female postabdominal segments unmodified.

Male genitalia (Figs 3A–C, 4A, B, D, E). Uncus absent. Tegumen broad, hood-shaped, mostly membranous, with shallow apical notch. Pair of long, distally narrower, membranous lobes arising ventrally beneath tegumen. Vinculum long, broadly V-shaped, extending laterally along base of valva. Saccus well developed, U-shaped; anterior process long and tubiform, $\sim 1/2$ length of valva, apex slightly capitate. Transtilla an

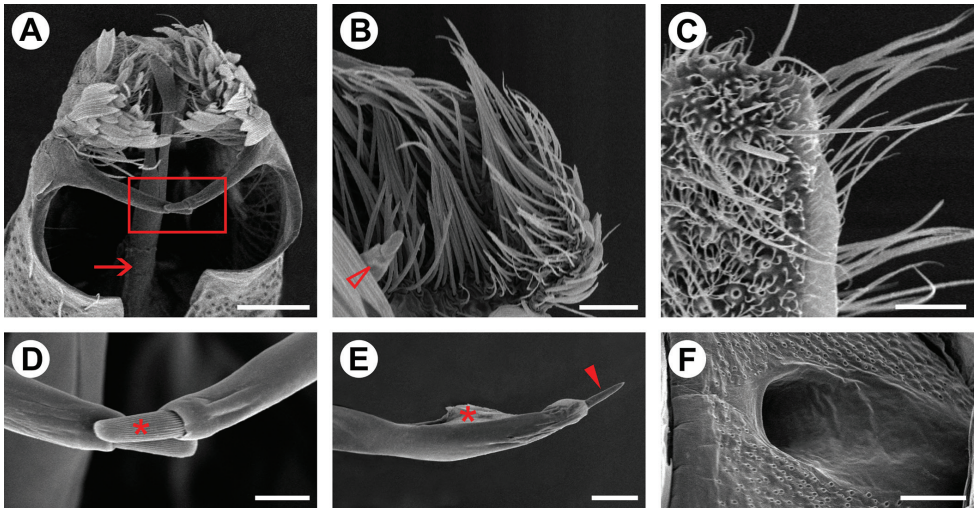


Figure 4. Genital morphology of *Spinivalva gaucha* under scanning electron microscopy: **A** male valvae (scales partly removed), showing saccular processes in crossed position and aedeagus (indicated by arrow), ventral view **B** setae of costa valvular in detail (open arrow indicates distal portion of saccular process), median view **C** female papilla annalis in detail, latero-dorsal view **D** saccular processes in detail (squared area in **A**; asterisk indicates distal sensillum of the right process) **E** caudal portion of aedeagus, showing terminal spine (indicated by closed arrow) and vesica (indicated by asterisk), lateral view **F** female ostium bursae, ventral view. Scale bars = 50, 25, 20, 10, 25, 50 μm , respectively.

arched, sclerotized plate joining bases of valvae. Juxta small, a dorsally concave, membranous plate, attached to middle of aedeagus. Aedeagus (Figs 3B, 4E) tubiform, slender, straight and long ($\sim 2\times$ valve length), slightly dilated caudally, with subapical, dorsally located concave aperture and ending as sharply pointed spine; entry of ductus ejaculatorius located at anterior end; vesica without cornuti. Valva (Figs 3C, 4A, B, D) broad at base, and deeply divided; costal margin relatively straight and distally rounded; cucullus densely covered by long piliform setae; sacculus with broad lobe abruptly narrowing distally, ending as a medially bent process with apex bearing a stout, blunt sensillum.

Female genitalia (Figs 3E, 4C, F). Sternum VII subtriangular; anterior margin linear; posterior margin with narrow notch. Tergum VIII subtriangular. Anterior apophysis with arms slightly curved, similar in length to posterior apophyses. Anal papillae connected dorsally, covered with long piliform setae and microtrichia. Ostium bursae moderately wide, located on anterior margin of sternum VII. Ductus bursa membranous, wider in middle, forming an accessory bursa $\sim 1/3$ length of corpus bursae. Corpus bursae membranous, gradually broadening posteriorly, \sim twice length of ductus bursae. Ductus seminalis membranous, narrow, inserted on distal portion of accessory bursa. Signum absent.

Etymology. The genus name is derived from the Latin *spina* (spine) and *valva* (valve), in reference to the conspicuous spine-like process present on the male valvae. Gender feminine.

***Spinivalva gaucha* Moreira & Vargas, sp. n.**

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http://species-id.net/wiki/Spinivalva_gaucha

Figs 1–11

Diagnosis. As discussed for the genus.

Description. Adult (Fig. 1). *Head.* Frons light gray; vertex covered mostly by white scaled tuft that curves forward to the frons. Antennae mostly dark gray; scape white ventrally with pecten of light-gray hairlike scales; pedicel and flagellum ventrally whitish gray. Maxillary and labial palpi mostly white, with scattered dark-gray scales laterally. *Thorax.* Forewing mostly covered by dark-gray scales. Narrow stripe of white scales along posterior margin; a zigzag edge, formed by short, oblique white fascia, separates this stripe from the remaining, mostly dark-gray area; distal portion of apical fascia bearing brownish scales. Apical portion with transverse bar of light-gray scales that separates distally two well-defined dots, one dark gray (toward anterior margin) and one white (toward posterior margin). Fringe with scales of two sizes, mostly white at base and dark gray apically. Hindwing completely covered by dark-gray scales and with concolorous fringe. Forelegs mostly dark gray, with some white scales basally and apically on each podite, particularly on coxa. Midlegs mostly white with scattered light-brown scales, and transverse dark-gray stripes on femur, tibia, tibial spurs and tarsomeres. Hindlegs similar to midlegs, but with hair-like scales on tibia. *Abdomen.* Mostly dark gray, with transverse, V-shaped white stripes on ventral surface of segments III–VI.

Male genitalia (Figs 3A–D; 4A, B, D, E). As described for genus.

Female genitalia (Figs 3E; 4C, F). As described for genus.

Type material. BRAZIL: Condomínio Alpes de São Francisco, 29°27'9.2"S, 50°37'6.6"W, São Francisco de Paula Municipality, Rio Grande do Sul State (RS), Brazil. All preserved dried and pinned, reared by the senior author from larvae and pupae collected on *Passiflora actinia* Hook. (Passifloraceae): LMCI 186, 26.V.2012, by G.R.P. Moreira, H.O. Vargas and S. Bordignon; LMCI 199, 19.XII.2012 by G.R.P. Moreira, R. Brito and F.A. Luz. HOLOTYPE: ♂ (LMCI 199-01), donated to DZUP (24.976). PARATYPES: 1♀ (LMCI 199-02), donated to DZUP (24.986); 1♂, 1♀ (LMCI 199-03 and 186-12), donated to MCNZ (81900 and 81903, respectively); 1♂, 1♀ (LMCI 199-04 and 186-15), donated to MCTP (31442 and 31443, respectively).

Other specimens examined. LMCI 156: Floresta Nacional de São Francisco de Paula, 29°25'21.4"S, 50°23'26.6"W, São Francisco de Paula Municipality, RS, Brazil, collected by K.R. Barão, 13–15.V.2011, on *P. actinia*. LMCI 157: Condomínio Alpes de São Francisco, 29°27'9.2"S, 50°37'6.6"W, São Francisco de Paula Municipality, RS, Brazil, collected by G.R.P. Moreira, R. Brito and G.L. Gonçalves, 28.V.2011, on *P. actinia*. LMCI 164: Campus da Vale, Universidade Federal do Rio Grande do Sul (UFRGS), 30°04'12.9"S, 51°07'11.5"W, Porto Alegre Municipality, RS, Brazil, collected by R. Brito, on *P. misera* Kunth and *P. suberosa* L. (Passifloraceae).

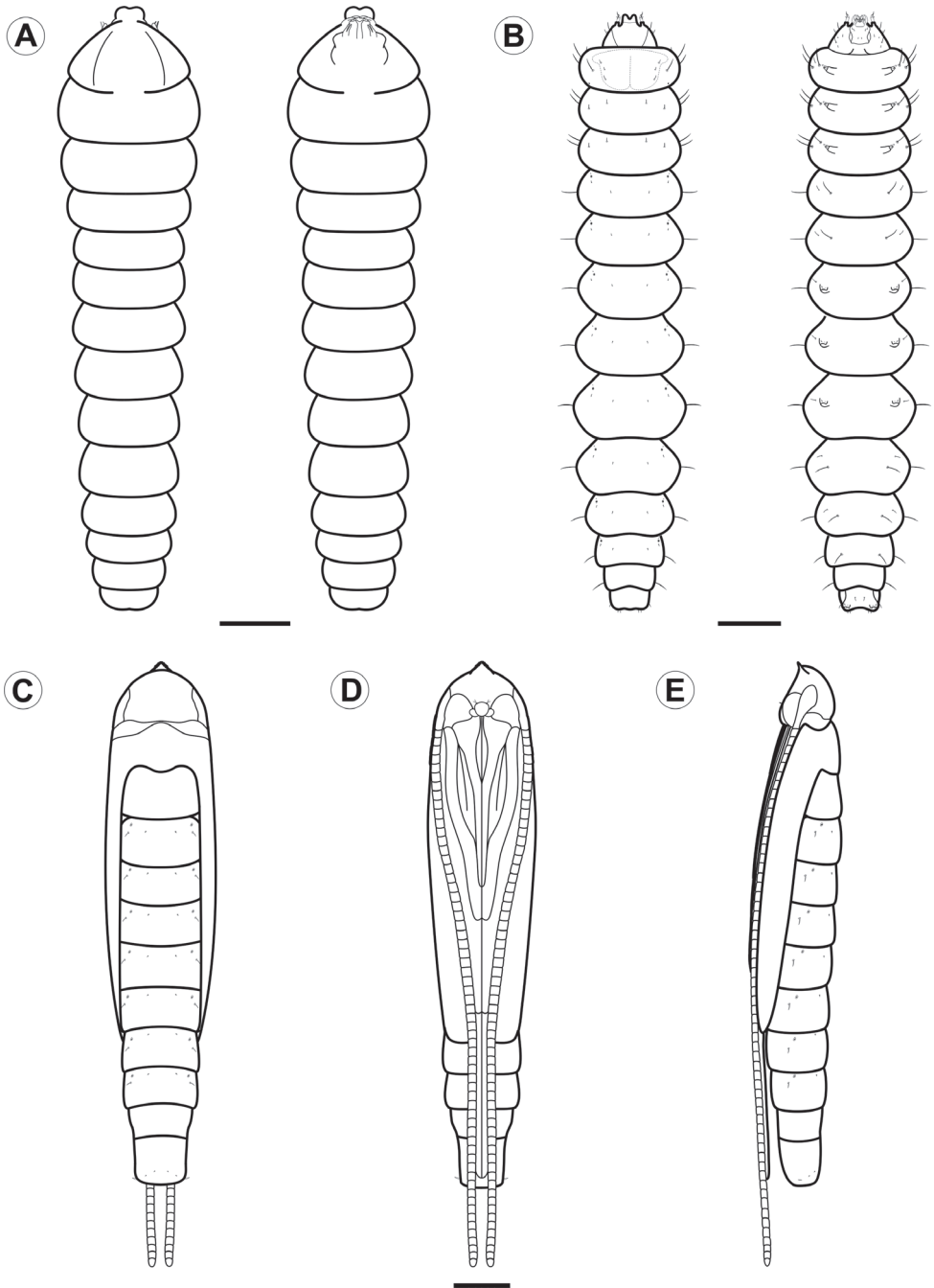


Figure 5. Larval and pupal morphology of *Spinivalva gaucha* under light microscopy: **A** first larval instar, dorsal and ventral views **B** fifth larval instar, dorsal and ventral views **C–E** pupa, dorsal, ventral and lateral views, respectively. Scale bars = 50 μ m; 0.5, 0.5 mm, respectively.

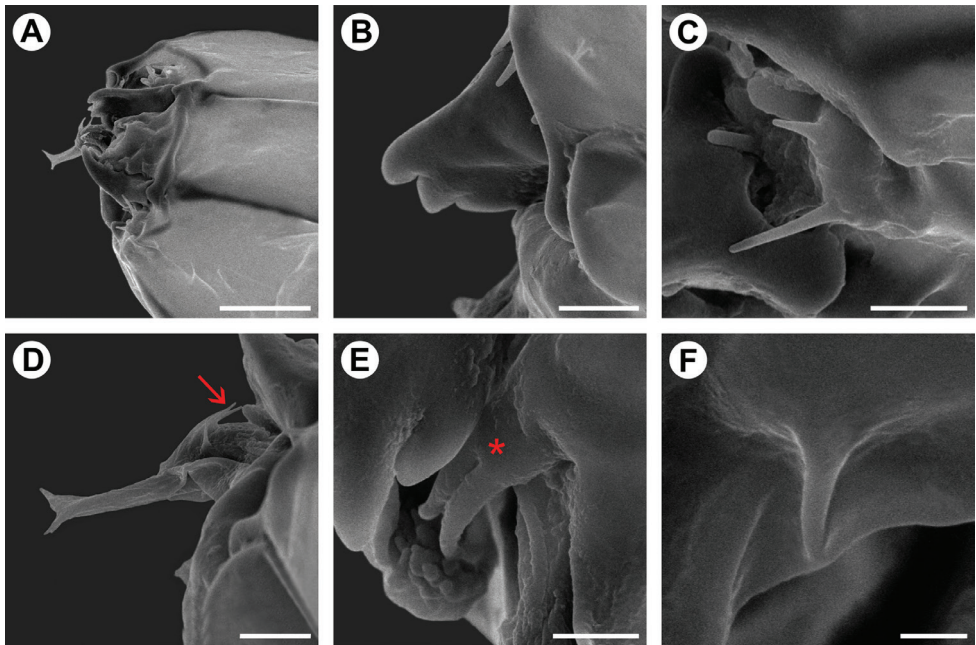


Figure 6. Scanning electron micrographs of *Spinivalva gaucha* first larval instar: **A** head, general, dorso-lateral view **B** mandible, dorsal view **C** antenna, lateral view **D** spinneret, lateral view; seta indicates hypopharyngeal papillae **E** maxilla (asterisk), lateral view **F** labial palpi. Scale bars = 20, 5, 5, 5, 3, 1 μm , respectively.

LMCI 169: Centro Politécnico da Universidade Federal do Paraná, 25°26'44.1"S, 49°13'56.8"W, Curitiba Municipality, Paraná State, Brazil; 5 larvae dissected from mines collected by G.R.P. Moreira, on *P. actinia*; used for DNA extraction only. Adults, dried and pinned, with the same collection data, deposited in LMCI: 4♂♂ (LMCI 156-9, 164-6, 7, 10); 1♀, (LMCI 164-9). Genitalia preparations, mounted in Canada balsam on slides, with the same collection data, deposited in LMCI: 4♂♂ (GRPM 50-11, 13, 21, 22); 4♀♀ (GRPM 50-12, 23, 32, 34). Immature stages, fixed in Dietrich's fluid and preserved in 70% ethanol, with the same collection data series, deposited in LMCI: 2 eggs (LMCI 157-2), 4 first-instar larvae (LMCI 157-8), 5 third-instar larvae (LMCI 157-4), 6 fifth-instar larvae (LMCI 157-10), and 9 pupae (LMCI 157-5, 6). Mature leaf mines ($n = 5$) containing larval exuvia, mounted in glycerin on slides and stained with rose bengal, with the same collection data, deposited in LMCI, under accession numbers LMCI 186-3, 7 and LMCI 199-5, 6, 7.

Etymology. The specific name is derived from the Portuguese “Gaúcho”, a term commonly used for natives of Rio Grande do Sul, the southernmost state of Brazil, where this new species was first found.

Immature stages. Egg (Fig. 10C). Flat, ellipsoid, laid on the abaxial surface, usually close to the leaf veins; chorion translucent, larva visible through transparent area of leaf before eclosion; chorionic ultrastructure, aeropyles and micropylar area not observed.

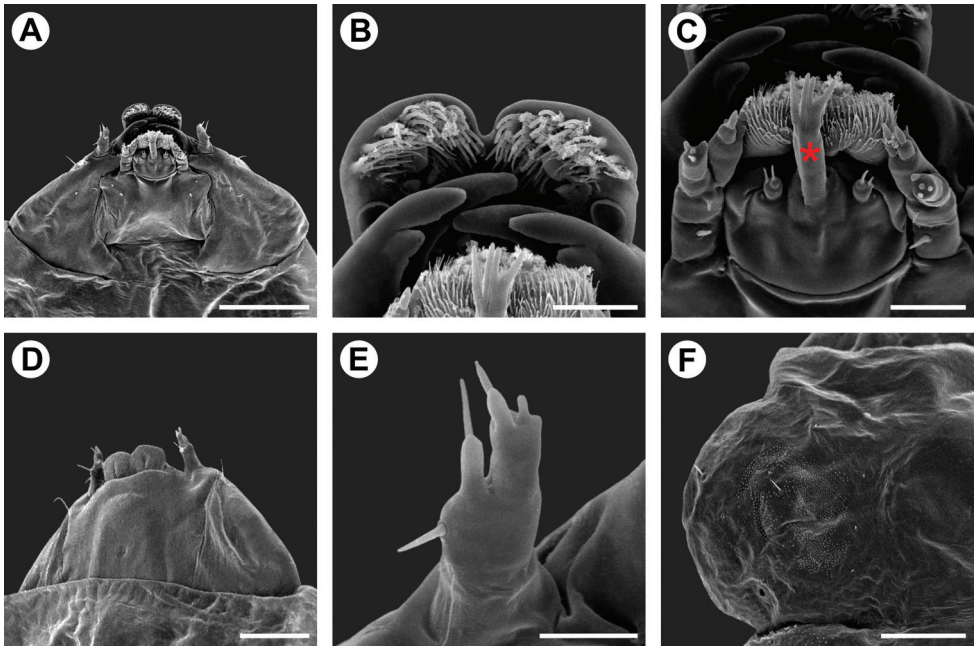


Figure 7. Scanning electron micrographs of *Spinivalva gaucha* third larval instar: **A** head, general, ventral view **B** labrum, ventral view **C** labium, ventral view (asterisk indicates the spinneret) **D** head, general, dorso-lateral view **E** antenna, antero-ventral view **F** left side of prothoracic shield, dorsal view. Scale bars = 75, 15, 15, 50, 10, 75 μm , respectively.

Larva (Figs 5A, B, 6, 7, 8, 10F, H). Head brown, thorax and abdomen yellowish. Leaf-miner, with hypermetamorphic development and five instars, all endophyllous, prognathous and tissue feeders; that is, there is no sap-feeder instar, and all larvae have a typical spinneret and functional mandibles of the chewing type. Instars change gradually in external morphology during ontogeny, and can be identified through measurements of the head capsule, since there is no overlap between the head-capsule size of succeeding instars (Table 2). The following exponential growth equation was adjusted for the head-capsule width from larvae reared on *Passiflora actinia*: $y = 0.078e^{0.420x}$; $n = 25$; $r = 0.99$; $p < 0.0001$. Preliminary observations suggested that the number of instars may vary from four to five as a function of the host plant, which should be further explored.

First instar (Figs 5A, 6A–F). Body depressed, without setae, legs or pseudopodia. Antennae (Fig. 6C) reduced, one-segmented, nearly flush with head capsule, with four short sensilla. Stemmata absent. Labrum (Fig. 5A) moderately bilobed, with slight central notch. Mandibles (Fig. 6B) of chewing type, with three blunt teeth. Maxilla (Fig. 6E) rudimentary, uni-segmented, with two finger-like, terminal lobes. Labium relatively broad, with well-developed tubular spinneret having flared terminal opening (Fig. 6D). Hypopharynx bearing few papilliform projections basally (Fig. 6D). Labial palpi (Fig. 6F) vestigial, reduced to pair of closely appressed, slender setae.

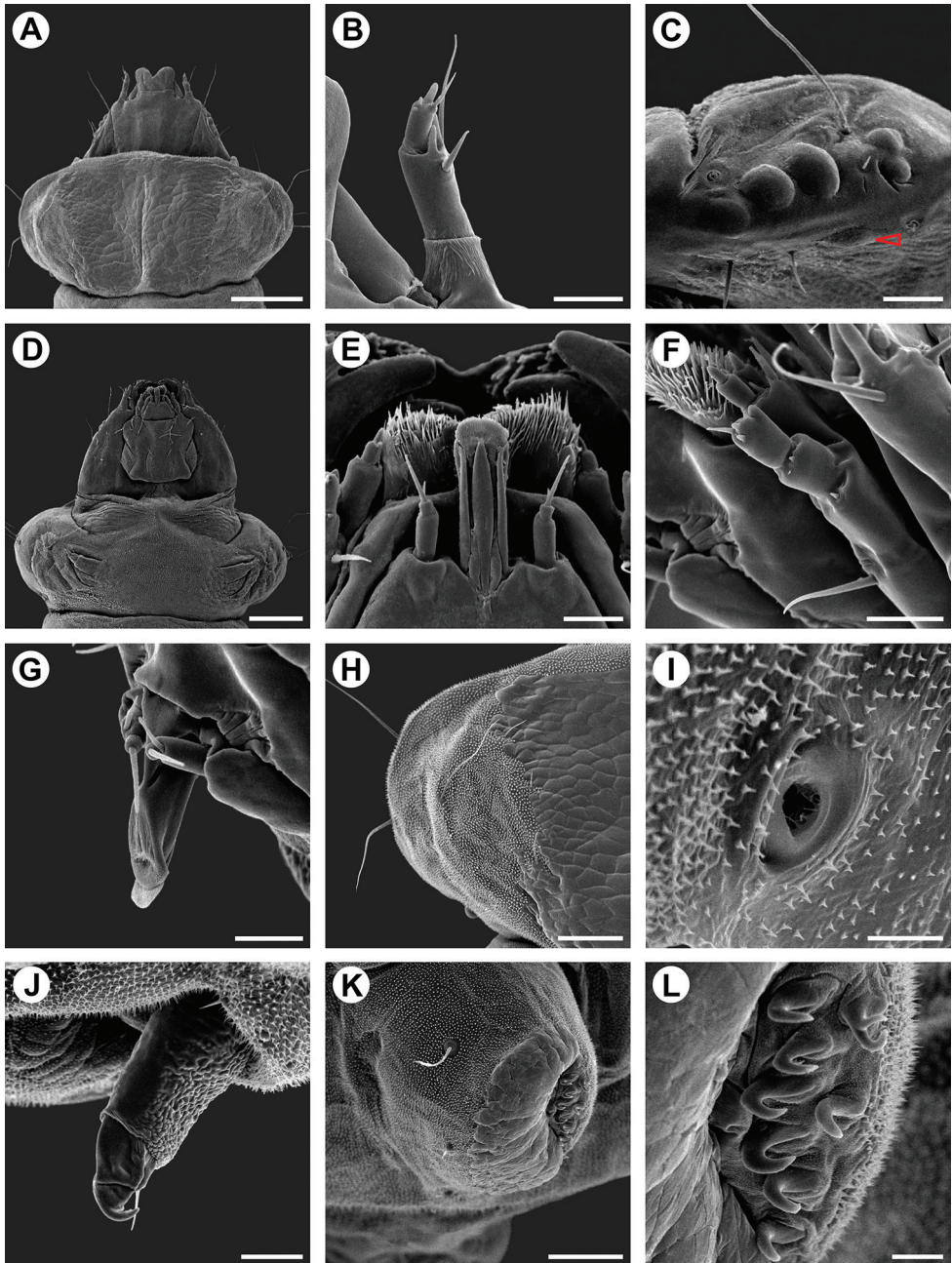


Figure 8. Scanning electron micrographs of *Spinivalva gaucha* fifth larval instar: **A** head and prothorax, general, dorsal view **B** antenna, dorsal view **C** stemmata (open arrow indicates sixth stemma), lateral view **D** head and prothorax, general, ventral view **E** labium, ventral view **F** maxilla, lateral view **G** spinneret, lateral view **H** left side of prothoracic shield, dorsal view **I** prothoracic spiracle, lateral view **J** prothoracic leg, postero-lateral view **K** pseudopodium on A4, antero-lateral view **L** crochets of pseudopodium A4 in detail. Scale bars = 200, 25, 25, 200, 20, 20, 20, 75, 10, 25, 75, 10 μm , respectively.

Table 2. Variation in size among head capsules of *Spinivalva gaucha* larvae reared on *Passiflora actinia* Hook (n = 5 per instar).

Instar	Head capsule width (mm)		
	Mean \pm standard error	Range	Growth rate
I	0.11 \pm 0.002	0.10–0.12	-
II	0.19 \pm 0.004	0.18–0.20	1.65
III	0.28 \pm 0.009	0.26–0.32	1.52
IV	0.43 \pm 0.012	0.39–0.46	1.52
V	0.57 \pm 0.140	0.57–0.58	1.33

Third instar (Figs 7A–F). Similar to first instar, but with body partly depressed and setae greatly reduced. Prothoracic shield slightly differentiated (Fig. 7F), nearly colorless; legs and pseudopodia absent. Antennae (Fig. 7E) bi-segmented, first segment stouter than second segment, each bearing three sensilla. Stemmata absent. Labrum (Fig. 7B) bilobed, with pronounced median notch, and several ventral, posteriorly bent papilliform projections. Mandibles of chewing type, with three teeth. Maxilla well developed, as shown in Fig. 7C. Labium broad, with spinneret similar to that of first instar, but shorter and stouter (Fig. 7C). Labial palpi (Fig. 7C) short, bi-segmented, each bearing apical sensillum. Hypopharynx with several papilliform projections basally (Fig. 7C).

Fifth instar (Figs 5B, 8A–L, 10F, H). Body subcylindrical, covered by microtrichia and with setae well developed; thoracic legs reduced; pseudopodia present on A3–5, A10. Head and prothoracic shield brown (Fig. 10F); remaining parts of body yellowish (Fig. 10F), changing to red before pupation (Fig. 10H). Maximum length of larvae examined 5.52 mm. Antennae (Fig. 8B) three-segmented, second segment longer than third, each bearing four sensilla. Stemmata six in number, five of them arranged close to lateral margin of head, and one inconspicuous stemma located ventrally (Fig. 8C). Labrum (Fig. 8A) bilobed, with deep median notch, similar to previous instars, but with ventral papilliform projections curved anteriorly. Mandibles similar to those of previous instars. Maxilla well developed, as shown in Fig. 8F. Labium broad, with stout, tubular spinneret having subapical opening (Figs 8G). Labial palpi (Fig. 8E) bi-segmented, basal segment longer than distal one, each bearing apical sensillum, that of distal segment longer. Hypopharynx with two sets of dense papilliform projections (Fig. 8E). Chaetotaxy: A group trisetose; L group unisetose; S group trisetose; SS group bisetose.

Thorax with prothoracic dark-brown dorsal shield well developed; one pair of legs on each thoracic segment; each leg with one pair of tarsal setae and one curved hook-like tarsal claw; one circular spiracle on each side of prothorax, near posterior margin and slightly displaced dorsally (Figs 8H–J). Protothorax chaetotaxy: D group bisetose, both located on dorsal shield; XD group bisetose, XD1 on dorsal shield and similar in length to D1 and D2; XD2 lateral to dorsal shield, about three times XD1 in length; L group bisetose, L1 dorsal to L2, slightly longer than XD2 and about three times L2 in

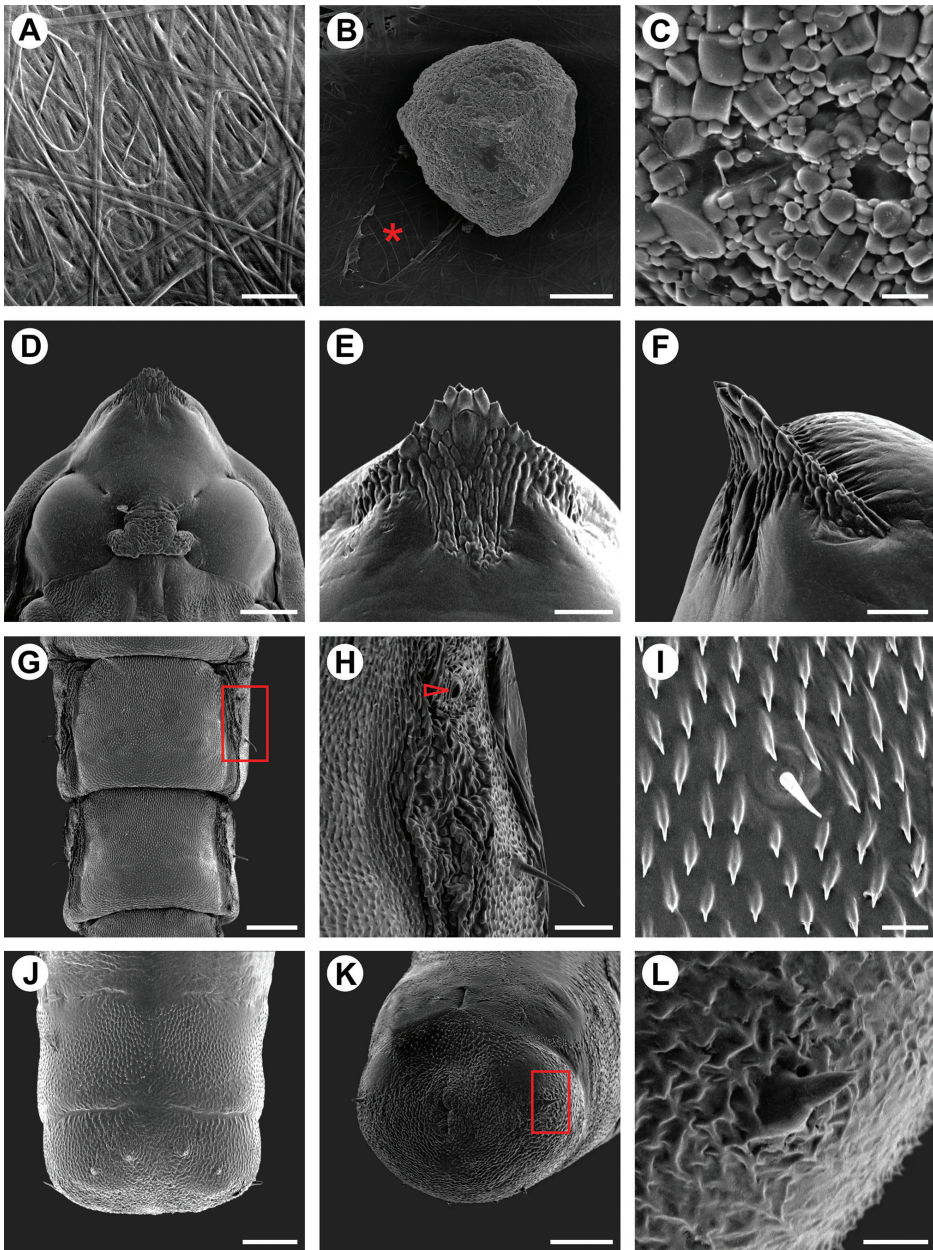


Figure 9. Scanning electron micrographs of *Spinivalva gaucha* pupal cocoon and pupa: **A** weaving pattern of the pupal cocoon upper surface **B** ornamental bubble (asterisk indicates a covered slit, used by the larva to attach the bubble on outside of the cocoon surface) **C** bubble surface in detail **D** head, ventral view **E–F** cocoon-cutter, ventral and lateral views, respectively **G** abdominal segments, dorsal view **H** abdominal segment A3 (detail of area marked with a rectangle in **G**; open arrow indicates spiracle) **I** setae and microtrichia occurring on central portion of A1–A7 **J–K** last abdominal segments, dorsal and ventro-posterior views, respectively **L** spine of last abdominal segment (detail of squared area marked in **K**). Scale bars = 20, 75, 5, 150, 50, 50, 200, 50, 10, 75, 75, 10 μm , respectively.

length; SV group bisetose, posteroventral to L2, both similar to L1 in length; V group absent. Meso- and metathorax chaetotaxy: D group bisetose, length of both setae similar to prothoracic D2; D2 posterolateral to D1; L group unisetose, L1 similar to that on prothorax in length; SV group bisetose, similar to prothoracic SV group in size and position; V group absent.

Abdomen with paired, circular spiracle laterally on A1-8; prolegs on A3-5 and A10, bearing uniordinal crochets in lateral penellipse (Figs 8K–L). Chaetotaxy of A1-2, 6-7: D group bisetose, both setae very small, D1 anterolateral to D2 and posterior to spiracle; SD group unisetose, SD2 anteroventral to spiracle, length of SD2 about half of D1; L group unisetose, L1 length similar to anterior segment; SV group unisetose, length of SV1 about half of L1; V group unisetose, length of V1 similar to L1. A3-5: Similar to anterior segment, but V1 located on proleg and extremely reduced. A8: Similar to anterior segment, but SV group absent. A9: All setae lost except L group, which is similar to anterior segment. A10: D group unisetose, D2 on posterior margin; SD group unisetose, SD1 lateral to D2; L group unisetose, L1 about 1/3 length of corresponding seta on A9; SV group on proleg, bisetose; V group unisetose.

Pupa (Figs 5C–E, 9D–L, 10J). Maximum length of specimens examined ranged from 3.69 to 5.10 mm. General coloration yellowish, with head, thorax, and corresponding appendices darkening later in development (Fig. 10J). Vertex bearing subtriangular acute process (= cocoon cutter; Figs 9D–F) with serrated anterior edge, formed by several pointed projections that are fewer and larger at apex. Frons with 2 pairs of short frontal setae (Fig. 9D). Antennae long and slender, extending longer than pupal length; forewing reaching anterior margin of A6; proboscis extending to A2; prothoracic, mesothoracic and metathoracic legs reaching A3, A5 and A9, respectively (Figs 5C–E). Abdominal integument dorsally covered with micotrichia (Figs 9G–I). Intermediate abdominal segments with lateral margin of terga corrugated (Figs 9G–H). From A1 to A7, two micro-setae, located medially on anterior margin of terga; additional micro-setae are found laterally, located posteriorly to spiracles (Figs 9H–I). Last abdominal segment with two pairs of spines dorsally and one pair laterally, on posterior margin of tergum (Figs 9J–L).

Host plants. Passifloraceae: *Passiflora actinia* Hook, *P. misera* Kunth and *P. suberosa* L. The former, where *S. gaucha* was most frequently collected, is found primarily in forest edges in the coastal mountains of southern Brazil, where it is endemic, distributed from the Brazilian states of Espírito Santo to Rio Grande do Sul. *Passiflora suberosa* and *P. misera* have broader distributions, extending to Central America, and also occur in relatively open areas occupied by shrubs and herbaceous vegetation. Details about the biology and distribution of these passion-vine species in southern Brazil were provided by Mondin et al. (2011) and Moreira et al. (2011), respectively.

Distribution. *Spinivalva gaucha* is known from the type locality (Condomínio Alpes de São Francisco) and the Floresta Nacional de São Francisco de Paula, both located in São Francisco de Paula Municipality, where *P. actinia* plants are used as larval host plants. A few scattered specimens were also collected from an additional population located in Porto Alegre Municipality. Both municipalities are located in Rio

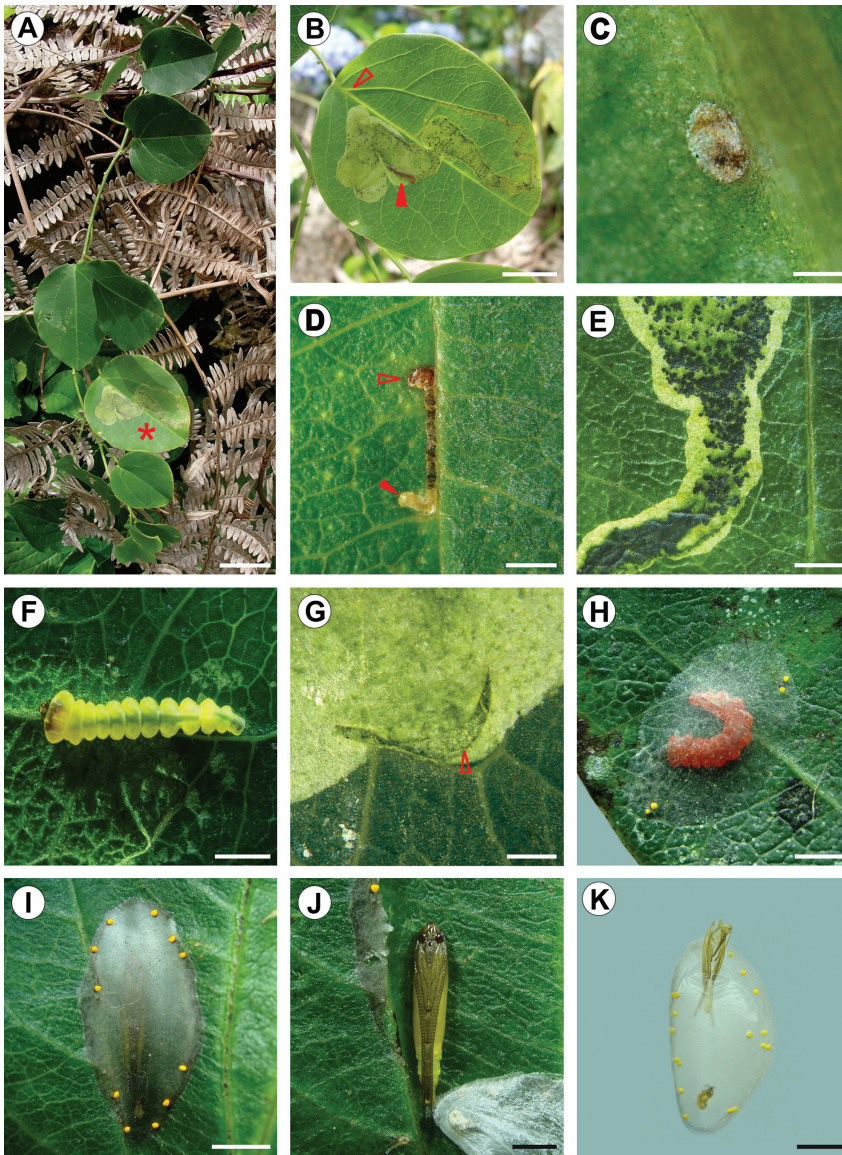


Figure 10. Life history of *Spinivalva gaucha*: **A** *Passiflora actinia* shoot at the type locality **B** *Spinivalva gaucha* mine on upper leaf surface (leaf marked with an asterisk in **A**; open and closed arrows indicate respectively the beginning of a mine and a last-instar larva visible through transparent blotch section of the mine); **C** chorion of empty egg on lower surface **D** first-instar larva (indicated by closed arrow) visible through transparent serpentine section of a young mine (open arrow indicates the beginning of the mine on the upper leaf surface) **E** initial portion of blotch section in detail, showing frass and damage to leaf parenchyma left by last-instar larva within the mine **F** fourth-instar larva in the mine **G** exit hole (arrow) used by a last-instar larva to leave the mine **H** last-instar larva after changing color, building the cocoon outside the mine on the leaf surface **I** cocoon, with pupa visible through transparency **J** pupa in detail, after removing the cocoon **K** pupal exuvium protruding from the cocoon exit hole onto plastic substrate, just after the adult emergence. Scale bars = 20, 10, 0.2, 1.5, 1, 0.5, 0.5, 2, 2, 1, 2 mm, respectively.

Grande do Sul (RS), Brazil. In the Porto Alegre population, *P. misera* and *P. suberosa* are used as hosts. We could not find conspicuous morphological differences among the specimens collected in RS, as also corroborated by the DNA analyses. Additional *Spinivalva* specimens were collected farther north in Curitiba Municipality, Paraná, also mining *P. actinia* leaves. However, as discussed below, analyses of the molecular data suggested that this population may correspond to a new species, a possibility that should be further explored. All these populations are located within the Atlantic Rain Forest domain *sensu lato* (Morellato and Haddad 2000).

Life history (Figs 9A–C, 10A–E, G–I, K, 11). Eggs of *S. gaucha* are deposited on the abaxial leaf surface, adhered by a cement substance, close to the midrib or secondary veins (Fig. 10C). Hatching occurs through the surface of the egg adhered to the leaf; the first-instar larva moves directly into the leaf lamina, easily reaching the adaxial side of the leaf (Fig. 10D). Initially, the mine is narrow, slightly serpentine in shape, increasing in width progressively during ontogeny and becoming a blotch during the last larval instar. The larva feeds on the palisade parenchyma from the beginning to the end of the mine (Figs 10B, 11). Dark-green granular frass pellets of increasing size are found in the larva's feeding path (Figs 10D, E), as are the head-capsule exuviae.

After the fifth-instar larva leaves the mine through a slit made in the blotch section (Fig. 10G) and prior to pupal moulting, it spins the pupal cocoon, usually on the adaxial leaf surface of adjacent leaves. The pupal cocoon is exophyllous, elliptical in general outline, transparent, from 7.76 to 8.74 mm long in the specimens examined. Silk filaments are woven in a tight pattern, forming a compact, flat wall that covers the pupa (Figs 9A, 10I). The cocoon periphery is adorned with several irregularly spaced, minute, light-yellow bubbles (Fig. 10I). These are not compartmentalized, showing a finely granular structured surface (Fig. 9C). They are discharged from the anus by the mature larvae to the outside through a slit made with the mandibles in the cocoon wall, which is closed soon after deposition (Fig. 9B). Throughout this process, the bubbles are manipulated by the spinneret. During adult emergence, one end of the pupal cocoon is split by the frontal process of the pupa (cocoon cutter). Generally after the adult emerges, the anterior half of the pupal exuvium (head and thorax) protrudes outside, while the posterior half remains in the pupal cocoon (Fig. 10K).

At the type locality, *S. gaucha* mines occur at low numbers on *P. actinia* plants (Fig. 10A). In most cases, only one mine was found per leaf, but up to three were collected in a single leaf, and several leaves may be used per plant. There was no indication that this behavior differed from that of the other passion-vine species and populations studied. We could not find a clear pattern for the number of generations per year and the flight period.

Molecular phylogeny (Fig. 12). A total of 1583 nucleotide sites were analyzed for *Spinivalva* from different localities and host plants; 110 (7%) were variable. An unrooted Bayesian tree recovered two major groups (Fig. 12A). The first included specimens from Porto Alegre (Pop. 1), hosted on either *P. suberosa* or *P. misera*, together with those from São Francisco de Paula / Condomínio Alpes de São Francisco (Pop. 2) hosted on *P. actinia*. The second group included individuals from Curitiba (Pop. 3) sampled on

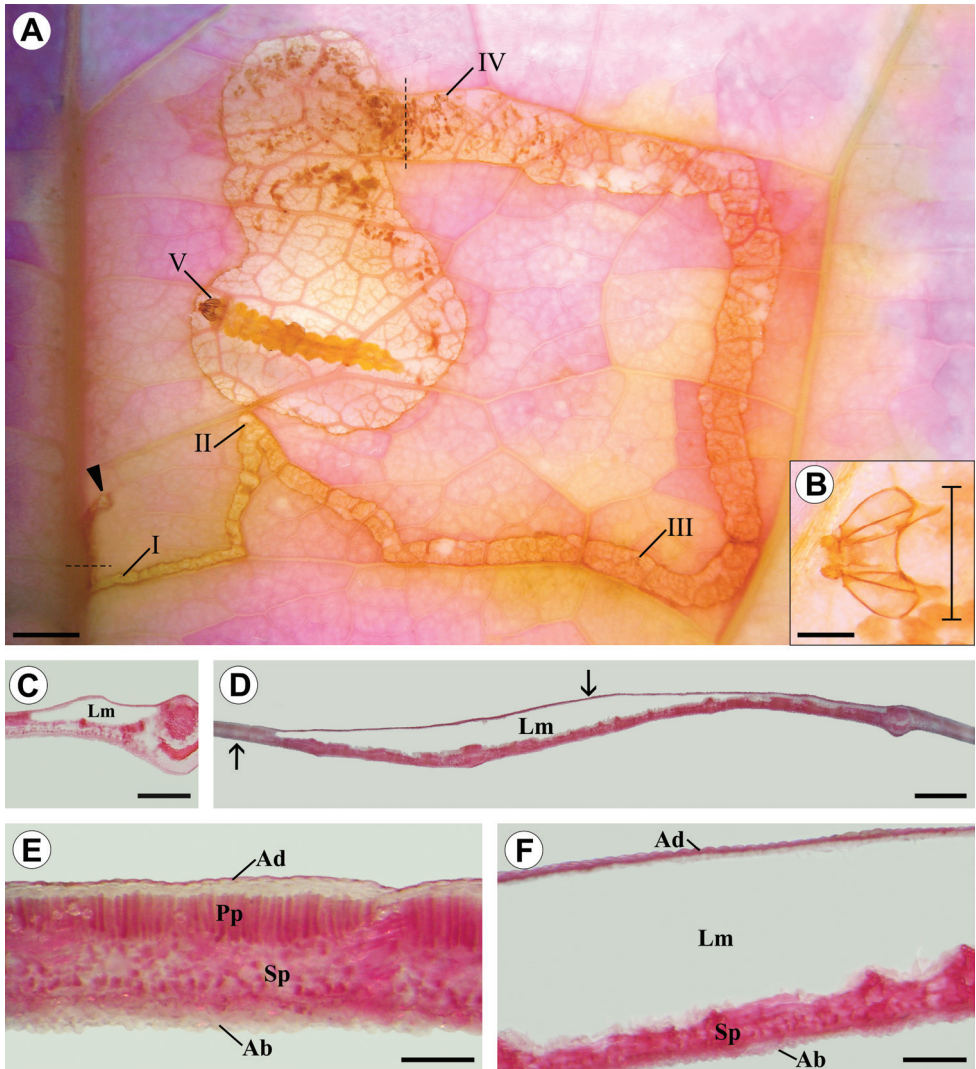


Figure 11. Diaphanized portion and histological sections of a *Passiflora actinia* leaf, showing through transparency the organization levels of a *Spinivalva gaucha* mine in relation to larval ontogeny: **A** general aspect of the mine, containing a last-instar larva; Roman numerals indicate larval instar numbers and corresponding positions of head capsules in the mine; closed arrow indicates the beginning of the mine **B** detail of head capsule shed by the fourth-instar larva (bar indicates position used for measurement of head-capsule width) **C** transverse section of serpentine portion of the mine (location indicated by the horizontal dashed line in A) **D** transverse section of blotch portion of the mine (location indicated by the vertical dashed line in A) **E** transverse section of intact portion of leaf lamina (indicated by left arrow in D) **F** transverse section of mined portion of leaf lamina (indicated by right arrow in D). **Ab** abaxial surface of epidermis; **Ad** adaxial surface of epidermis; **Lm** leaf mine; **Pp** palisade parenchyma; **Sp** spongy parenchyma. Scale bars = 1.5, 0.15, 2.0, 3.0 mm; 500, 600 μm, respectively.

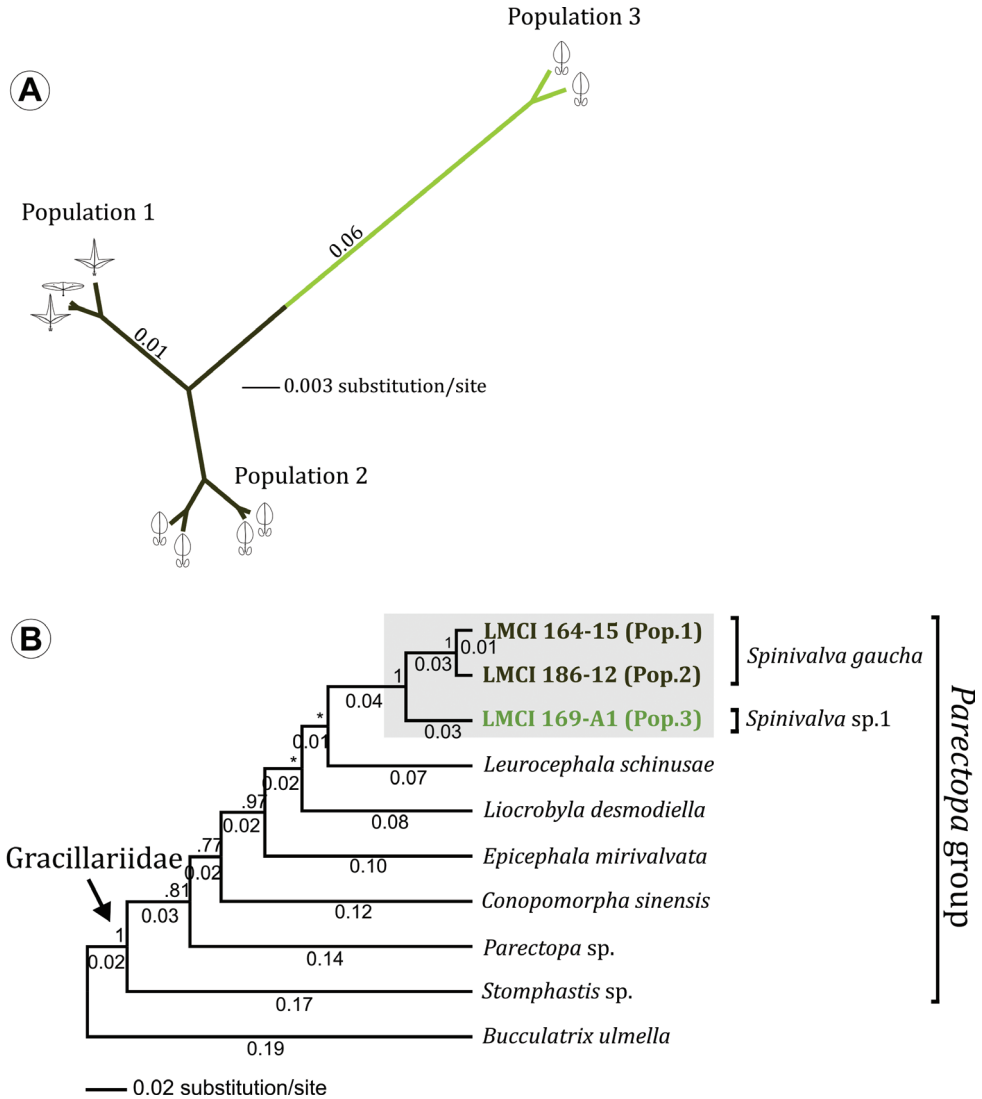


Figure 12. Bayesian consensus phylogeny of *Spinivalva*. **A** unrooted tree based on 1.5 Kb bp of the mitochondrial genes cytochrome oxidase *c* subunit I, tRNA-Leu and cytochrome oxidase *c* subunit II. Specimens from three different localities (termed Populations 1, 2 and 3; see Material and Methods for details), field-collected from different host plants (*P. suberosa* [✱], *P. misera* [✱] and *P. actinia* [✱]) were analyzed. Numbers indicate raw branch lengths **B** phylogenetic relationships of *Spinivalva* within the *Parectopa* group of gracillariids (sensu Kawahara et al. 2011), based on 610 bp of the barcoding region (cytochrome oxidase *c* subunit I gene). Numbers above branch indicate node support (posterior probability); those located below represent the raw branch length. A species of Bucculatricidae (*Bucculatrix ulmella*) was used to root the tree.

P. actinia. The genetic divergence between these major groups was 7% (Fig. 12A). The intraspecific difference between localities in the first group was 1%. In addition, the barcode fragment analyzed recovered 610 nucleotides, including 236 (38%) variable sites. According to our phylogenetic hypothesis, *Spinivalva* was strongly supported as a monophyletic lineage within the *Parectopa* group of gracillariids (Fig. 12B). Despite the strong statistical support within this lineage of gracillariids, the internal relationships for the genera included in the *Parectopa* group were poorly resolved. *Leurocephala schinusae* and *Liocrobyla desmodiella* were placed as closest to *Spinivalva* (showing lower genetic divergence), but with weak posterior probability of node support.

Discussion

The following characteristics suggest that *Spinivalva* gen. nov. belongs to the subfamily Gracillariinae (*sensu* Davis et al. 2011): 1) flat, scaled head; 2) maxillary palpi with four segments; 3) male abdomen bearing two coremata; 4) pupation occurring outside the mine; 5) adults resting with the anterior portion of the body inclined circa 45°. Our molecular analysis placed it within the *Parectopa* group (*sensu* Kawahara et al. 2011) in the Gracillariinae, near the genera *Leurocephala* Davis and McKay and *Liocrobyla* Meyr. From a morphological perspective, the forewing of adults of *Spinivalva* resembles those in the *Parectopa* group in general coloration, fascia arrangement, presence of apical dot, and venation pattern (Vári 1961). When compared to *Leurocephala*, a recently described genus also found in the Atlantic Rain Forest of Brazil (Davis et al. 2011), additional similarities are found in the males, in particular regarding the reduced segment VII that bears two pairs of coremata, the elongated tergum VIII, and the presence of paired gnathal lobes. However, as noted above, males of *Spinivalva* differ markedly from those of *Leurocephala* and the remaining genera of the *Parectopa* group in relation to the valva. Unlike them, it has a saccular extension with a conspicuous process bearing a stout sensillum, in association with an aedeagus that is tubular, long and slender, and a saccus with the anterior process long and tubular. These differences extend to additional lineages related to the *Parectopa* group that were not included in our molecular analysis, for example *Micrurapteryx* Spuler, 1910, *Neurobathra* Ely, 1918 (Kawahara et al. 2011), and *Chileoptilia* Vargas and Landry, 2005 (C. Lopez-Vamoonde, unpubl. data), and other genera described by Vári (1961). As far as we are aware, the existence of a saccular tubiform portion associated with the hair pencils in the coremata of *Spinivalva* has not been reported within Gracillariidae. However, detailed descriptions for coremata structures are rarely provided in the gracillariid literature, and thus one should use caution regarding the validity of this apomorphy. Bubbles adorning the pupal cocoon similar to those described here for *S. gaucha* have been found not only in other phylogenetically related genera such as *Conopomorpha* Meyrick, 1885, *Epicephala* Meyrick, 1880 and *Leurocephala* Davis & Mc Kay, 2011, but also in other lineages that are not closely related to the *Parectopa* group (*e.g.*, Wagner et al. 2000, Davis et

al. 2011, Hu et al. 2011). Wagner et al. (2000) speculated they provide a physical barrier, thus protecting the pupa against the attack of parasitoids and predators.

The existence of at least one “sap feeding” instar early in larval ontogeny has been considered a synapomorphy for all Gracillariidae (Kumata 1978, Davis 1987, Davis et al. 2011). However, our data showed clearly that this is not the case for *S. gaucha*, where all instars are of the “tissue feeding” type. That is, although the larvae are hypermetamorphic (early instars apodal and without stemmata, later instars with legs) as in other Gracillariidae, there is no sap-feeding in *S. gaucha*. Early-instar larvae also have mandibles of a chewing type combined with a well-developed spinneret, and with the remaining mouth parts differentiated; and after they hatch, these larvae feed on the palisade parenchyma. Palisade cells typically have well-developed, compact walls compared to those in the spongy parenchyma. The morphological characteristics in *S. gaucha* are associated with feeding on tough tissues after hatching, contrary to other gracillariid species that have sap-feeder early instars that feed by dilacerating either the leaf epidermis layers or the spongy parenchyma (e.g., Kumata 1978, Wagner et al. 2000, Brito et al. 2012). The absence of a sap-feeding instar was suggested for the life cycle of *Chileoptilia yaroella* Vargas & Landry, 2005, although the first instar was not described by the authors at that time. Additional studies using scanning electron microscopy recently conducted by two of us (Vargas and Moreira, unpublished data) confirmed this prediction; in this case, however, the first instar is not a leaf miner, but feeds on the tiny gynoecia within the calyx of flowers of *Acacia macracantha* Willd. (Mimosaceae) in northern Chile. These discoveries will certainly have important implications for future studies concerning the evolution of the wide diversity in feeding habits known to exist within Gracillariidae.

We found no conspicuous morphological differences at any life stage among populations of *Spinivalva* occurring in Rio Grande do Sul, independently of the host plant. These observations were corroborated by the molecular data, which showed a low divergence rate among the different populations. Consequently, we consider all these specimens to be conspecific; that is, a set of variations exists within *S. gaucha* species boundaries and among the host plants used. However, comparison of these specimens from Rio Grande do Sul with those collected from Curitiba revealed a greater divergence in mitochondrial DNA sequences. We did not study genitalia morphologies of the latter, or their immature stages, and so a decision about their taxonomic status awaits further investigation. Thus, specific diversity within the genus *Spinivalva* might be higher than described here. As discussed for the flora in general, many passion-vine species occur in the Atlantic Rain Forest, and several of them are endemic to this biome (Stehmann et al. 2009). In the future, they should be searched for the presence of this and other lineages of gracillariids. Another gracillariid species, *Phyllocnistis tethys* Moreira & Vargas, 2012, has been associated with a different passion-vine species in southern Brazil (Brito et al. 2012). However, *Phyllocnistis* larvae use a wide range of plant families as hosts (Kawahara et al. 2009). Therefore, *Spinivalva* is the first genus that is known to be particularly associated with the Passifloraceae. Passion vines are toxic to most lepidopterans, and the biological implications, if any, for such a peculiar association in herbivory also remain unknown (Brito et al. 2012).

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References

- Becker VO, Adamski D (2008) Three new cecidogenous *Palaeomystella* Fletcher (Lepidoptera, Coleophoridae, Momphinae) associated with Melastomataceae in Brazil. *Revista Brasileira de Entomologia* 52: 647–657. doi: 10.1590/S0085-56262008000400017
- Brito R, Gonçalves GL, Vargas HA, Moreira GRP (2012) A new species of *Phyllocnistis* Zeller (Lepidoptera: Gracillariidae) from southern Brazil, with life-history description and genetic comparison to congeneric species. *Zootaxa* 3582: 1–16.
- Brown JW, Baixeras J, Solórzano-Filho J, Kraus JE (2004) Description and life history of an unusual fern-feeding tortricid moth (Lepidoptera: Tortricidae) from Brazil. *Annals of the Entomological Society of America* 97: 865–871. doi: 10.1603/0013-8746(2004)097[0865:DA LHOA]2.0.CO;2
- Carnaval AC, Hickerson MJ, Haddad CFB, Rodrigues MT, Moritz C (2009) Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. *Science* 323: 785–789. doi: 10.1126/science.1166955
- Caterino MS, Sperling FAH (1999) *Papilio* phylogeny based on mitochondrial cytochrome oxidase I and II genes. *Molecular Phylogenetics and Evolution* 11: 122–137. doi: 10.1006/mpev.1998.0549
- Davis DR (1987) Gracillariidae. In: Stehr FW (Ed.) *Immature Insects*. Kendall/Hunt Publishing Company, Dubuque, 372–374.
- Davis DR (1994) New leaf-mining moths from Chile, with remarks on the history and composition of Phyllocnistinae (Lepidoptera: Gracillariidae). *Tropical Lepidoptera* 5: 65–75.
- Davis DR, Mc Kay F, Oleiro M, Vitorino MD, Wheeler GS (2011) Biology and systematics of the leafmining Gracillariidae of Brazilian pepper tree, *Schinus terebinthifolius* Raddi, with descriptions of a new genus and four new species. *Journal of the Lepidopterists' Society* 65: 61–93.

- Davis DR, Miller SE (1984) Gracillariidae. In: Heppner JB (Ed.) Atlas of Neotropical Lepidoptera, Checklist: Part 1, Micropterigoidea – Immoidea. Dr W Junk Publishers, The Hague, 25–27.
- Davis DR, Wagner DL (2011) Biology and systematics of the New World *Phyllocnistis* Zeller leafminers of the avocado genus *Persea* (Lepidoptera, Gracillariidae). ZooKeys 97: 39–73. doi: 10.3897/zookeys.97.753
- De Prins J, De Prins W (2013) Global Taxonomic Database of Gracillariidae (Lepidoptera). <http://www.gracillariidae.net> [accessed on January 6, 2013]
- Drummond AJ, Suchard MA, Xie D, Rambaut A (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. Molecular Biology and Evolution 29: 1969–1973. doi: 10.1093/molbev/mss075
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3: 294–299.
- Freitas AVL, Mielke OHH, Moser A, Silva-Brandão KL, Iserhard CA (2011) A new genus and species of *Euptychiina* (Lepidoptera: Nymphalidae: Satyrinae) from Southern Brazil. Neotropical Entomology 40: 231–237. doi: 10.1590/S1519-566X2011000200012
- Fujihara J, Sato H, Kumata T (2001) The pupal cremasters as a diagnostic character for species of *Phyllonorycter* (Lepidoptera: Gracillariidae), with description of a new species of the *nipponicella* complex from Japan. Insect Systematics and Evolution 31: 387–400. doi: 10.1163/187631200X00435
- Hasegawa M, Kishino H, Yano T (1985) Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. Journal of Molecular Evolution 21: 160–174. doi: 10.1007/BF02101694
- Hu B, Wang S, Zhang J, Li H (2011) Taxonomy and biology of two seed-parasitic gracillariid moths (Lepidoptera, Gracillariidae) with description of a new species. Zookeys 83: 43–56. doi: 10.3897/zookeys.83.783
- Kawahara AY, Nishida K, Davis DR (2009) Systematics, host plants, and life histories of three new *Phyllocnistis* species from the central highlands of Costa Rica (Lepidoptera, Gracillariidae, Phyllocnistinae). ZooKeys 27: 7–30. doi: 10.3897/zookeys.27.250
- Kawahara AY, Ohshima I, Kawakita A, Regier JC, Mitter C, Cummings MP, Davis DR, Wagner DL, De Prins J, Lopez-Vaamonde C (2011) Increased gene sampling strengthens support for higher-level groups within leaf-mining moths and relatives (Lepidoptera: Gracillariidae). BMC Evolutionary Biology 11: 182. doi: 10.1186/1471-2148-11-182
- Kobayashi S, Huang G-H, Hirowatari T (2011) Two species of Gracillariidae (Lepidoptera) new to China, and description of the pupal morphology of the genera *Corythoestis* and *Eumetriochroa*. Zootaxa 2892: 25–32.
- Kumata T (1978) A new stem-miner of alder in Japan, with a review of the larval transformation in the Gracillariidae (Lepidoptera). Insecta Matsumurana, New Series 13: 1–27.
- Meyrick E (1921) Exotic Microlepidoptera. Exotic Microlepidoptera (Marlborough) 2: 289–480.
- Meyrick E (1928) Exotic Microlepidoptera. Exotic Microlepidoptera (Marlborough) 3: 65–416.
- Meyrick E (1932) Exotic Microlepidoptera. Exotic Microlepidoptera (Marlborough) 4: 257–288.

- Mondin CA, Cervi AC, Moreira GRP (2011) Sinopse das espécies de *Passiflora* L. (Passifloraceae) do Rio Grande do Sul, Brasil. *Brazilian Journal of Biosciences* 9 (s1): 3–27.
- Moreira GRP, Ferrari A, Mondin CA, Cervi AC (2011) Panbiogeographical analysis of passion vines at their southern limit of distribution in the Neotropics. *Brazilian Journal of Biosciences* 9(s1): 28–40.
- Moreira GRP, Gonçalves GL, Eltz RP, San Blas G, Davis DR (2012) Revalidation of *Oliera* Brèthes (Lepidoptera: Cecidosidae) based on a redescription of *O. argentinana* and DNA analysis of Neotropical cecidosids. *Zootaxa* 3557: 1–19.
- Morellato LP, Haddad CFB (2000) Introduction: The Brazilian Atlantic Forest. *Biotropica* 32: 786–792.
- Myers N, Mittermeier RA, Mittermeier CG, Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858. doi: 10.1038/35002501
- Oliveira-Filho AT, Fontes MAL (2000) Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and the influence of climate. *Biotropica* 32: 793–810.
- Patočka J (1989) Pupae of Central European Tischeriidae (Lepidoptera, Tischerioidea). *Biologia (Bratislava)* 44: 923–932.
- Stehmann JR, Forzza RC, Salino A, Sobral M, Costa DP, Kamino LHY (2009) Plantas da Floresta Atlântica. Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rio de Janeiro, 516 pp.
- Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2011) MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance and maximum parsimony methods. *Molecular Biology and Evolution* 28: 2731–2739. doi: 10.1093/molbev/msr121
- Vargas HA, Landry B (2005) A new genus and species of Gracillariidae (Lepidoptera) feeding on flowers of *Acacia macracantha* Willd. (Mimosaceae) in Chile. *Acta Entomológica Chilena* 29: 47–57.
- Vargas HA, Parra LE (2005) Un nuevo género y una nueva especie de Oecophyllembiinae (Lepidoptera: Gracillariidae) de Chile. *Neotropical Entomology* 34: 227–233. doi: 10.1590/S1519-566X2005000200011
- Vári L (1961) South African Lepidoptera. Volume I, Lithocolletidae. *Transvaal Museum Memoir* 12: 1–238.
- Wagner DL, Loose JL, Fitzgerald TD, Benedictis JA, Davis DR (2000) A hidden past: the hypermetamorphic development of *Marmara arbutiella* (Lepidoptera: Gracillariidae). *Annals of the Entomological Society of America* 93: 59–64. doi: 10.1603/0013-8746(2000)093[0059:AHPTHD]2.0.CO;2

Phylogenetic systematics of *Schacontia* Dyar with descriptions of eight new species (Lepidoptera, Crambidae)

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Abstract

The Neotropical genus *Schacontia* Dyar (1914) is reviewed and revised to include eleven species. *Schacontia replica* Dyar, 1914, **syn. n.** and *S. pfeifferi* Amsel, 1956, **syn. n.** are synonymized with *S. chanesalis* (Druce, 1899) and eight new species are described: *Schacontia umbra*, **sp. n.**, *S. speciosa*, **sp. n.**, *S. themis*, **sp. n.**, *S. nasa*, **sp. n.**, *S. nyx*, **sp. n.**, *S. clotho*, **sp. n.**, *S. lachesis*, **sp. n.**, and *S. atropos*, **sp. n.** Three species, *S. medalba*, *S. chanesalis*, and *S. ysticalis*, are re-described. An analysis of 64 characters (56 binary, 8 multistate; 5 head, 13 thoracic, 13 abdominal, 25 male genitalic, and 8 female genitalic) scored for all *Schacontia* and three outgroup species (*Eustixia pupula* Hübner, 1823, *Glaphyria sesquialis* Hübner, 1823, and *Hellula undalis* (Fabricius, 1781)) retrieved 8 equally most parsimonious trees (L=102, CI=71, RI=84) of which the strict consensus is: [((((*medalba* + *umbra*) + *chanesalis*) + *speciosa*) + (*ysticalis* + [*rasa* + *themis* + (*atropos* + *lachesis* + *nyx* + *clotho*)])]. The relevance of male secondary sexual characters to the diagnosis of *Schacontia* species is discussed.

Keywords

Schacontia, Crambidae, Glaphyriinae, Brassicales, secondary sexual characters

Introduction

Schacontia Dyar, 1914: 400 represents a small cluster of species recently transferred to the Glaphyriinae (Solis 2009) (Figs 1–12). Both the male genitalia and the external appearance of described *Schacontia* are atypical for pyraloids, so much so that the type species was originally described by Schaus as a member of the noctuid genus *Acontia* Ochsenheimer (as “*Acontia*? [sic] *medalba*”; Schaus, 1904: 163). The subsequent taxonomic history of these moths is one of taxonomic curiosity and nomenclatural flux. *Schacontia* caught the attention of taxonomists in part by virtue of its unusual male genitalic apparatus, which comprises a uniquely configured gnathal complex and reduced valvae. *Schacontia* was originally described in the Schoenobiinae, retained there by Amsel (1956), transferred to the Epipaschiinae (Pyralidae) by Munroe (1958), and then tentatively transferred to the Cybalomiinae (Munroe 1995). It was most recently transferred to the Glaphyriinae by Solis (2009) based in part on the external morphology and genitalia, but mostly based on the morphology of the tympanal organs. Solis (2009: 493) characterized the subfamily with the following combination of characters: chaetosemata absent; concavity on the costa of the forewing present; fovea between Rs_{2+3} and Rs_4 present; forewing with Rs_4 in a non-apical position and a costal crescent present; and lateral indentations of Sternite 2 present (Luquet and Minet 1982).

With respect to their actual biology, *Schacontia* larvae have been variously associated with Capparaceae (Brassicales) and have been recently reported as parasites of cassidine chrysomelid beetles (Cuignet et al. 2008), but that latter report is unverified as *Schacontia*. Without more life history data and more taxon-rich analysis, it is not possible at this time to address life history evolution, the macroevolution of host plant associations, or larval feeding behaviors in *Schacontia*. It is in the widespread species (*S. chanesalis*, *S. themis*, *S. ysticalis*) that life history and larval data are most sorely needed rangewide. The association of some species with Capparaceae is not unusual for crambids (cf. Solis et al. 2009), and as such, *Schacontia* may provide a forum for exploring its origin(s). The evolution of glucosinolates in the Brassicales (e.g., Mithen and Marquez 2010) may bear on the origins of these moths’ specialized feeding habits, including the gall-forming behavior and internal feeding reported by Solis et al. (in prep.).

In the present work, we treat newly assembled historical and recent material from the Western Hemisphere. Our purpose is to refine the circumscription and composition of *Schacontia* by identifying and describing new species and presenting a phylogenetic analysis of their relationships. Recent collecting and rearing work, including the efforts in Costa Rica by D. Janzen and W. Hallwachs, have generated life history information, most importantly the association of *Schacontia* with capparaceous plants. Those potentially allied with *Schacontia* on the basis of wing venation and features of the gnathos and tegumen, comprise eight undescribed species ranging from Mexico through Central and South America and the Caribbean, some narrowly endemic, others widespread.

Materials and methods

Pinned specimens were examined with an incandescent light source (reflected light). Male and female genitalic preparations varied, some of those pre-dating this study having accumulated from several sources. Most were prepared following Clarke (1941), using chlorazol black and in some cases mercurochrome as staining agents; Eosin-Y was used in some preparations [those originating with Dr. V.O. Becker]. The more recent dissections were made following a hot soak in supersaturated sodium hydroxide, and held in glycerine caps or temporary slides for character scrutiny. Some older preparations of wings were prepared following Borror, Triplehorn, and Johnson (1989): soaked in bleach, stained with Eosin-Y, and slide mounted in Canada balsam. Slide preparations were examined with dissecting and compound microscopes. Photographs were made using the Microptics and Visionary Digital imaging systems and images manipulated with the Gnu Image Manipulation Program (The GIMP Team, gimp.org) and, when appropriate, retouched with Adobe Photoshop® (Adobe Systems, Mountain View, CA). All measurements were made with the aid of an ocular micrometer. Forewing length was measured from the center of the axillary area up to the apex of the forewing (FW). Terminology follows Wootton (1979), Klots (1970), Maes (1985, 1995), Yoshiyasu (1985), Phillips and Solis (1996), Solis and Maes (2002), and Mally and Nuss (2011), except where noted (Figs 63, 64). The terminology of Maes (1985, 1995) is adhered to strongly with respect to the tympanal organs; Mally and Nuss (2011) are consulted as a more recent reference with respect to coding the female genitalic characters.

Material examined

This work drew in part from an effort to treat taxa with taxonomic and nomenclatural problems identified during preliminary surveys of pyraloids in the extensive Costa Rican collection of D. Janzen and W. Hallwachs. Because the genitalic characters of *Schacontia* species had not been adequately explored, specimens of all known Costa Rican species were initially dissected to survey diagnostic characters of each species and putative synapomorphies for the genus. In order to determine the nomenclatural status of Costa Rican species, types of all neotropical species at the Zoologische Staatssammlung München, Munich, Germany (ZSM), Naturhistorisches Museum, Vienna (NHMV), The Natural History Museum, London (BMNH), and the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM) were examined. Following this preliminary work, a more expansive series of material (all the specimens of *Schacontia* we could locate) was examined, most recently including Bolivian and Puerto Rican material housed at the Carnegie Museum of Natural History (CMNH) as well as at Cornell University Insect Collection (CUIC), and all the available material at USNM, including material from the V.O. Becker collection (VOB). Specimens are listed for each species with all attendant label data, including

genital dissection slide numbers and record numbers from the database of Janzen and Hallwachs (<http://Janzen.sas.upenn.edu>). Primary types are deposited at the USNM (Washington, DC) and the CMNH (Pittsburgh, PA).

Repository abbreviations

The following abbreviations refer to collections from which specimen material forms the basis of this work:

BMNH	The Natural History Museum [statutorially: British Museum (Natural History)], London, UK
CMNH	Carnegie Museum of Natural History, Pittsburgh, PA, USA
CNC	Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Ontario, Canada
CUIC	Cornell University Insect Collection, Ithaca, NY, USA
INBio	Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica
MGCL	McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL, USA
NHMV	Naturhistorisches Museum, Vienna, Austria
USNM	National Museum of Natural History [formerly, United States National Museum], Washington, District of Columbia, USA
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany
ZSM	Zoologische Staatssammlung, Munich, Germany

Following the identification of a suite of male secondary sexual characters suspected of diagnosing multiple species pairs, we undertook a preliminary DNA barcoding exploration of two putative species for which relatively recent (~20 year old) material existed. Sequencing was done using standard protocols at the Biodiversity Institute of Ontario (Hrcek et al. 2011; Wilson 2012).

Character coding and cladistic analysis

All characters were equally weighted and coded as unordered. Preference was given to combinations of binary and inapplicable coding schemes over multistate characters. Conspecificity of male and female specimens was inferred by locality when other biological information was unavailable. Preliminary phylogenetic analysis involved parsimony searches via the ratchet routine (island-hopper, 1000 iterations per rep) in Winclada/Winclada (1000 iterations per rep; Nixon 1999–2002). Character selection and coding schemes were reevaluated repeatedly following successive rounds of tree search as the matrix was developed. The Winclada (.winc) file was re-saved as a NONA (.ss)

file and then as a TNT file, using a text editor to ensure rooting at the first terminal encountered. Exhaustive searches (implicit enumeration) were then run in TNT (Willi Hennig Society edition; Goloboff et al. 2008). Bremer values (Bremer 1988) were calculated in TNT from exhaustive searches of progressively longer suboptimal trees (increments of 1 step). Synapomorphies were mapped with Winclada.

Systematics

Taxonomic scope and outgroup selection

The scope of our treatment of described *Schacontia* is based on Munroe (1995); type material is deposited at USNM except where designated in text. We treat the taxonomic and nomenclatural issues in the subfamilial placement of the genus only insofar as they pertain to outgroup selection and rooting.

Initial examination of specimens tentatively identified as *Schacontia* revealed, first, a cohesive group of species comparable to the type species [*S. medalba* (Schaus, 1904)] unified by a uniquely hood-like or mucronate uncus, reduced male valvae, a divided tegumen with a prominent medial sulcus, and a gnathos with a unique, four-armed configuration. A somewhat more variable group, including *S. ysticalis* (Dyar, 1925) and several undescribed species, appeared to bear similarities to *Schacontia* in forewing pattern and, in modified form, features of the male valva, tegumen, and gnathos. Bearing in mind that member species of *Schacontia* have been placed in several subfamilies prior to the genus' transfer to Glaphyriinae by Solis (2009), and in the interest of being thorough, type species of all 33 known glaphyriine genera were examined as outgroup candidates. We also surveyed types of *Cybalomia* Lederer, 1863 and a range of crambid subfamilies in order to mine specific character systems for putative synapomorphies of *Schacontia* and to ensure proper character polarization. We selected three glaphyriine outgroup taxa, all type species of their respective genera: *Eustixia pupula* Hübner, 1823, *Hellula undalis* Fabricius, 1781, and *Glaphyria sesquialis* Hübner, 1823, at which our tree is rooted. These outgroups were chosen both on the basis of their status as name-bearers and on the basis of what we estimated to be comparable suites of observable similarities (putative homologies) with *S. medalba*. The rooting at *G. sesquialis* was implied by the current classification, but more importantly was based on a preliminary screening of male and female genitalia and tympanal structures. These include the configuration of the saccus tympani and corpus bursae.

A total of 64 characters (56 binary, 8 multistate; 5 head, 13 thoracic, 13 abdominal and tympanal, and 25 male genitalic, and 8 female genitalic) were adduced and coded (below; see Appendix I for the full matrix). Inapplicable and missing data were coded with “-” and “?”, respectively.

Head [Figs 13, 14]

0. Ocelli: (0) absent; (1) present

1. Proboscis: (0) reduced, inconspicuous; (1) conspicuous (Figs 13, 14)

2. Frons: (0) of normal contour, evenly rounded; (1) conical or expressed as a small hump; (2) carinate or otherwise modified (Figs 13, 14)
3. Length of labial palpus: (0) extending beyond clypeus; (1) not extending beyond clypeus
4. Maxillary palpi: (0) extending anteriorly beyond frons; (1) not reaching anterior margin of frons

Thorax [Figs 15–20]

5. Forewing (Rs_3 , Rs_4): (0) bases separate; (1) stalked (Figs 16, 17)
6. Forewing (M_1 , M_2): (0) bases separate; (1) stalked (Figs 16, 17)
7. Medial area: (0) contrast with basal and postmedial areas subtle, almost unicolorous except for lines, spot; (1) contrast between medial area and basal and postmedial areas sharp
8. Forewing coloration: (0) compound, ground color not uniform in any given area (antemedial, medial, postmedial; Fig. 15); (1) two-toned, medial area contrasts with basal and apical area in ground color
9. Concentration of white scales apical to antemedial line: (0) absent, or if present then only diffusely; (1) present (Fig. 15)
10. Hindwing (HW) postmedial line: (0) not conspicuous or nearing inner margin; (1) distinct, approaching or reaching inner margin (Fig. 15)
11. Distance between postmedial line and wing terminus: (0) narrow (Fig. 15); (1) wide
12. Wing lines: (0) dark on light ground; (1) light on dark ground (Fig. 15)
13. HW ($M_2M_3+CuA_1$): (0) bases separate; (1) stalked (Figs 16, 17)
14. Male hind leg secondary sexual complex consisting of a flattened hind tibial spur with flattened scales and basal tarsus with concave spoon-like modification: (0) absent; (1) present (Figs 18–20)
15. Dark patch amidst hind tibial scales: (0) absent; (1) present (Figs 18, 19)
16. Tufts of epipleural setae: (0) absent; (1) present
17. Female medial hind tibial spurs: (0) one pair (medial pair absent); (1) two pair (medial pair present)

Abdomen - Tympanal characters [Figs 21–32]

18. Bullae tympani invaginated in Sternum 2: (0) not (all ingroup taxa; Figs 21–32); (1) slightly to strongly
19. Saccus tympani invagination: (0) short, not beyond puteolus; (1) deep, with posterior ridge, but not prominently invaginated posteriad (Figs 21–23); (2) capacious, ovate chamber; conspicuous broad lip (Figs 24–32)
20. Saccus: (0) not prominent (Figs 21–23); (1) prominent (Figs 24–32)
21. Mesal extent of saccus (@ pons): (0) short (Figs 21–23); (1) intermediate (Figs 24–32);
22. Puteoli: (0) absent or indistinguishable from saccus tympani (all ingroup taxa; Figs 21–32); (1) present, if small

23. Processus tympani: (0) inconspicuous; (1) approximately semi-circular (Figs 21–23); (2) thumblike, lobulate (Figs 24–32)
24. Fornix, protrusion over venula prima: (0) protruded over slightly, flat; (1) far removed from edge (all ingroup taxa; Figs 21–32)
25. Fornical ulna: (0) > 90 degrees or low arc (all ingroup taxa; Figs 21–32); (1) < 90 degrees
26. Sclerotization of fornix: (0) light to moderate; (1) heavy (all ingroup taxa; Figs 21–32)
27. Fornix: (0) robust, broad (Figs 21–24); (1) narrow, ribbonlike (Figs 24–32)
28. Venulae secundae: (0) wide, gently tapered (Figs 21–24); (1) more sharply tapered, elongate, forming a neck (Figs 24–32)
29. Tergo-sternal sclerite: (0) present, not elongate (Figs 21–24); (1) prominent, elongate, roughly equivalent in length to that of bulla tympani (Figs 24–32)

Abdomen - Post-tympanal characters [Figs 33–35]

30. Coremata on 4th abdominal segment: (0) absent; (1) present (Figs 33–35)

Male genitalia [Figs 36–65, part]

31. Gnathos-ventrotergal rods complex: (0) absent; (1) present (all ingroup taxa; Figs 36–65, in part)
32. Gnathos, middle process: (0) absent; (1) present (all ingroup taxa; Figs 36–65, in part)
33. Dorsal ridges of tegumen: (0) absent, split to uncus, or inverted U; (1) cruciate, crossing near uncus (Figs 46, 49, 52, 55, 58, 61, 64); (2) inverted epsilon with medial ridge (Figs 36, 39, 42, 44)
34. Teguminal sulcus: (0) absent; (1) present (all ingroup taxa; Figs 36–65, in part)
35. Uncus tip trefoil shaped: (0) absent (Figs 36, 39, 42, 44, 46); (1) present (Figs 49, 52, 55, 58, 61, 64)
36. Shape of trefoil, if present: (0) reduced, rhomboid (Figs 55, 58, 61, 64); (1) expanded, hastate (Figs 49, 52)
37. Uncus edges: (0) simple, undifferentiated (Figs 36, 39, 42, 44, 46, 55, 58, 64); (1) modified, swollen (Figs 49, 52, 61)
38. Uncus, interior (under-surface): (0) clear, without relief (Figs 36, 39, 42, 44, 46, 55, 58, 64); (1) with elongate central development appearing as a raised ridge (Figs 49, 52)
39. Valva - outer margin: (0) entire or emarginate, but continuous, such that trajectory of valval membrane continues apically (Figs 36, 39, 42, 44); (1) trajectory of valval membrane recurves such that upper and lower extensions are evident, a fleshy lobe bearing a setal tuft associated with end of costa, and the subcostal projection sclerotized dorsally (Figs 46, 49, 52, 55, 58, 61, 64)
40. Glabrous central area of valva: (0) Absent [valva elongate, setose]; (1) truncate - squared or subquadrate (emarginate) (Figs 36, 39, 42); (2) ~subtriangular or subrectangular, ~1.5 x long as wide (Figs 44, 46, 49, 52); (3) about as long as wide, sub-symmetrical (Figs 55, 58, 61, 64)

41. Intra-saccular process: (0) absent; (1) slightly raised bump, flange, or paddle centrally located on inner face of valva (Figs 36, 39, 42, 44, 46); (2) trigger-like extension at outer margin of lower lobe of valva (Figs 49, 52, 55, 58, 61, 64)
42. Intra-saccular process, adornment: (0) denticled or rugose (Figs 39, 44, 46, 49, 52, 55, 58, 61, 64); (1) naked (Figs 36, 42)
43. Saccular bend: (0) absent (Figs 36, 39, 42, 44); (1) present (Figs 46, 49, 52, 55, 58, 61, 64)
44. Saccular margin: (0) angled close to vinculum (Figs 46, 49, 52); (1) angled or rounded with apex at saccular midpoint (Figs 55, 58, 61, 64)
45. Saccular bend angled versus rounded: (0) angled, 90 degrees (Figs 61, 64); (1) rounded (Figs 55, 58)
46. Ventro-medial setal comb: (0) absent; (1) present (Figs 55, 58)
47. Localized patch or cluster of ventral, saccular spine-like setae: (0) absent; (1) present (Figs 36, 39, 42, 46, 49, 52, 55, 58, 61, 64)
48. Ventro-marginal setae: (0) absent or rudimentary (Figs 36, 39, 42, 44); (1) distributed along length of outer margin of sacculus (Figs 61, 64); (2) localized or concentrated at ventral bend (Figs 46, 49, 52, 55, 58)
49. Isolation of costal bar: (0) <75% along length of costa (Figs 46, 49, 52); (1) > 75% along length of costa (Figs 55, 58, 61, 64)
50. Secondary lobe of valva: (0) absent (Figs 46, 49, 52); (1) present, extending not beyond distal end of costa; (2) pronounced, finger-like (Figs 55, 58, 61, 64)
51. Recurved or decumbent setal plume associated with end of costa: (0) absent (Figs 36, 39, 42); (1) present (Figs 44, 46, 49, 52, 55, 58, 61, 64)
52. Setae arranged in recurved hook-shaped cluster: (0) absent; (1) present (Figs 58, 61, 64)
53. Scales arranged in terminal black dots on male abdomen: (0) absent; (1) present, conspicuous (all ingroup taxa)
54. Phallus - cornuti: (0) absent (Figs 37, 40, 43, 44); (1) present (Figs 47, 50, 53, 56, 59, 62, 65)
55. Number of cornuti: (0) one (Fig. 47); (1) two (Figs 50, 53, 56, 59, 62, 65)

Female Genitalia [Figs 38-63, part]

56. Antrum: (0) present, chalice-like (Figs 38, 41); (1) elongate, diffuse/indistinct from ductus bursae (Figs 45, 48, 51, 54, 57, 60, 63)
57. Colliculum: (0) absent (Fig. 38); (1) present, even if inconspicuous as in *chanesalis* (Figs 41, 45, 48, 51, 54, 57, 60, 63)
58. Narrow, differentially sclerotized band around center of colliculum: (0) absent (Figs 41, 45, 48, 54, 60); (1) present (Figs 51, 57, 63)
59. Ductus bursae: (0) effectively absent or inconspicuously short (Figs 38, 41); (1) present, variously sclerotized anterior to colliculum (Figs 45, 48, 51, 54, 57, 60, 63)
60. Sclerotization on floor of ductus bursae: (0) absent, indiscernable (Figs 45, 48); (1) present, either weak and diffuse or strong and conspicuous (Figs 51, 54, 57, 60, 63)
61. Corpus bursae: (0) elongate (Figs 38, 41, 45, 48); (1) globular (Figs 51, 54, 57, 60, 63)

62. Attachment of ductus bursae to corpus bursae: (0) basal (Figs 38, 41, 45); (1) sub-basal, creating shoulders on corpus bursae, associated with migration of point of attachment of ductus seminalis to sub-basal position of corpus bursae (Figs 48, 51, 54, 57, 60, 63)
63. Modification of Sternum 8: (0) absent; (1) present (all ingroup taxa)

After surveying all the described *Schacontia* species and determining there was insufficient evidence to retain *S. replica* and *S. pfeifferi*, these characters were scored (Appendix I) for three described *Schacontia* species (*medalba*, *chanesalis* and *ysticalis*), eight undescribed species, and three outgroups (*E. pupula*, *G. sesquialis*, and *H. undalis*).

Phylogenetic relationships

We were unable to discern consistently different characters among *S. chanesalis*, *S. pfeifferi*, and *S. replica*, but in view of there being extremely limited material of *S. pfeifferi* in particular, and despite Amsel's description's being the only detailed and well-figured one to date, we elected to synonymize *S. replica* and *S. pfeifferi* with *S. chanesalis* based in large part on a lack of discernable discrete variation in the male genitalia.

From cladistic analysis eight most parsimonious trees obtain (L=102, CI=71, RI=84), the strict consensus of which (L=108, CI=67, RI=81) is presented (Fig. 66) with the topology: *Glaphyria sesquialis* [root] + [*Hellula undalis* + [*Eustixia pupula* + [[*S. speciosa* + [*S. chanesalis* + [*S. medalba* + *S. umbra*]]] + [*S. ysticalis* + [*S. rasa* + *S. themis* + [*S. lachesis* + *S. atropos* + *S. nyx* + *S. clotho*]]]]].

The monophyly of *Schacontia* is supported by synapomorphies enumerated in the diagnosis of the genus (below). Two primary groupings appear in the strict consensus (character numbers given parenthetically). The first comprises the type *S. medalba*, *S. chanesalis* and the newly described species *S. umbra* and *S. speciosa*; these are united by the absence of ocelli (0); reduced proboscis (1); a compound, non-uniform ground color that does not sharply delineate the medial area (8); a distinct hindwing postmedial line approaching or reaching the inner margin (10); robust, broad fornix (27); and wide, gently tapered venulae secundae (28). In these species the outer margin of the valva is also continuous, the valva highly reduced in all but *S. speciosa* (40), and without a conspicuous saccular bend; phallus simple, without cornuti (55); attachment of the ductus bursae basal (63). Three of these species (excluding *S. speciosa*) are characterized by having the saccus tympani deep, with a posterior ridge, but not invaginated posteriad (19) and a tipped, mucronate uncus that is not conspicuously obovoid and is longer than its width at the base. As will be discussed, 4 of 5 described species - all but one of which fall within this group - were described on the basis of female types. The morphology of the female genitalia is rather uniform among the species in this group; their putative association with males is based on a combination of wing pattern and geographical proximity.

The second major intrageneric grouping, the *ysticalis-themis* group comprises *S. ysticalis* and six newly described species, whose association with *Schacontia* had been hypothesized initially. This group is united by a forewing pattern that is either essentially unicolorous excepting the antemedial and postmedial lines and orbicular spot, or two toned, but with the basal area unbroken and the medial area contrasting with the basal and apical areas (8); an inconspicuous hindwing postmedial line not nearing the inner margin (10); the saccus tympani a capacious ovate chamber with a conspicuous broad lip, comparable to that of *Cybalomia* Lederer (19); the dorsal ridge of the tegumen cruciate, crossing near the base of the uncus (33); the uncus either gently tapered and bluntly rounded, wider at the base than long, or variously nipped, trefoiled, and/or conspicuously obovoid (35, 36); the outer margin of the valva with upper and lower lobes, not with a continuous edge (39), but with a saccular bend or elbow either at its midpoint or proximal to the vinculum (44, 45); ventro-marginal setae present and well-developed (48); costal setae present, sometimes arranged in a recurved, fish-hook-shaped cluster (52); phallus with cornuti (54); attachment of the ductus bursae sub-basally, creating the shouldered appearance on the corpus bursae (62).

Morphologically, this second, perhaps more enigmatic species-group, is less homogeneous than that surrounding the type species of *Schacontia*. Its most basal member (*S. ysticalis*) retains numerous features common to the latter group, viz. concentration of white scales apical to the postmedial line (character 9), the narrow distance between the postmedial line and the wing terminus (character 11), the light wing lines in contrast with the dark ground color (character 12), the undifferentiated uncus (character 35), the configuration of the intra-saccular process (character 41), and the elongate corpus bursae (character 61). The remaining species, all hitherto undescribed, form a complex of species exhibiting a heterogeneous collection of male secondary sexual characters, including unusual metatarsal structures, tibial scales and spurs, and abdominal coremata. These appear somewhat homoplastically, such that their down-weighting or removal results in a more decisively resolved topology, but we retain them in analysis to emphasize their relevance to future work.

***Schacontia* Dyar, 1914: 400**

<http://species-id.net/wiki/Schacontia>

Type species. *Acontia medalba* Schaus, 1904: 163, by subsequent designation.

Type locality: Brazil.

Etymology. “*Schacontia*” seems to be Dyar’s contraction of Schaus and *Acontia*, the noctuid genus in which Schaus mistakenly attributed *medalba* and subsequently designated by Dyar as the type species of *Schacontia*.

Diagnosis. *Schacontia* species may be recognized by (character numbers listed parenthetically): Forewing Rs_3 and Rs_4 stalked (5); M_1 and M_2 stalked (6); hindwing M_2M_3 + CuA_1 stalked (13); bullae tympani invaginated in S2 (18); absence of puteoli (22); fornix heavily sclerotized and far removed from the edge of $Ve1$ (24); fornical

angle a low arc > 90 degrees (25); presence of gnathos-ventrotergal rods complex (31), bearing a finger-like middle process (32); presence of teguminal sulcus (34); intrasaccular process a bump or flange towards base of valve or as a trigger-like process at margin of lower lobe of valve (41); pair of terminal black dots on abdominal dorsum of male (53); uncus hood-like, mucronate, or obovoid, with variously modified terminal nipple (35, 36). In addition, the costal bulge in the FW postmedial line is frequently coupled with a color contrast between the FW medial area and the basal and terminal areas, often involving white scaling. Unlike the *medalba* group (for present purposes including *S. speciosa*), the proboscis is not reduced in the *yisticalis-themis* group, the labial palpi droop, the tympanal fornix is narrow, ribbonlike; venulae secundae tapered to form a “neck.”

Habitus. In the species most readily identifiable as *Schacontia* (by virtue of their similarity to the type species *S. medalba*), hereafter referred to as the *medalba* group, the forewings are gray with a metallic sheen and the antemedial and postmedial lines variously suffused with white, the exception being *S. umbra*, which may be almost uniformly shaded dark brown. Towards the costa, the postmedial line bulges outward; the hind wings are by and large nondescript in pattern beyond the presence of a faint postmedial line. The *yisticalis-themis* group including the *S. themis-rasa* sister pair and the *S. nyx* complex [*S. nyx*+*S. clotho*+*S. lachesis*+*S. atropos*], are distinguished from these in having ocelli present; frons with normal, convex contour, except in *S. yisticalis*; and labial palps porrect, extending beyond the clypeus.

Male genitalia. All *Schacontia* bear a modification of the intrasaccular region of the valva. In the case of those species surrounding the type species of *Schacontia*, this comprises a naked or denticled flange; the valvae are characteristically reduced, if not truncate, and the uncus prominent but unadorned, mucronate. The valvae become progressively more complex in the *yisticalis-themis* group, with the intrasaccular feature transposed laterally to form a sclerotized trigger-like structure. Also in the *yisticalis-themis* group: the dorsal ridges of the tegumen are cruciate, meeting near the uncus; the tegumen is much wider than the uncus such that the lateral edges of the tegumen appear to taper/fall away from the uncus gradually; the outer margin of the valva is complex, including a variously adorned subcostal process, the costa associated with a fleshy lobe at its terminus and at least one setal tuft; the sacculus bears a localized patch or cluster of setae ventrad; and a membranous area exists between the costa and the subcostal process.

Description. Head - In *medalba* group, ocelli and chaetosemata absent; proboscis reduced; frons conical; labial and maxillary palpi straight. In *yisticalis-themis* group, ocelli present; frons of normal, convex contour except in *S. yisticalis*; labial palps porrect, extending beyond clypeus. **Thorax** - In *medalba* group, pronotum, mesonotum, legs gray; hind leg of female with 1 pair of tibial spurs. Males of several members of *yisticalis-themis* group bear a flattened, hind tibial spur, specialized hind tibial scales, a shallow concave spoon-like metatarsal modification, and coremata on 4th abdominal segment (on *S. themis*, *S. nyx*, *S. clotho*, *S. lachesis*, and *S. atropos*); in addition, epipleural setae may be present (in *S. rasa*, *S. clotho*, *S. lachesis*, and *S. atropos*); and female

hind tibia usually bear two pair of spurs (a medial pair present) except in *S. ysticalis* and *S. rasa*. *Forewing* (FW) - *Schacontia* exhibit a characteristic curvature of postmedial line, outwardly bulging towards costa. In *medalba* group FW medial area partially suffused with white; in *ysticalis-themis* group, FW either unicolorous with basal and postmedial areas or polymorphic, with some specimens more darkly shaded. Rs_3 and Rs_4 stalked; M_1 and M_2 stalked. *Hindwing* - In *medalba* group, HW generally pale with few contrasting markings; female frenulum with a single seta; postmedial line sometimes present, conspicuous, but never in *ysticalis-themis* group. $[M_2M_3]+CuA_1$ stalked. **Abdomen** - Scales arranged in two terminal black dorsal spots in males, more conspicuous in *ysticalis-themis* group. Tergites gray with dark-gray scaling in *medalba* group. Tympanal organs crambiform (tympanum and conjunctivum not co-planar, praecinctorium present, bullae tympani open anteromedially), but somewhat variable. In *medalba* group, bullae tympani broad, tympanal assemblage wider than long (cf. Solis 2009: 503); processi tympani present, towards antero-lateral end of fornix, prominent, lamellate, hemi-circular; processus spiniformis present; fornix tympani strongly sclerotized, broad, removed from edge of venula prima; fornical ulna gradually arched at approximately $>90^\circ$ angle; pons short, broad, V-shaped, length more or less equivalent to breadth of fornix; rami (posteromedial margins of sacci) weakly sclerotized, arcuate, not strongly angled medially; venulae secundae present, tapering gently such that posterior width only slightly less than anterior width; puteoli absent; posterior lip of saccus weakly sclerotized, saccus indistinct and grading into second sternite; posterior width of tympanal organs narrower than anterior width, but venulae secundae not tapering sharply to form a neck; bullae not conspicuously invaginated in S2. In *ysticalis-themis* group, tympanal assemblage less asymmetrical than in *medalba* group (i.e., not conspicuously wider than long); tergo-sternal sclerite robust, conspicuous; bullae tympani longer than wide, saccus or rim of bullae tympani sclerotized at base; processi tympani present, lamellate, thumb-like, towards antero-lateral end of fornix; fornix tympani sclerotized; angle of fornical ulna obtuse; pons elongate, comprising (in part) two parallel, elongate, sclerotized prongs, divergent only at anterior terminus (posteromedial margin of saccus appears delimited by sclerotized rami, extends and remains parallel to pons for most of its length, pons extending towards bottom of saccus); saccus deep, pronounced (cf. “poches ou dépressions tympaniques” of Minet 1985); venulae secundae prominent, tapering such that “partie libre” (*sensu* Minet) of second sternite forms a “neck” as in *S. speciosa*; puteoli absent; posterior width of tympanal organs roughly half of anterior width. **Male genitalia** (Figs 36–60, part). *Medalba* group: Uncus oblong, cuspidate or mucronate, terminal edge entire; tegumen robust, divided into two dihedral, di-trapezohedral, or hemispherical bubbles that meet for a length that varies across species such that its dorsal ridges appear cruciate; juncture may appear as an elongate strut that divides anterior to base of uncus, such that anterior margin of tegumen may appear moderately emarginate (as in *S. chanesalis*) or more deeply invaginate (as in *S. medalba* and *S. umbra*). A transparent, membranous or sub-sclerotized area within uncus overlies a finger-like process arising from within center of gnathos, configuration harness-like, comprising a plate suspended by four

arms, one pair extending to and (apparently) articulating with base of uncus dorso-caudally; other subtergal pair extending ventrally to and articulating with vinculum; connection between gnathal plate and tegumen membranous. Lower arms of gnathos appear to represent a fusion with ventro-tergal rods (Cf. Yoshiyasu 1985). Characteristic reduced male valvae extend straight out at roughly a 90° angle, and with a localized patch or cluster of ventral, filiform saccular setae. Valvae either simple and rounded or broadly emarginate to bilobed; reduced, their most prominent feature a pair of intrasaccular processes (one in each valva) oriented dorsally and variously naked or adorned with spines or denticles. Ventro-marginal setae absent or rudimentary. Juxta U-shaped or broadly V-shaped, robust at base, vaguely taurean. Phallus simple, cornuti absent.

Ysticalis-themis group: Uncus obovoid or superficially tridentate (appearing trefoil- or spade tipped); tegumen robust, divided into two obliquely-oriented oval sections meeting caudally near base of uncus, but diverging widely cephalad such that anterior margin of tegumen appears deeply invaginated; gnathos comprising a suspended rectangular plate with arms arising from each corner and a small, nub-like process arising centrally; dorsal arms wrap around anal tube, a ventral pair extend to termini of vinculum, such that gnathos almost appears to articulate both with uncus-tegumen and with vinculum, which is variously U-shaped or horseshoe shaped with pronounced pockets at each terminus. Valvae complex, comprising regions and processes that are variously sclerotized, fleshy in appearance, and/or bearing tufts of setae: intrasaccular flange located towards latero-ventral edge and sclerotized to form a trigger-shaped process; robust, spine-like setae on valva; ventro-marginal setae present on valva, either distributed evenly along length of outer margin of sacculus or concentrated at ventro-saccular “ulna”; costa robust and joined to rest of valva by a narrow membranous area; valva with secondary outer fleshy setose lobe or process below costa; recurved/decumbent setal plume associated with terminus of costa. Juxta robust, V-shaped or broadly U-shaped, ventral tip curved outward forming a small chin-like platform in *S. themis* and *S. rasa*; a less robust, more open U-shape in *S. nyx* complex. Phallus with two cornuti.

Female genitalia (Figs 38–63, part) - *Medalba* group: Papillae anales convex, partially appressed but separate, setose; posterior and anterior apophyses roughly equivalent in length, not especially robust; antrum may be conspicuous, chalice-like; ductus bursae short, not discretely circumscribed; corpus bursae membranous, elongate, without signa; ductus seminalis arising from posterior end of corpus bursae. *Ysticalis-themis* group: Papillae anales setose, rounded, not conspicuously dihedral (except in *S. lacheisis*); colliculum, if present, a partial collar, sometimes shortened to form a narrow ring immediately outside corpus bursae, ductus bursae per se all but eliminated; note that in contrast to *Udea* Guenée (1845), for example, ductus bursae, if present, developed posterior to colliculum (cf. Mally and Nuss 2011: 63, Fig. 3), an elongate band or partial sleeve immediately occupying antrum, appearing as a sclerotized band on floor of ductus bursae; corpus bursae globular or ovoid (more elongate in *S. ysticalis*), without signa, one or two accessory bursae posteriad where ductus seminalis attached.

Species variation. Individual species variation with respect to wing polymorphism is especially acute in the *S. nyx* complex; of particular interest here are the male sec-

ondary sexual characteristics, which covary imperfectly across species and are discussed below. *Schacontia* species may vary greatly in size (>100% wingspan).

Distribution. Collectively, *Schacontia* species are distributed across Mexico, south to Central America (Guatemala, Costa Rica, Panama) and South America (Bolivia, Brazil, Ecuador, Venezuela) and the Caribbean (Puerto Rico, Cuba, Hispaniola). A single North American record of *Schacontia themis* is reported here from Sanibel Island, Florida (USA: Lee Co.).

Biology. Larvae are internal feeders that may induce galls, and pupate within the host. The only known host plant records are in Capparaceae: in Costa Rica, larvae have been reared from *Podangrogyne decipiens* (Triana & Planch.) Woodson (Solis, Nishida and Metz, in preparation); *Cleome spinosa* Jacq. has been reported as host for *S. chanesalis*; *Capparis frondosa* Jacq., and *C. verrucosa* Jacq. are reported for other *Schacontia* species.

Remarks. *Schacontia* was described by Dyar (1914) to accommodate three species, whose original descriptions were based primarily on wing pattern: the type species *Schacontia medalba* (Schaus, 1904; formerly *Acontia medlba*); *S. chanesalis* (Druce, 1899), formerly *Pionea chanesalis*; and *Schacontia replica* Dyar, 1914, the last of which accompanied the generic description (Druce 1899: 557, Schaus 1904: 163, Dyar 1914: 400). Dyar (1925: 8) later described *Thlecteria ysticalis* from a female specimen, also on the basis of wing pattern, and this species was later removed to *Schacontia* by Munroe (1995: 42), who also recognized *S. pfeifferi* Amsel, 1956, raising the total number of species recognized in the genus to five. Amsel's (1956: 101–102) description of *S. pfeifferi*, which placed *Schacontia* in the Schoenobiinae, is the most complete description to date and one of only two works prior to the present to figure or characterize genitalia (the other being Solis 2009). Neither Schaus nor subsequent authors were explicit in their characterization of what makes *Schacontia* unique or in their rationale for describing and including new species in the genus.

Key to species of *Schacontia*

Key to species of *Schacontia*: Male Genitalia + Habitus + Female genitalia (part)

- 1 Forewing generally silvery gray or gray brown with white shading in vicinity of antemedial and postmedial lines, particularly in medial area and at outermost edge of postmedial line; or dark brown with poorly contrasted markings except for postmedial line. Hindwing postmedial line conspicuous, nearing inner margin. Frons conical. Valva simple or reduced, sub-quadrate or emarginate/mildly bilobed; lacking a straight, prominent coastal arm; medial projection or flange arising from within sacculus; apex of costa lacking a tuft or plume, or a fleshy, setose subcostal lobe. Uncus mucronate, hood-like. Tegumen divided wherein the two tablet-shaped, bubble-like sections meet centrally for some or most of their length. Juxta more or less horseshoe shaped. Tympanal apparatus with saccus indistinct, posterior ridge lightly if

- at all sclerotized, grading into second sternite; venulae secundae not sharply tapering inward caudally; fornix broad, robust..... **2**
- 1' Forewing ground color straw or light gray, uniform or with a contrasting gray medial area suffused with white; or with outer margin and basal areas rust colored (*S. jysticalis*) or yellowish brown (*S. lachesis* and *S. atropos*); ante-medial and postmedial lines conspicuous; HW postmedial line faint, without secondary postmedial shading, not reaching inner margin. Frons with normal undifferentiated convex contour. Valva broad with a distinct costal bar or boom and either a faint, rudimentary hump appearing in the ventro-saccular region or as a more prominent, lateral sclerotized process at ventro-marginal edge of sacculus; a tuft or plume associated with costal terminus, each of which may also bear a fleshy, setose subcostal lobe. Uncus, either gently tapering to a wide rounded tip, or obovoid or squared, bearing a trefoil-like tip, in the last case appearing nearly tridentate, with a raised central ridge resulting in a webbed appearance (this feature may vary in prominence). Tegumen deeply divided such that two ovular sections meet obliquely towards base of uncus. Juxta robust, V- or broadly V-shaped. Tympanal saccus distinct, with posterior ridge or lip heavily sclerotized; venulae secundae tapered inward caudally; fornix narrow, ribbon-like..... **4**
- 2(1) Forewing medial area variously but diffusely shaded, generally without sharp contrast or orbicular spot; basal area not traversed by a white band. Uncus tapering to a distinct, ventrally directed squared tip. Tegumen invaginate such that sulcus joining two teguminal hemispheres extends less than 40% of length of tegumen. Intra-saccular process smooth, not conspicuously denticled..... **3**
- 2' Forewing medial area variously shaded, but often with contrast, an orbicular spot varyingly distinct or inconspicuous, if present; the basal area usually traversed by a white band. Uncus broadly tapered with a simple rounded nipple. Teguminal sulcus extends most of length of tegumen. Intra-saccular process rugose or denticled..... ***S. chanesalis***
- 3(2) Forewing color variously shaded with white scaling; lines or variously shaded regions conspicuous. Orbicular spot faint, if present. Hind wing slate gray. Valva truncate, rounded, entire..... ***S. medalba***
- 3' Forewing shaded chocolate brown, markings not obvious. Hind wings dark gray. Valva slightly emarginate..... ***S. umbra***
- 4(1') FW medial area suffused with white basad; postmedial line with broad, gentle costal bulge. Uncus dorsoventrally flattened, edges nearly carinate; uncus tip broad, neither acutely sharp nor sculpted with trefoil shape. Valva lacking a trigger-like process below costa; costa with mane-like tuft of elongate setae, recurved medially. Phallus simple, cornuti absent. Corpus bursae elongate, without signa **5**
- 4' FW shading either unicolorous or with medial area more darkly shaded than both basal and postmedial areas. Uncus tip swollen, either obovate or

- squared, in latter case with lateral edges thickened. Valva with a trigger-like process arising from within sacculus along ventral edge, and a conspicuous fleshy subcostal lobe and setose plume; costa lacking tuft of elongate setae medially recurved. Phallus with two prominent cornuti. Corpus bursae more or less globular, rarely with signa **6**
- 5(4) Basal area of FW with a brown ovoid spot, delineated by white bands crossing from wing base to antemedial line. Uncus tapered towards blunt squarish tip at a roughly 60 degree angle. Valva entire, not emarginate, without distinct upper and lower extensions; center of valva unadorned; intra-saccular structures indistinct. Phallus simple, naked, without cornuti ***S. speciosa***
- 5' Basal area of FW rust colored, mottled. Uncus broad, lateral edges parallel, tapering to a wide, gently rounded tip at a roughly 45 degree angle. Valva with upper and lower extensions, the lower sclerotized dorsad; intrasaccular flange conspicuous, adorned with both surficial and adjacent setal clusters. Phallus with a single cornutus. ***S. ysticalis***
- 6(4') FW uniform mouse gray or mottled, in latter case with medial area more darkly shaded. Uncus rounded, obovate with distinct, rhomboid nipple; uncal edges not reinforced or swollen. Valva gently rounded ventrally with moderate to elongate lateral process, ventro-medial edge with a distinct comb of elongate setae **7**
- 6' FW ground color gray or straw colored, contrasting gray medial area in some specimens. Uncus squared or scooplike in appearance with lateral edges swollen, sometimes conspicuously so, with or without a pronounced central ridge, tip hastate or trefoil-like; valva either elbowed or sharply angled towards midpoint, but not gently rounded, lacking an elongate process distally, ventro-medial edge without a distinct comb of elongate setae **8**
- 7(6) FW mottled in appearance, medial area slightly darker than basal and post-medial areas; orbicular spot pronounced. Epipleural setae absent. Ventral trigger-like process on valva rudimentary, if present; subcostal lobe robust, squat, $\leq 3\times$ longer than wide ***S. nyx***
- 7' FW gray, unicolorous; orbicular spot faint. Epipleural setae present. Ventral trigger-like process pronounced; subcostal lobe elongate and narrow, $\sim 5\times$ longer than wide ***S. clotho***
- 8 (6') Uncus with conspicuous, prominent central ridge. Elongate lateral lobe of valva absent; subcostal lobe not elongate; ventral edge of valva not conspicuously elbowed close to vinculum; central membranous area of valva conspicuously longer than wide **9**
- 8' Uncus with a uniformly smooth contour. Subcostal lobe pronounced, finger-like; ventral edge of valva angled or elbowed sharply (not rounded) approximately mid-way between vinculum and lateral edge of valva; central membranous area of valva not conspicuously longer than wide **10**
- 9(8) Female with two pairs of hind tibial spurs; male with coremata present on 4th abdominal segment, flattened hind tibial spur, specialized hind tibial scales

- with embedded dark patch, cuplike metatarsal modification, epipleural setae *S. themis*
- 9' Female with single pair of hind tibial spurs; male secondary sexual features above absent *S. rasa*
- 10(8') Male secondary sexual characters (including coremata on 4th abdominal segment, cf. 10) all present *S. lachesis*
- 10' Male secondary sexual characters (cf. 10) absent *S. atropos*

***Schacontia medalba* (Schaus, 1904)**

http://species-id.net/wiki/Schacontia_medalba

Figs 1, 21, 36–38

Acontia? *medalba* Schaus, 1904: 163. Type Locality: Brazil.

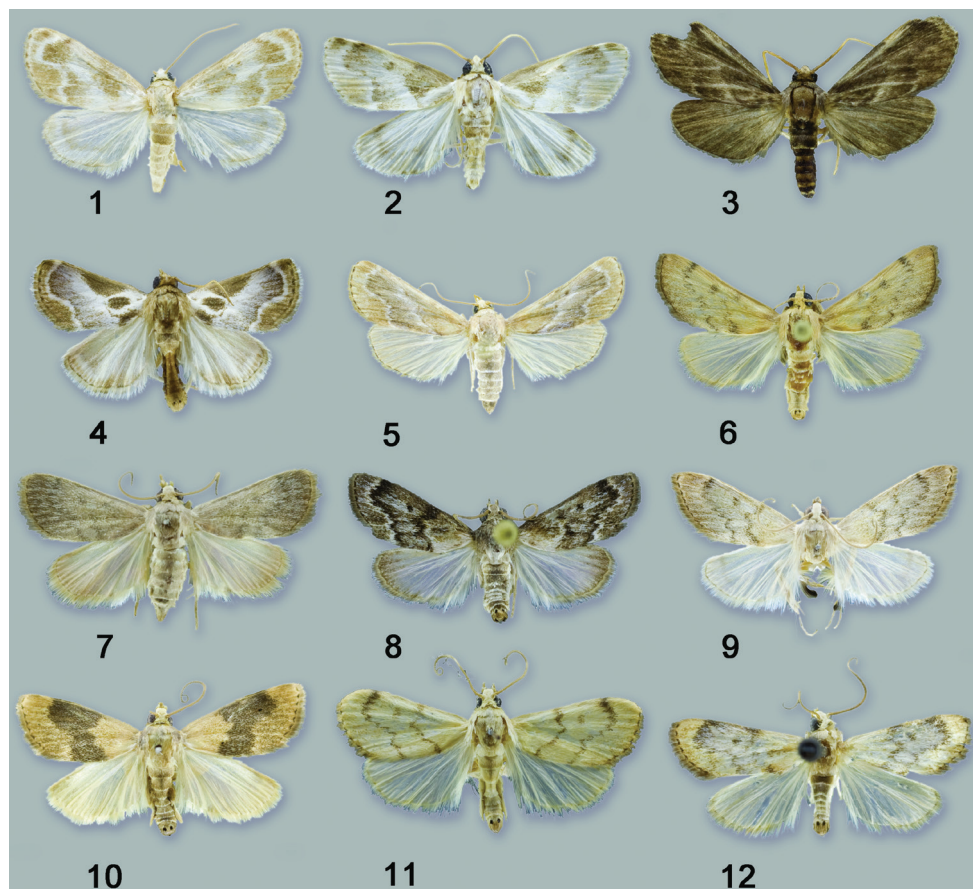
Material examined. (19♂, 10♀, 1 sex undet.).

Type material. Holotype (♀, USNM): Castro, Parana; Collection Wm Schaus; [red type label] type 10575; *Acontia?* *medalbi* [sic] sp. Schs; Pyralie Schoenobiana gen. nov.; USNM Genitalia Slide by DA ♀ 107,899.

Other material examined. Brazil: (19♂, 8♀, 1 sex undet.): Bnito Prov. Pernmbuco Brazl 83, unknown [illegible] 84 W.S. 165, genitalia slide by DA ♂ USNM 107,909 (1♂); Bnito Prov., Pernmbuco Brazl 83, [illeg.], Collection C.V. Riley, Genitalia slide by DA ♂ USNM 107,887 (1♂); Bnito Prov., Pernmbuco Brazl 83, [illeg.], Collection C.V. Riley, Genitalia slide by DA ♀ USNM 107,888 (1♀); Pernambuco, Brazil, coll. Pickel, 17 II 929 2065, Genitalia slide by DA ♀ 107,910 (1♀); Pernambuco Tapera, 1934. VIII.24, 2087♀ (1♀); Bnito Prov., Pernmbuco, Brazl. 6/1 83, Not known [illeg.], Collection of C.V. Riley ♂ (1♂); Pernambuco, Brazil, Coll. Pickel ♂ (1♂); 28, Bnito Prov., Pernmbuco, Brazl 8 3, 2, Fernald ♂ (1♂); 73, Not in BM 1925, W Schaus ♂ (1♂); 2♂ 1♀, as previous; Castro, Parana, Collection Wm Schaus, incl. 1: Genitalia slide by MAS ♀ USNM 107,011 (1♀); 1♂ as previous; Brazil: Nova Teutonia, F. Plaumann (1♂); Col. Becker No. 4601, Rio Brilbante, Mato Grosso, Brasil, 25.I.1971, V. O. Becker Col., *Schacontia medalba* det. M.A. Solis [on one only] (2♀); Col. Becker No. 9164, Rio Brilbante, Mato Grosso, Brasil, 24.X.1970, Becker leg. (1♀); Nova Teutonia, 27°11'S 52°23'W, Brazil, 300–500 m, 4-IV-1954, Fritz Plaumann [CNC] (4♂); Nova Teutonia, 27°11'S, 52°23'W, Brazil, 300–500 m, 10-IV-1954 Fritz Plaumann [CNC] (4♂); as above, "Slide No. 3645M.S." (1 sex undet.); Nova Teutonia, 27°11'S, 52°23'W, Brazil, 300–500 m, 3-III-1954, Fritz Plaumann, *Schacontia* n. sp. 7, Det. E.G. Munroe 1998 [CNC], Genitalia slide by JAL ♂ (1♂). **Peru** (1♀): Boniti P, Peru, Jan 7. 83.

Diagnosis. Specimens of *S. medalba* are most readily diagnosed from those of *S. chanesalis* by male genitalia, specifically the reduced, unlobed valvae and the naked intrasaccular process, features they share with *S. umbra*.

Re-description (Fig. 1). Forewing length 6.5–1.0 mm. **Head** - Frons conical; labial palpi straight, extending as far as clypeus. **Thorax** - Female with one pair of hind tibial



Figures 1–12. Habitus of adults. **1** *S. medalba* male, Peru, 1883, “Boniti P., Peru, Jan. 7. 83” **2** *S. chanesalis* male, Mexico, Becker 68741, Tam El Ensino 250 m, 4–13.viii.1988, V.O.Becker Col. **3** *S. umbra* male paratype, “Col. Becker 100503, Ecuador: Past. Mera, 1300 m, xii 1992, V.O. Becker Col, *Schacontia* n. sp. #3 det. M.A. Solis” **4** *S. speciosa* male holotype, “Col. Becker 65271, Brasil, RJ Marica, 5 m, 11.x.1985, V.O. Becker Col. **5** *S. ysticalis* Sirena, Corcovado Nat. Pk., Osa Penin., Costa Rica, 19–27 Mar 1981, DH Janzen, W. Hallwachs **6** *S. themis* Venezuela, Guarico, Hato Masaguaral, 45 km S Calabozo, 8.57N, 67.58W, Galry For #20, 75 m, 13–16 May 1988, uv lt., M. Epstein & R. Blahnik **7** *S. rasa* male holotype, Col. Becker 110514, Mexico, Tam San Fernando, 50 m, 28.vi.1997, V. O. Becker Col. **8** *S. nyx* “Venezuela: Guarico, Hato Masaguaral, 45 km S Calabozo, 8.57N, 67.58W, Galry Forest #20, 75 m, 13–16 May 1988, uv lt., M. Epstein & R. Blahnik **9** *S. clotho* male holotype, Col. Becker 102660, Ecuador, Loja Catamayo 1300 m, 20.xii.1992, V.O. Becker Col., Genitalia 1287 **10** *S. lachesis* male, “Col. Becker 55439, Brasil, RJ Arrai al do Cabo, 50 m, 29.i.1985, V.O. Becker Col.” **11** *S. lachesis* male, “Bolivia, Santa Cruz, Puerto Suarez, 150 m, Nov 1908, J. Steinbach, CMNH Acc. 3758” **12** *S. atropos* male holotype, “San Estaban, Carabobo, Venez., Dec. 1–20 1939, Pablo J. Anduze.”

spurs (medial pair absent); legs uniform gray brown. *Forewing*. Basal area primarily gray brown, undivided; antemedial (am) line meets anal margin. Subterminal line interrupted by wing veins; medial area partially suffused with white, especially basad; white

postmedial line appears shaded basally, interrupts/traverses dark shading between apical area and distal region of medial area; this “double” line faintly common to HW; FW fringe gray-brown. *Hindwing*. Postmedial line present, conspicuous (see above); terminal area lightly shaded, fringe white. **Abdomen** - Apical bands of pale scales on abdominal segments; terminal dots grayish brown, faint if present. *Tympanal organs* (Fig. 21). As for the *medalba* group, *vide supra*. **Male genitalia** (Figs 36, 37). Teguminal sulcus short, such that anterior margin of tegumen appears deeply invaginate; juxta U-shaped; valvae simple, reduced, rounded, not bilobed or emarginate; intrasaccular process a simple flange; intrasaccular process naked; phallus simple, cornuti absent. **Female genitalia** (Fig. 38). Antrum wider than deep, chalice-like; ductus bursae inconspicuous, no colliculum apparent; corpus bursae indistinct, weakly sclerotized, elongate.

Immature stages. Unknown.

Variation. Variable in size; forewings vary with respect to obfuscation in medial area.

Biology. Unknown.

Distribution. Brazil, Peru.

Schacontia chanesalis (Druce, 1899)

http://species-id.net/wiki/Schacontia_chanesalis

Figs 2, 13, 15–17, 22, 39, 41

Pionea chanesalis Druce, 1899, p. 557.

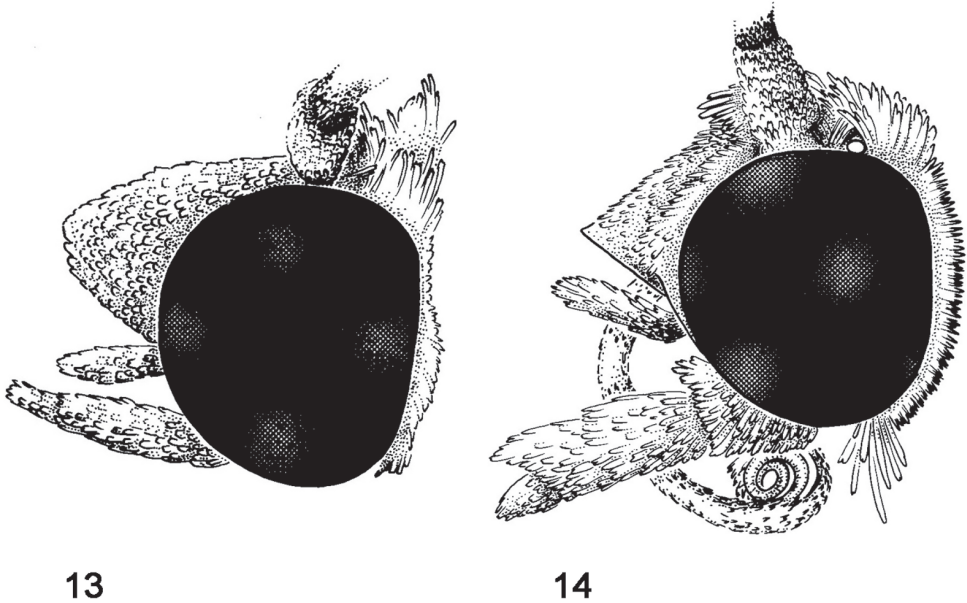
Schacontia replica Dyar, 1914, p. 400, **syn. n.** (Holotype ♀, Mexico, USNM).

Schacontia pfeifferi Amsel, 1956, p.101, **syn. n.** (Holotype ♂, Guatemala, ZSM, Munich).

Material examined. Below we summarize material examined for *S. chanesalis*. We include material previously determined as its new synonyms, *S. replica* and *S. pfeifferi*, and list them accordingly. We acknowledge that cryptic species may yet be identified pending the accumulation of molecular data.

Type material. Holotype (♀, BMNH): Holotype [round white label w/ red border]; El Tumbador, Guatemala, Champion; Godman-Salvin, Coll. 1904-1., B.C.A. Lep.-Het., *Pionea chanesalis* Druce; *Pionea chanesalis* Druce, type [hand written]; Genitalia Slide by DA, ♀. [Holotype of *Schacontia replica*]: March 1912, Orizaba, Mex, 3414, R Muller Collector, [red type label] Type 15484, *Schacontia replica* Dyar Type, [green label] USNM Genitalia Slide by DA ♀ 107,898, left FW missing (1♀). [Holotype; ZSM, Munich]; Typus ♀ leg. H. Amsel; Venezuela Maracay leg. P. Vogl.; Genitalia slide by DA 108,040 ♀, det. Amsel 1953 *Schacontia pfeifferi* Ams. [“Allotype”, ZSM, Munich].

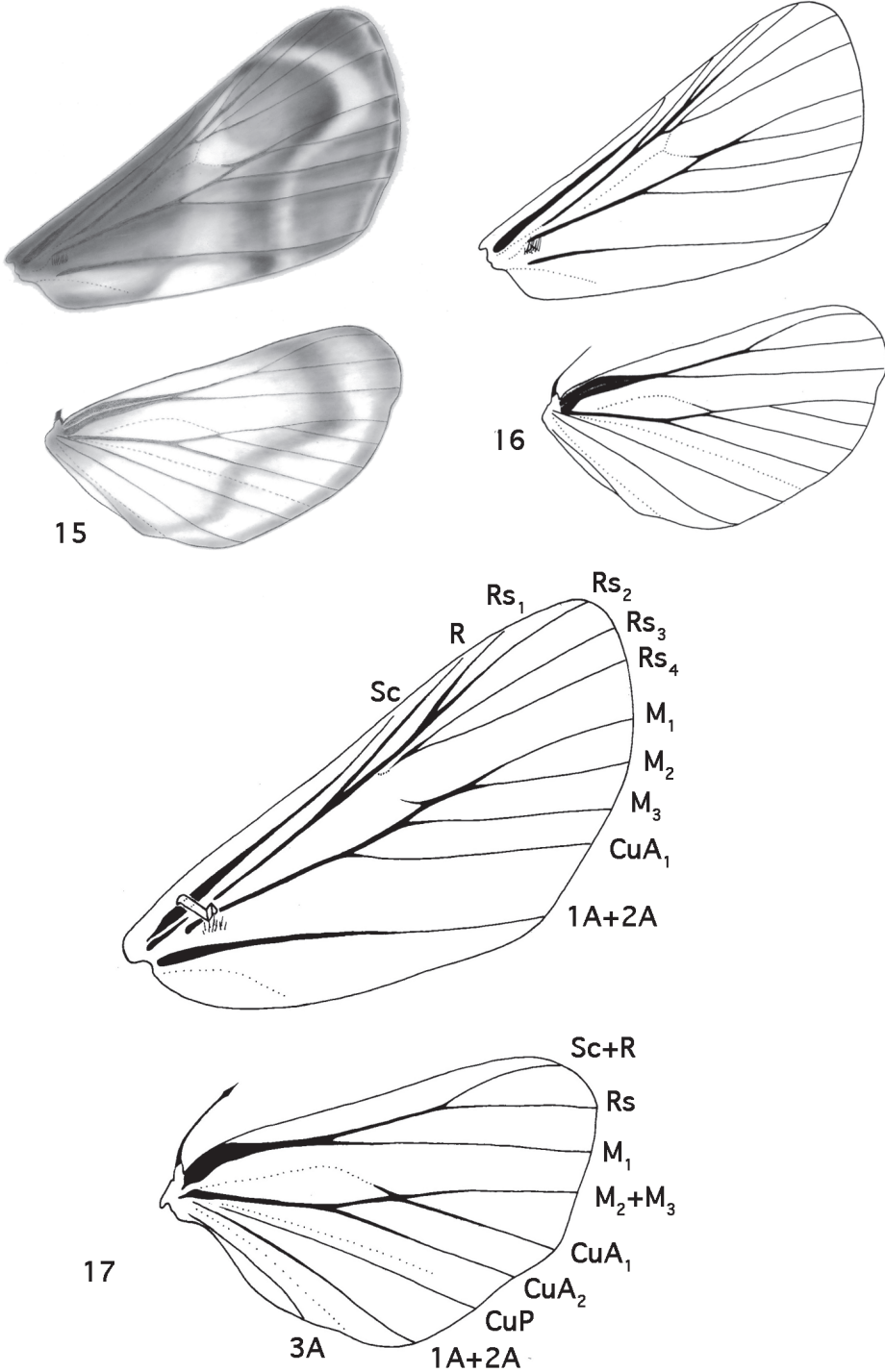
Other material examined. **Costa Rica** (8♂, 11♀, 4 sex undet.): Santa Rosa National Park Guanacaste Prov. Costa Rica 2–4 May 1980 DH Janzen & W. Hallwachs, Genitalia Slide by DA ♂ USNM 107,903, INBio Barcode # CR1001 115186 (1♂) as previous [no slide label], #CR1001 115190 (1♀); Estac. Quebrada Bonita, 50m R.B. Carara Puntarenas Pr. Costa Rica Nov 1989. R. Zuniga. 194500, 469850, Geni-



Figures 13, 14. Head, lateral view. **13** *S. chanesalis*; frons “normal” **14** *S. ysticalis*; frons carinate.

talia Slide by DA ♂ USNM 105,819, head illustrated; INBio Barcode # CR1000 120043 (1♂); Estac. Quebrada Bonita, 50m R.B. Carara Puntarenas Pr. Costa Rica April 1989. R. Zuniga. 194500, 469850, Genitalia Slide by DA ♂ USNM 106,418 [v. poor specimen], INBio Barcode # CR1001 103073 (1♂); Estac. Quebrada Bonita, 50m R.B. Carara Puntarenas Pr. Costa Rica Oct 1989. R. Zuniga. 194500, 469850, Genitalia Slide by DA ♀ USNM 105,820, INBio Barcode # CR1000 160925 (1♀); Estac. Quebrada Bonita, 50m R.B. Carara Puntarenas Pr. Costa Rica Set 1989. R. Zuniga. 194500, 469850, INBio Barcode # CR1001 103076 (1♀[?]); Est. Sta. Rosa, 800m, P.N. Guanacaste, Prov. Guan. Costa Rica, I. Curso Microlepidopt., Jul 1990 L-N-313000, 359800, INBio Barcode # CR1000 182323 (1♀); Est. Maritza, 600 m, Lado oeste del Volcan Orosi I curso Microlepidopt., July 1990 L-N-326900, 373000, INBio Barcode # CR1000 181312 (1♂); Santa Rosa National Park Guanacaste Prov. Costa Rica 7–9 July 1980 DH Janzen & W. Hallwachs, INBio Barcode # CR1001 115188 (1♀); Santa Rosa Nat. Pk., Prov Guanacaste, Costa Rica 10–12 Nov 1979 D.H. Janzen, INBio Barcode # CR1001 115187 (1♂); 97-SRNP-320, 8, Genitalia Slide by JAL ♀ (1♀); 97-SRNP-320, [right FW detached] (1♀); Prov. Guanacaste, Z.P. Nosara, Sector of Mirador, 800 m 2–8 Nov 2002. H. Mendez. Tp. De Laz. L N 220750 383450 #72175, INB0003554509 (1♀); Estac. Quebrada Bonita 50m R.B. Carara Puntarenas Pr. Costa Rica Oct 1989. R. Zuniga. 194500, 469850, INBio Barcode # CR1000 196823 (1♂); Fca. Cafrosa, Est. Las Mellizas, P.N. Amistad, 1300m Prov. Punt. COSTA RICA M. Ramirez & G. Mora, Nov. 1990 L-S-316100-596100, INBio Barcode # CR1000 278769 (1♀); Estac. Quebrada Bonita, 50m R.B. Carara Puntarenas Pr. Costa Rica Set 1989. R. Zuniga. 194500, 4698500 (1 sex undet.); Est.

Sta. Rosa, 800m, P.N. Guanacaste, Prov. Guan. Costa Rica, I. Carso Microlepidopt., Jul 1990 L-N-313000, 359800 (1 sex undet.); *Schacontia* sp. Crambidae, Costa Rica, Cartago prov. Parque National Tapanti near the ranger station 1250m, 25-V-2005 (adult emergence) Col/rear: Kenji NISHIDA Host Plant: Podandrogynne decipiens (Capparidaceae), gall inducer on the stem unknown family, female (1♀); *Schacontia* sp. Crambidae, Costa Rica, Cartago prov. Parque National Tapanti near the ranger station 1250m, 25-V-2005 (adult emergence) Col/rear: Kenji NISHIDA Host Plant: Podandrogynne decipiens (Capparidaceae), gall inducer on the stem, *Schacontia* n. sp. 2/06 det. M.A. Solis (1 sex undet.); *Schacontia* sp. Crambidae, Costa Rica, Cartago prov. Parque National Tapanti near the ranger station 1250m, 25-V-2005 (adult emergence) Col/rear: Kenji NISHIDA Host Plant: Podandrogynne decipiens (Capparidaceae), gall inducer on the stem Deformed adult caught in its pupal shell x1 Pupated 15-VI-2005 (pupal stage 1 month) (1♂); *Schacontia* sp. Crambidae, Costa Rica, Cartago prov. Parque National Tapanti near the ranger station 1250m, 25-V-2005 (adult emergence) Col/rear: Kenji NISHIDA Host Plant: Podandrogynne decipiens (Capparidaceae), gall inducer on the stem unknown family, female (1♀); *Schacontia* sp. Crambidae, Costa Rica, Cartago prov. Parque National Tapanti near the ranger station, 1250m, 25-V-2005 (adult emergence) Col/rear: Kenji NISHIDA Host Plant: Podandrogynne decipiens (Capparidaceae), gall inducer on the stem unknown family, male (1♂); Costa Rica: Estac. Biol. Las Cruces 6 km SE San Vito Rio Jaba 1150m X-20/21/1993, blacklight in secondary forest J. Powell coll. (1sex undet.); Voucher: D.H. Janzen & W. Hallwachs DB: <http://Janzen.sas.upenn.edu> Area de Conservacion Guanacaste Costa Rica 97-SRNP-320.1, "legs away for DNA" (1 sex undet.); same as previous, 97-SRNP-320.2, 97-SRNP-320.3, and 11-SRNP-12677 (1♂, 1♀, 1 sex undet., respectively). **Guatemala:** Cayuga Guat, Dec, Schaus and Barnes coll, Genitalia slide by DA ♂ USNM 108,097 (1♂); Quirigua Guat, Schaus and Barnes coll, Genitalia slide by DA ♀ USNM 107, 892, FW in capsule (1♀); Grutas de San Pedro Martir, Guatemala Escuintla VIII-10-1965 P.J. Spangler 1♀[?]. **Honduras:** El Hatillo Honduras Black light 3-VIII-1972 Robert D. Lehman (1 sex undet., obscured by mold). **Mexico** (22♂, 3♀, 3 sex undet.): Col. Becker 44006, Mexico: Veracruz Huatusco 1300m 19–23. Viii. 1981 V.O. Becker col., Comp. c/tipo USNM 1981 V.O. Becker (1♂); Nov '11, Orizaba Mex, R Muller collector, 3414, Chanesalis or [illeg.] desc. as *Pionea* [illeg.] *Schoenobiinae*, ♀ USNM 197,890 Genitalia slide by DA (1♀); Mexico: 2 mi. N. Tamazunchale, S.L.P. 400', July 16–18, 1963, Duckworth & Davis, Genitalia slide by DA ♂ USNM 108,099 (1♂); Mexico: 2 mi. N. Tamazunchale, S.L.P. 400', July 16–18 1963, Duckworth & Davis, Genitalia slide by DA ♂ USNM 108,889 (1♂); Mexico: El Salto Falls, 26 mi W. Antiguo Morelos, Tamps., 2000', July 11–14 1963, Duckworth & Davis (1♀); Mexico: .2 mi. N. Tamazunchale, S.L.P., 400', Aug. 2 1963, Duckworth & Davis (1♂); (17♂, 1♀, 1 sex undet. [genitalic slide unavailable, "1291"]); Col. Becker 68741, Mexico, Tam El Encino, 250 m, 4–13.viii.1988, V.O.Becker Col., Genitalia Slide ♂ by JAL [one specimen only]; Col. Becker 108733, Mexico: Tam El Encino, 250 m, 21–31.v. 1997, V. O. Becker Col. (1♂); Mex: Ver., 7 km NNW Huatusco, 1300 m, VIII-15-1987, J.T. Doyen (1 sex



Figures 15–17. Wings. **15** *S. chanesalis* female underside **16** *S. chanesalis* female underside **17** *S. chanesalis* male underside.

undet.). **Venezuela** (3♂): Venezuela: Guarico, Hato Masaguaral, 45 km S Calabozo, 8.57N, 67.58W, Galry Forest #20, 75 m, 3–5 June 1988, uv light, M. Epstein Genitalia slide ♂ by JAL USNM 108,083] (1♂); VENEZUELA: San Esteban Carabobo, Venez., Dec. 1–20 1939, Pablo J. Anduse, Illustration of wing pattern (1♂); Venezuela Maracay leg. P. Vogl., Jan.–Febr.35, Typus ♂ leg. H. Amsel, Genitalia slide by DA 108,039 ♂ (1♂).

Diagnosis. Specimens of *S. chanesalis* are best distinguished from those of *S. medalba* by the male genitalia, specifically a more sinuate valva and more denticled or rugose (as opposed to naked) intrasaccular process. The valvae are less conspicuously lobate than in *S. umbra* (below). Forewing pattern somewhat variable, as in *S. medalba*, but antemedial area more often traversed by white bar originating at scapula, enhancing the baso-costal patch.

Re-description (Fig. 2). Forewing length: 4.5–9.0 mm. **Head** - Ocelli and chaetosemata absent; proboscis reduced. Labial palpi porrect, extending slightly beyond clypeus. Frons conical; vertex and frons grayish brown, intermixed with white scales medially and along anterior bases of antennae. **Thorax** - Prothoracic collar light gray intermixed with gray-brown and white scales. Tegula and mesoscutum mostly gray, intermixed with light-gray and/or grayish-brown scales, the posterior apex of tegulae pale gray. Legs predominantly white, gray shading throughout foreleg; female with one pair of hind tibial spurs (medial pair absent). **Forewing.** Baso-costal triangle flanked by white scaling towards inner margin and in medial area, which is outwardly shaded brown (suffused with white basad). Postmedial area (between postmedial line and subterminal line) grayish brown. Subterminal line white; terminal line black, interrupted. Marginal scales brown. Basal area grayish brown traversed by a white band. Fringe scales light gray. **Hindwing.** Ground color white/very light gray, darker postmedially; postmedial lines grayish brown, white distally, conspicuous and common with FW. Subterminal area shaded darker brown; fringe white. Sc+R1 and Rs anastomosed slightly beyond dilated base of former. Male and female acanthae of frenulum fused from near base to apex to form one bristle. **Abdomen** - Ground color mostly dark gray intermixed with gray and light-gray scales above, white on undersurface. **Tympanal organs** (Fig. 22). As above for *medalba* group, *vide supra*. **Male Genitalia** (Figs 39, 40) - Tegumen divided dorsally into two dihedral or hemi-spherical “bubbles” that meet at a central sulcus, which divides anterior to base of uncus and forms a Y-shaped strut. Teguminal sulcus long, extending length of two teguminal lobes, such that anterior margin of tegumen appears emarginate, but not deeply invaginated. Uncus oblong, mucronate or miter-like, culminating in a distinct tip; concave or spatulate, setose on inner (ventral) surface. A membranous, more or less circular region at base of uncus positioned directly above (dorsal to) finger-like projection of gnathos, which also comprises a floating sub-teguminal plate with four arms. Finger-like process arises from center of gnathos; dorsal pair of arms, which meet at juncture of uncus and tegumen, appearing to fulfill traditional description of gnathos by enveloping the anal tube, and the anterior pair extending ventrolaterally towards the vinculum, resembling a wish-bone. Gnathos thus appears as a subteguminal (ventrad) suspension. Valvae reduced,

broadly emarginate, bilobed; intrasaccular process a simple flange, denticled or rugose; subapical setal cluster near saccular margin. Costa robust, curved, appearing to arise near the respective vincular terminus. Juxta horseshoe-shaped, the base wider than the lateral “arms.” Phallus simple, moderately sclerotized throughout; cornuti absent. **Female Genitalia** (Fig. 41) - Papillae anales appressed; antrum apparent, chalice-like; ductus bursae short; corpus bursae elongate, without signa, caeca, or appendix bursae; ductus seminalis originating from posterior portion of corpus bursae. Ostium bursae with membrane between seventh and eighth segments.

Biology. Larvae have been reared from *Podandrogynae decipiens* (Capparaceae) (D. Janzen, pers. comm.).

Distribution. Mexico, Guatemala; Costa Rica; Venezuela.

Immature stages. Unknown.

Variation. In size, with Mexican specimens appearing smaller in wingspan (FW length 4.5–7.0 mm) than Central American specimens.

Remarks. It is with some trepidation that we synonymize both *replica* and especially *pfeifferi* with *chanesalis*. *Pfeifferi* in particular was, until this work, the only *Schacontia* for which a detailed description had been published, and its continental separation from the type locality and primary distribution of *chanesalis* might suggest the potential for as yet unrecognized diagnosable species.

***Schacontia umbra* Solis & Goldstein, sp. n.**

urn:lsid:zoobank.org:act:524F3C52-1E37-4E82-B0F8-AF4485B49E2C

http://species-id.net/wiki/Schacontia_umbra

Figs 3, 23, 42, 43

Material examined. Type material. Ecuador: Holotype (♂, USNM): Ecuador, Past. Mera: 1300 m xii. 1992 V.O. Becker Col; Col. Becker 100503, (1♂). Paratypes (4♂), USNM. Ecuador, Past. Mera: 1300 m xii. 1992 V.O. Becker Col, Col. Becker 100503, (♂); Ibidem, 100504, (1♂); Ecuador, Past. Puyo: (22 km W) 5 February 1976 Blacklite [sic] Spangler, et al., Ecuador, Peace Corps. Smithsonian Institution Aquatic Insect Survey, Genitalic slide by DA ♂108,095, (1♂); (27 km N) Est. Fluv. Metrica 4 February 1976 Spangler, et al. (1♂).

Diagnosis. *Habitus, male genitalia* (Figs 3, 42). This species is most readily diagnosed by the darkly shaded forewings and by the male genitalia, which have the following features in common with *medalba*: anterior margin of tegumen deeply invaginate, outer margin of valva entire, intra-saccular process naked.

Description. (Fig. 3). Forewing length: 7.5–8.0mm (n=5). **Head** - Ocelli absent; proboscis reduced; frons conical; labial and maxillary palpi straight, not extending beyond clypeus. **Thorax** - Female with one pair of hind tibial spurs (medial pair absent). *Forewing*. Shaded gray brown, hind wings dark gray brown; postmedial line, when evident, characteristic of genus, outwardly bulged towards costa, sinuous towards inner margin, but entire forewing more darkly shaded than in other species. Medial area

partially suffused with white in some but not all specimens. Subterminal line pale, unbroken; fringe gray. *Hindwing*. Uniformly brown gray; subterminal line pale tawny, unbroken; fringe gray. **Abdomen** - Uniformly covered in gray-brown scales. *Tympanal organs*. (Fig. 23). As for *medalba* group, *vide supra*. **Male genitalia** (Figs 42, 43) - Teguminal sulcus short, such that anterior margin of tegumen appears deeply invaginate; juxta a U-shaped plate; valvae simple, reduced, rounded, not bilobed or emarginate; intrasaccular process a simple flange, naked; phallus simple, cornuti absent. **Female genitalia** (Fig. 44) - Unknown.

Immature stages. Unknown.

Variation. Markings may be obscured in some specimens, rendering them more or less uniformly gray brown.

Etymology. The specific epithet refers to the dark wing shading of this species and is treated as a noun in apposition.

Biology. Unknown.

Distribution. Central Ecuador.

***Schacontia speciosa* Solis & Goldstein, sp. n.**

urn:lsid:zoobank.org:act:77C2883E-34CB-4725-8AEC-A6C530C487F9

http://species-id.net/wiki/Schacontia_speciosa

Figs 4, 24, 44, 45

Material examined. Type material. Brazil: Holotype male, USNM (Fig. 4): Col. Becker 65271; Brasil: RJ Marica 5m, 11. x.1985, V.O.Becker Col. **Paratypes** 10♂, 1♀, 2 sex undet., USNM. Brazil: Same data as holotype (9♂, with additional label “Genitalia 1290”); BRAZIL: BA Jequié, 600–750 m; Col. Becker 105714 (1♀); BRAZIL: Rio Jan. 10 km SW Maricá “restinga” sand dune, 11–12-X-85 Scott E. Miller (1♂, 2 sex undet, ex abd.).

Diagnosis. *Habitus, male genitalia* (Figs 4, 44). The forewing pattern of this species makes it unmistakable; readily diagnosed by a combination of the frosted medial area common to other *Schacontia* and the interruption of the brown basal area to render a medio-basal patch encircled in white. Male genitalia diagnosed from those of other *Schacontia* species by the combination of expanded (not truncate) but inornate valvae, and reduced features associated with them, such as the inconspicuous intrasaccular flange; and a blunt, squarish, barely-tapering uncus.

Description. Male (Fig. 4). Forewing length: 7.5–8.0 mm, (n=14). **Head** - Ocelli absent; proboscis normal; frons expressed as a small hump, but not conspicuously conical; labial palpi correct, extending beyond clypeus. **Thorax** - Vertical scales mocha; female with one pair of hind tibial spurs (medial pair absent). *Forewing*. Medial area gray, partially suffused with white basad; postmedial line shaded white outwardly, brown inwardly; basal and submarginal areas primarily mocha brown; basal area interrupted by oblong basal patch surrounded by white. Subterminal line dark, unbroken; fringe scale gray, darkest at termini. *Hindwing*. Brownish white, no contrasting markings,

postmedial line inconspicuous if present; subterminal line dark, unbroken; fringe scales brown, pale gray at margin. **Abdomen** - Scales arranged in two terminal black dorsal spots in males. *Tympanal organs* (Fig. 24). Tergo-sternal sclerite robust, conspicuous; bullae tympani longer than wide, saccus or rim of bullae sclerotized at base; processi tympani present, lamellate, thumblike, towards anterolateral end of fornix; processus spiniformis present; fornix tympani sclerotized; angle of fornical ulna obtuse; pons of intermediate length, roughly half the depth of saccus, component rods broad, separate along entire length, diverging at anterior termini; posteromedial margin of saccus extends and remains parallel to pons for most of its length, pons extending towards bottom of saccus; saccus pronounced; venulae secundae prominent, tapering slightly at base of tympanal case such that “partie libre” (*sensu* Minet) of second sternite forms a neck; puteoli absent. **Male genitalia** (Fig. 44) - Teguminal sulcus short, not apparent; juxta U-shaped, lateral arms modestly recurved; valvae simple, broad, not truncate; intra-saccular process rudimentary, if present; costa with recurved, elongate tufts of setae but no conspicuous fleshy lobe; phallus simple, cornuti absent. **Female genitalia** (Fig. 45) - Papillae anales separate, round, swollen; colliculum present as faintly sclerotized collar embedded in ductus bursae, which is short, inconspicuously delimited and unsclerotized anterior to colliculum; corpus bursae elongate, membranus, without signa or appendix bursae; ductus seminalis inserted between antrum and ductus bursae.

Immature stages. Unknown.

Etymology. The specific epithet is from the Latin for showy or handsome.

Biology. Unknown. Adults active in October.

Distribution. Southeastern Brazil (Bahia, Rio de Janeiro).

Schacontia ysticalis (Dyar, 1925)

http://species-id.net/wiki/Schacontia_ysticalis

Figs 5, 25, 46–48

Thlecleria ysticalis Dyar, 1925, p. 8.

Material examined. (16♂, 16♀, 1 sex undet.).

Type material. **Mexico:** Holotype (♀, USNM).

Other material examined. **Bolivia:** Puerto Suarez, Bolivia, 150 m, Dec. 1908, J. Steinbach C.M. Acc. 3758 (1♂) [CMNH]. **Costa Rica** (4♂, 6♀): Santa Rosa National Park, Guanacaste Prov., Costa Rica, D.H. Janzen, 12 Dec 1978–10 Jan 1979, Genitalia Slide by DA ♂ USNM 107,905, INBio Barcode # CR 1001 115170 (1♂); Santa Rosa National Park, Guanacaste Prov., Costa Rica, D.H. Janzen, 12 Dec 1978–10 Jan 1979, Genitalia Slide by DA ♂ USNM 107,904, INBio Barcode # CR 1001 115169 (1♂); Playa Naranjo, Sta Rosa P.N., Guanacaste Prov., Costa Rica, E. Alcazar, Ene 1991 L-N-309300-353300, INBio Barcode # CR 1000 640648 (1♂); Santa Rosa National Park, Guanacaste Prov., Costa Rica, D.H. Janzen, 12 Dec 1978–10 Jan 1979, Genitalia Slide by DA ♀ USNM 107,906, INBio Barcode # CR 1001

115171 (1♀); Est. Queb. Bonita, 50 m, Res. Biol. Carara, Prov. Punt., Costa Rica, R. Zuniga, Jun 1991, L-N-194500, 469850, INBio Barcode # CR 1000 343579 (1♀); Estac. Quebrada Bonita, 50 m, R.B. Carara, Puntarenas Pr., Costa Rica, R. Zuniga, April 1989, 194500, 469850 INBio Barcode # CR 1000 017910 (1♀); Sirena, Corcovado Nat. Pk., Osa Penin., Costa Rica, 19–27 Mar 1981, DH Janzen, W. Hallwachs, INBio Barcode # CR 1001 115172 (1♀); Est. Quebrada Bonita, R.B. Carara, Prov. Punta, Costa Rica, 50 m, Mar 1994, R. Guzman, L N 194500_469850 #2803, INBio Barcode # CR1001 754072 (1♀); Est. Quebrada Bonita, R.B. Carara, Prov. Punta, Costa Rica, 100 m, ENE 1995, R. Guzman, L_N_195250_469850 #4433, INBio Barcode # CR1002 243527 (1♀); Costa Rica, Prov. Limon, Sector Cedrales de la Rita, 3 km N del Puente Rio Suerte, Ruta Puerto Lindo, 10 m, Feb 1997, E. Rojas, L_N_278600_566500 #45311, INBio Barcode # CR1002 499299 (1♂). **Mexico** (2♂, 4♀): Col. Becker 42358, Mexico: Veracruz Est. Biol. Tuxtla, 11–16.vi.1981, V. O. Becker Col., *Schacontia ysticalis* Dyar, Det. M.A. Solis (1♀); Ibid. x4 exc. Col. Becker 42297 (3♀, 1♂); Venadio, Sinaloa, Mex, B P Clark donor, Not in BM 1925 W Schaus (1♂). **Nicaragua** [CMNH]: Managua Dist., Laguna de Xiloa, 23 April 1996, E. van den Berghe (3♂, 1♀); Managua Dist., Laguna de Xiloa, 14 April 1996, E. van den Berghe (2♂); Managua Dist., Laguna de Xiloa, 8 March 1997, E. van den Berghe (1♂) [CMNH]. **Venezuela** (7♂, 5♀): Venezuela, Guarico, Huato Masaguaral, 45 km S Calabozo, 8.57°N, 67.58°W, Galry For#4, 75 m, 12–13 Apr 1988, uv light, M. Epstein, R. Blahnik, Genitalic Slide by DA ♀ USNM 107,896 (1♀); same as previous (2♂, 4♀, 1 sex undet.), “hind leg used for illustration” [Fig. 20]); Venezuela, Guarico, Huato Masaguaral, 45 km S Calabozo, 8.57°N, 67.58°W, Galry For#4, 75 m, 13–16 May 1988, uv light, M. Epstein, R. Blahnik [3♂, incl. 1w/ label Genitalic Slide by DA ♂ USNM 108,100]; Venezuela, Guarico, Huato Masaguaral, 45 km S Calabozo, 8.57°N, 67.58°W, Galry For#4, 75 m, 23–24 Apr 1988, uv light, M. Epstein, R. Blahnik, Genitalic Slide by DA ♂ USNM 107,895, “Head illustrated” (1♂); Venezuela, Guarico, Huato Masaguaral, 45 km S Calabozo, 8.57°N, 67.58°W, Galry For#4, 75 m, 25 May, uv light M. Epstein & C. Canaday (1♂).

Diagnosis. *Habitus, male and female genitalia* (Figs 5, 46–48). Distinct by virtue of orange cast to basal and postmedial areas of forewing. Male genitalia distinct by virtue of wide, rounded uncus without modifications; heavy, long recurved setal tufts at costa of valva; and intrasaccular patch of heavy setae. Female genitalia distinct by virtue of elongate, robust bursa combined with conspicuous appendices bursae.

Re-description. Male (Fig. 5). Forewing length: 7.0–11.0 mm (n=14). **Head** (Fig. 14) - Ocelli present; proboscis normal; frons conical or expressed as a small hump; labial palpi porrect, extending beyond clypeus. **Thorax** - Legs white, forelegs cupreous dorsally, as basal tarsomeres on all legs. Female with two pair of hind tibial spurs (medial pair present). *Forewing*. Basal, antemedial, and subterminal fasciae brownish orange, shaded distally with white (dark basad). Both antemedial and postmedial lines shaded distally with white (dark basad); antemedial and postmedial areas rust colored/cupreous; medial area sparsely suffused with white. FW fringe brown. *Hindwing*. postmedial line faint if present; HW yellowed at margin, sub-

terminal line interrupted; fringe whitish beige. **Abdomen** - Cupreous sheen; white abdominal bands on all segments. Scales arranged in two terminal black dorsal spots in males. *Tympanal organs* (Fig. 25). As for *ysticalis-themis* group, *vide supra*. **Male genitalia** (Figs 46, 47) - Teguminal sulcus short, such that anterior margin of tegumen appears deeply invaginate, the two oblong teguminal lobes joined obliquely. Uncus wider than long; terminal edge of uncus entire. Gnathos quadrate. Juxta an inverted triangular plate or robust “V”, less sclerotized at center. Valvae complex; costa robust with recurved, elongate tufts of setae; subcostal lobe with petiolate scales, most arched towards dorsal articulation of valva; with secondary outer, oblong lobe or process below costa; with fleshy setose lobe associated with terminus of costa and located between distal portion of costa and lower portion. Intrasaccular process a simple flange, the inner surface of which bears chisel-shaped setae; with robust, spine-like setae at base; submarginal area of sacculus setose. Saccular margin angled close to vinculum, not at saccular mid-point; ventro-marginal setae concentrated at saccular ulna. Phallus moderately sclerotized; vesica with a small cornutus. **Female genitalia** (Fig. 48) - Papillae anales separate, more or less round, flat, and swollen; ostium bursae with membrane between seventh and eighth segment; antrum membranous; colliculum present as a sclerotized collar of intermediate length embedded within ductus bursae; two conspicuous appendices bursae located at posterior end of corpus bursae; corpus elongate, membranous, without signa; ductus seminalis near posterior end of corpus bursae.

Immature stages. Unknown.

Variation. Unremarkable.

Biology. Unknown. Recorded adult activity mid-June (Mexico), January–June (Costa Rica), 8 March–23 April (Nicaragua), 12 April–25 May (Venezuela), December (Bolivia).

Distribution. Mexico, Costa Rica, Nicaragua, Venezuela, Bolivia.

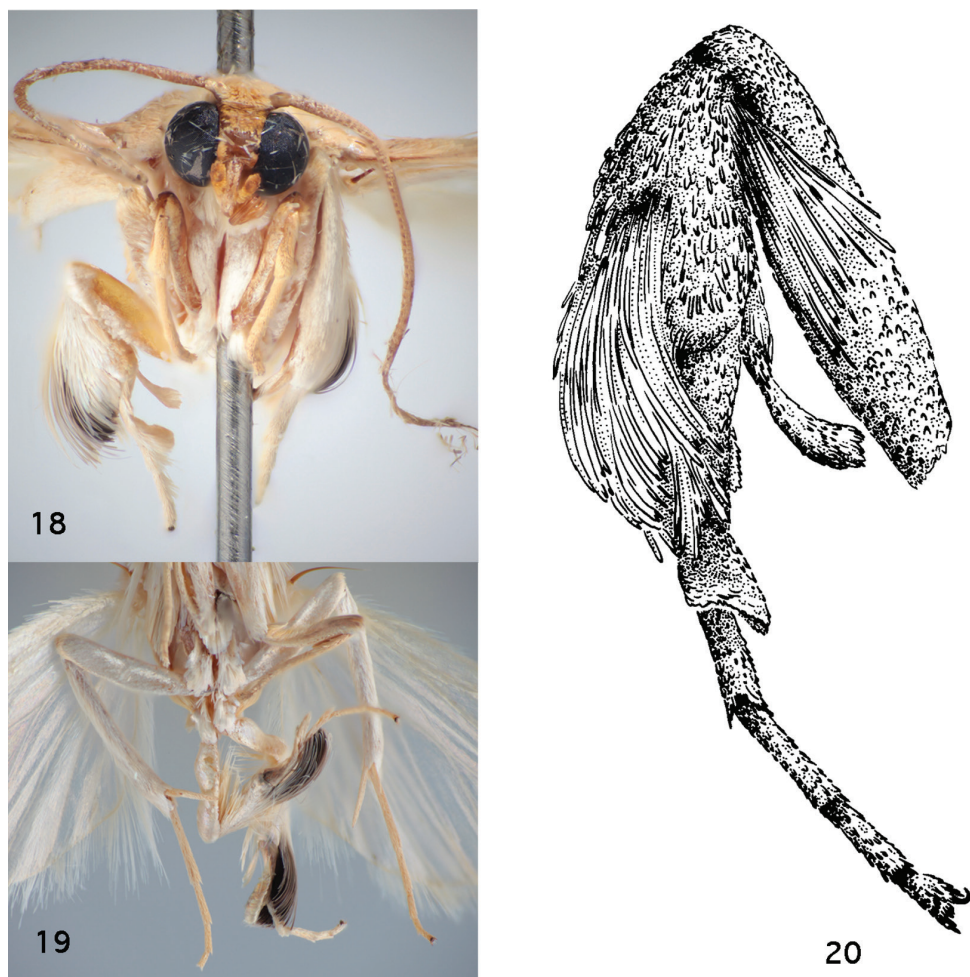
***Schacontia themis* Solis & Goldstein, sp. n.**

urn:lsid:zoobank.org:act:81B6D7E0-F6F0-44C8-B4B7-BB8424FE4B9F

http://species-id.net/wiki/Schacontia_themis

Figs 6, 19, 26, 49–51

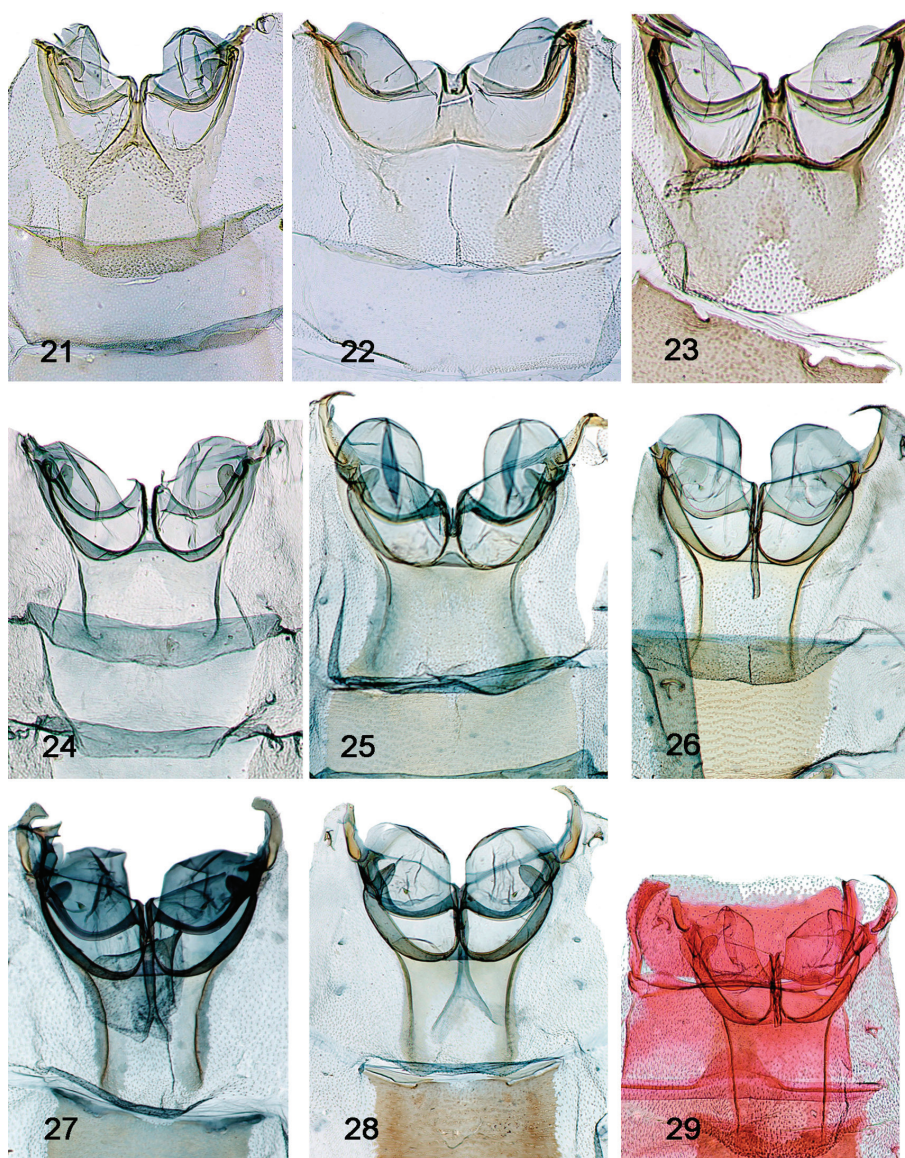
Material examined. Type material. Holotype (♂, CMNH). **Dominican Republic:** La Altagracia. 2 km N Bayahibe, 18–23N, 68–51W, 10 m, 3 July 1992, C. Young, R. Davidson, S. Thompson, J. Rawlins, Dry seasonal forest on limestone, USNM ENT 00808538, DNA 2012 (1♂) [GenBank Accession #KC789515]. Paratypes (41♂, 19♀) USNM, except where otherwise designated. Costa Rican paratypes with an INBio barcode label deposited at INBio. **Brazil** (5♂, 1♀, 1 sex undet.): Unit. Amaz. Taperinha b. Santarem 1–10 VI '27, Zerny (1♂) [NHMV]; Unit. Amaz. Taperinha b. Santarem, 1–10 VIII '27, Zerny (1♂) [NHMV]; Unit. Amaz. Taperinha b. Santarem, 21–31 VII '27, Zerny (1♂) [NHMV]; Unit. Amaz. Taperinha b Santarem 1–10 VII '27, Zerny,



Figures 18–20. Thoracic and leg structures in *Schacontia clotho* and *S. themis*. **18** *S. themis*, hind leg, frontal view, illustrating secondary sexual characters: flattened hind tibial spur, scales with dark patch, and flattened concave metatarsal modification, and epipleural setae (data Fig. 6) **19** *S. clotho*, ventral view, illustrating darkened hind tibial scales. Ecuador: Loja Catamayo, 1300 m, 20.xii.1992, V.O. Becker Col; Col. Becker 102660 **20** *S. themis*, hind leg, lateral view.

86 (1♂) [NHMV]; Col. Becker 105713, Brasil: BA Jequié, 600–750 m, 11–22 xi 1995, V.O. Becker Col. [1 sex undet.]; Unit. Amaz. Taperinha b. Santarem 1–7 IX '27, Zerny, 43, genitalia slide by JAL ♀ USNM 108,870 (1♀); Unit. Amaz. Taperinha b. Santarem 1–10 VII '27, Zerny, 43, Genitalia slide by JAL ♂ USNM 108,880 (1♂). **Cayman Islands** (7♂, 1♀): N.B. Certain Cayman Islands specimens have multiple data labels with conflicting dates. 17 iv–26.viii 1938, Oxf. Un. Cayman Is. Biol. Exped., Coll. by C.B., G.H. Thompson, 18 v 1938, Cayman Brac., N. coast of Stakes Bay, Light trap A, [yellow tag PARATYPE, *in errato*], *Proboscontia amica* Munroe, CNC (2♂); 17 iv–26.viii 1938, Oxf. Un., Cayman Is. Biol. Exped., Coll. by C.B. Lewis, G.H. Thomp-

son, 4 v 1938, Grand Cayman, N coast of Rum Point, Light trap (1♂) [BMNH] [red Holotype label, *in errato*]; 17 iv–26 viii 1938, Oxf. Un. Cayman Is. Biol. Exped., Coll. by C.B. Lewis, G.H. Thompson, 1 vii 1938, Grand Cayman, East end of Interior, The Cliff, Light trap, ♀ Pyralidae Brit. Mus. Slide No. 19801, Slide No. 3663 MS (1♀) [BMNH]; 17 iv–26 viii 1938, Oxf. Un. Cayman Is. Biol. Exped., Coll. by C.B. Lewis, G.H. Thompson, 14 v 1938, Grand Cayman, East End light trap B (1♂) [BMNH]; 17 iv–26 viii 1938, Oxf. Un. Cayman Is. Biol. Exped., Coll. by C.B. Lewis, G.H. Thompson, 7 v 1938, Grand Cayman, N coast of, Rum Point, Light trap (1♂) [BMNH]; 17 iv–26 viii 1938, Oxf. Un. Cayman Is. Biol. Exped., Coll. by C.B. Lewis, G.H. Thompson, 22 v 1938, Cayman Brac., N coast of Stakes Bay, Light trap A, ♂ Pyralidae Brit. Mus. Slide No. 19802 (1♂) [BMNH]; 17 iv–26 viii 1938, Oxf. Un. Cayman Is. Biol. Exped., Coll. by C.B. Lewis, G.H. Thompson, 11 vii 1938, Grand Cayman, N coast of North Side, Light trap B (1♂) [BMNH]. **Costa Rica** (5♂, 6♀, 1 sex undet.): Guanacaste. Voucher INBio data base Costa Rica 97-SRNP-2346 Testigo Base de datos INBio Costa Rica (1♂); Voucher INBio data base Costa Rica 97-SRNP-2354.2 Testigo Base de datos INBio Costa Rica, Genitalia slide ♀ by JAL (1♀); Voucher INBio data base Costa Rica 97-SRNP-2349 Testigo Base de datos INBio Costa Rica (1♀); Sirena, Corcovado Nat. Pk. Osa Penin. Costa Rica 10–12 Aug. 1980, D.H. Janzen & W. Hallwachs, Genitalia slide by DA ♀ USNM 107,907, INBio Barcode #CR1001 115167, “Head illustrated” (1♀); Est. Cacao, 1000–1400 m, Lado SO Vol. Cacao, P.N.G. Prov. Guan, Costa Rica, C. Chaves, Abr 1991, L-N-323300, 375700 (1♀); INBio Barcode # CR1000 700522, Est. Santa Rosa, Prov. Guana, Costa Rica, 300 m, 25 Feb–5 MAR 1995, B. Gamboa, L N 313300 #4730 (1♀); INBio Barcode # CR1000 187409, Est. Sirena, 0–100 m, P.N. Corcovado, Prov. Punt., Costa Rica, G. Fonseca, May 1991, L-S-270500, 508800, INBio Barcode # CR1000 563282 (1♀); Voucher INBio data base Costa Rica 97-SRNP-2352 Testigo Base de datos INBio Costa Rica, “S. mootii #4” (1♂); Voucher INBio data base Costa Rica 97-SRNP-2354.1 Testigo Base de datos INBio Costa Rica, genitalia slide ♂ by JAL (1♂); Sirena, Corcovado Nat. Pk., Osa Penin., Costa Rica 5–11 Jan 1981, D.H. Janzen & W. Hallwachs, Genitalia slide by DA ♂ USNM 107, 908, INBio Barcode #CR1001 115168 (1♂); 80.SRNP.47, Santa Rosa National Park, Guanacaste Province, Costa Rica, D.H. Janzen, genitalia slide ♂ by JAL (1♂); 1sex undet.: Santa Rosa National Park, Guanacaste Prov., Costa Rica, 1 May 1980, D.J. Janzen & W. Hallwachs, INBio Barcode # CR1002 506841. **Cuba** (2♂): Col. Becker 72733, Cuba: Gtnmo Imias, 10 m, 17 vii 1990, V.O. Becker, 17, Genitalia slide by JAL ♂, USNM ENT 00808541, DNA 2012 (1♂); Col. Becker 73068, Cuba: Stgo. Siboney, 20 m, 23 vii 1990, V.O. Becker, 15, genitalia slide by JAL ♂, USNM ENT 00808540, DNA 2012 (1♂). **Dominican Republic** (1♂, CMNH): Same data as holotype, USNM ENT 00808539 [GenBank Accession # KC789516] (1♂). **Jamaica** (9♂, 1♀): Jamaica: Clar. Par., Mason River Station 4 mi NW Kellits, DNA 2012, 2200 ft, 16–19 Apr ’73, Don & Mignon Davis (1♂); Jamaica: Clar. Par., Portland Ridge nr. Jackson Bay Cave, 40 ft, 4 May 1973, Don & Mignon Davis (1♂); Jamaica: Ann Par., nr. Runaway Bay Cave, 50 ft, 1–2 May 1973, Don & Mignon Davis (1♂); Jamaica: Clar. Par., nr. Jackson Bay Cave, 1.5 mi SE Jack. Beach, 50 ft, 4



Figures 21–29. Tympanal organs. Collection and/or dissection numbers follow country of origin; when label data presented elsewhere, annotated as such. **21** *Schacontia medalba*, Brazil, “Bnito Prov., Pernmbuco, Brazil 83; Collection C.V. Riley; USNM genitalia slide 107887 **22** *S. chanesalis* male, Guatemala: Quirigua Guat; Schaus and Barnes coll; Genitalia slide by DA ♂ USNM 107,891 **23** *S. umbra* male Holotype, Ecuador, Past. Mera: 1300 m, xii.1992, V.O. Becker Col; Col. Becker 100504 **24** *S. speciosa* male, Paratype, Brazil (data Fig. 4) **25** *S. ysticalis* male 108100; Venezuela Guarico, Huato Masaguaral , 45 km S Calabozo, 8.57°N, 67.58°W, Galry For#4 75 m, 13–16 May 1988, uv light, M. Epstein R. Blahnik **26** *S. themis*, male, Costa Rica, Guanacaste, Santa Rosa Nat’l Pk., 97 SRNP 2354.1 JAL, 2 May 2003, #5 **27** *S. rasa* male Holotype, Mexico, Col. Becker 110514, Mexico, Tam San Fernando, 50 m, 28.vi.1997, V. O. Becker Col., [green USNM genitalia slide label “JAL 18”] **28** *S. nyx* male, Venezuela, Lara, 4 km NW of La Pastora, 2–3.III.1978, riparian forest, blacklight, J.B. Heppner, Genitalia slide by DA ♂ USNM 108,101 **29** *S. clotho* Cf Fig. 9.

May 1973, Don & Mignon Davis (6♂, 1♀) [incl. 1♂ genitalia slide ♂ by JAL USNM 108,879, + 1♀ genitalia slide ♀ by JAL USNM 108,868]. **Panama** (5♂, 2♀ males): Panama: Canal Zone, Barro Colorado Isl., 21 Mar 1979, Silberglied/Aiello, at light, 35, Genitalia slide by JAL USNM 108,874 (1♂); Panama: Canal Zone, Barro Colorado Isl., 7 Mar 1979, Silberglied/Aiello, at light (1♂); Panama: Canal Zone, Barro Colorado Isl., 31 Mar 1979, Silberglied/Aiello, at light (1♂); Panama: Canal Zone, Barro Colorado Isl., 19 Mar 1979, Silberglied/Aiello, at light (1♂); Panama: Canal Zone, Barro Colorado Isl., 18 Mar 1979, Silberglied/Aiello, at light (1♂); Panama: Canal Zone, Barro Colorado Isl., 12 Mar 1979, Silberglied/Aiello, at light, 34, Genitalia slide ♀ by JAL USNM 108,873 (1♀); Panama: Canal Zone, Barro Colorado Isl., 1 Apr 1979, Silberglied/Aiello, at light (1♀). **Puerto Rico** (4♂, 2♀): Puerto Rico, Guanica, Bosque Estatal de Guanica, 3.6 km E Guanica, 17-58-11N, 66-52-28W, Thornscurb, 100 m, 12 June 1996, J. Rawlins, R. Davidson, C. Young, M. Klingler, W. Zanol, S. Thompson, Carnegie Museum Specimen Number 65,312 (1♂) [CMNH]; Puerto Rico, Guanica, Bosque Estatal de Guanica, 3.6 km E Guanica, 17-58-11N, 66-52-28W, thornscurb, 100 m, 12 June 1996, J. Rawlins, R. Davidson, C. Young, M. Klingler, W. Zanol, S. Thompson, Carnegie Museum Specimen Number 65,695 (1♂) [CMNH]; Col. Becker 67784, Puerto Rico, Guanica, 170 m, 20 viii 1987, V.O. Becker (2♂, 1♀) [incl. 1 genitalia slide ♂ by JAL]; Col. Becker 67782, Puerto Rico, Guanica, 170 m, 20 viii 1987, V.O. Becker (1♀). **Venezuela** (3♂): Venezuela, Guarico, Hato Masaguaral, 45 km S Calabozo 8.57N, 67.58W, Galry For #10, 75 m, 23–24 Apr 1988, uv lt., M. Epstein & R. Blahnik (2♂); Venezuela, Guarico, Hato Masaguaral, 45 km S Calabozo 8.57N, 67.58W, Galry Forest #20, 75 m, 13–16 May 1988, uv lt., M. Epstein & R. Blahnik [x2 incl. 1w/Genitalia slide ♂ by JAL USNM 108,869] (1♂) [Fig. 6].

Additional material examined: British Virgin Islands (BVI) (29♂, 16♀): Brit. Virgin Isl., Guana Island, 0–80 m, 5–23 July 1985, S.E. & P.M. Miller, Clubhouse 60 m, U.V. light trap, 9–15 July 1985 (1♂); same as previous, 36, VOB ♀ USNM 108,875 (1♀); Brit. Virgin Isl., Guana Island, 0–80 m, 5–23 July 1985, S.E. & P.M. Miller (5♂); same as previous, VOB ♂ USNM 95900 (1♂); Col. Becker 66651, Brit. Virgin Isl., Guana I., 0–80 m, 9–23.vii.1987, V.O. Becker & S.E. Miller, Genitalia 1260 (1 sex undet.); Col. Becker 70821, Brit. Virgin Isl., Guana X. 1989 V.O. Becker (10♂, 3♀) [incl. ♂ “slide 21”, hair pencils and abdominal coremata present]; same as previous, Genitalia slide by JAL ♂ (1♂, 1♀); same as previous, Genitalia 1261 and 1262 (2♀); Col. Becker 66649, Brit. Virgin Isl., Guana I., 0–80 m, 9–23 vii 1987, V.O. Becker & S.E. Miller, 11, Genitalia Slide ♂ by JAL (1♂) [hair pencils and abdominal coremata present]; Col. Becker 66651, Brit. Virgin Isl., Guana I, 0–80 m, 9–23 vii 1987, V.O. Becker & S.E. Miller (1♂, 2♀); Col. Becker 66650, Brit. Virgin Isl., Guana I., 0–80 m, 9–23 vii 1987, V.O. Becker & S.E. Miller (3♂, 1♀); Col. Becker 66649, Brit. Virgin Isl., Guana I, 0–80 m, 9–23 vii 1987, V.O. Becker & S.E. Miller (2♂, 5♀); same as previous, Genitalia 1296 [Abdomen remains on specimen (!)] (1♂); Brit. Virgin Isl., Guana Island, 0–80m, 13–26 July 1986, S.E. Miller & M.G. Pogue, North Bay, *Coccoloba* forest, U.V. light trap. sea level, 15–25 July 1986, [note label dates contradict], #25 (1♂); Brit. Virgin Isl., Guana I, 0–80 m, 24–31.x. 1990, S.E. Miller & T.M.

Kuklenski, Collectors Bishop Museum, n. gen. + sp, Schacontiinae det. E.G. Munroe, 1991, *Schacontia* n. sp. det. M.A. Solis (1♂); Brit. Virgin Isl., Guana I, 0–80 m, 10–25.vii.1988, S.E. Miller & C. O'Connell, Colls. Bishop Museum, 89: 13 Apr #1 EGM (1♂); Brit. Virgin Isl., Guana Island, 1–14 July 1984, S.E. & P.M. Miller, 39, Genitalia Slide by JAL ♀ USNM 108,878 (1♀); Anomalous BVI specimens with tibial hair pencils but no abdominal coremata (3♂): Col. Becker 70821, Brit. Virgin Isl., Guana X. 1989 V.O. Becker, 23, Genitalia slide ♂ by JAL (1♂); Col. Becker 66650, Brit. Virgin Isl., Guana I., 0–80 m 9–23.vii.1987 V.O. Becker & S.E. Miller, 13, Genitalia slide ♂ by JAL (1♂); Brit. Virgin Isl., Guana Island, 0–80 m, 5–23 July 1985, S.E. & P.M. Miller, Clubhouse, 60 m, U.V. light trap, 9–15 July 1985, 38, VOB ♂ USNM 108,877 (1♂). **Mexico** (4♀). Chichen Itza. Yucatan, Mexico. EC Welling Coll. 5.III.1956 (1♀) [CNC]; Chichen Itza, Yucatan, Mexico, EC Welling Coll., 2.III.1956 (1♀) [CNC]; Mexico, Mazatlan, July 10, 1969, El 50', James H. Baker collection 1978 (1♀); Taboga Isl Pan, Febr 12 August, Busck (1♀). **United States** (1♀): Florida. "Sanibel Island, Lee Co., FLA.", "30-VI-1984 Leg. W.L. Adair", MGCL slide no. 687 [MGCL].

Diagnosis. *Habitus* (Fig. 6). Unlike many *Schacontia*, there is little to no contrast between the medial area and the rest of the forewing; although this holds for both *S. rasa* and *S. clotho* as well, those two are readily distinguished on other grounds. Male *S. themis* exhibit the full range of secondary sexual features known from the genus (flattened hind tibial spur, elongate hind tibial scales with embedded dark patch, epipleural setae, and concave metatarsal structure) as well as long abdominal coremata (Fig. 19; Table 1); *S. rasa* (below), the putative sister species of *S. themis*, has none of these (but see remarks). Two other *Schacontia* species (*S. clotho* and *S. lachesis*) do share these features in part, but not the genitalic configuration that characterizes *S. themis* and *S. rasa* (see below). *Male and female genitalia* (Figs 49–51). As with the remaining *Schacontia*, males of this species are most readily diagnosed by a combination of genitalic and external secondary sexual characteristics. The male genitalia best distinguish this species and its putative sister, *S. rasa* (below), from other *Schacontia*: The uncus has a characteristic, expansive trefoil-shaped tip and lateral edges that appear swollen or re-enforced (as *S. lachesis* and *S. atropos* do), and a raised, pronounced medial ridge (as they do not). The intrasaccular flange is robust and forms a trigger-shaped process at the latero-ventral edge of the valva.

Description. Male. (Fig. 6). Forewing length: 5.3–10.0 mm. **Head** - Ocelli present; proboscis with pale basal scales in males, light brown basal scales in females. Vertex and frons yellowish white in males, intermixed with brownish-gray scales in females; frons of normal (convex) contour; maxillary palpi uniformly grayish brown; labial palpi grayish brown in males, fading to gray apically in females; labial and maxillary palpi porrect, extending well beyond clypeus; antennal scape and pedicel yellowish white, flagellomeres grayish brown. **Thorax** - Thoracic collar, tegula and mesoscutum yellowish white in males, brownish gray in females. Males with flattened hind tibial apical spur, hind tibial tuft of long black scales intermixed with pale yellowish-white scales, epipleural setae, and shallow concave metatarsal modification. Females with two pair of hind tibial spurs (medial pair present). Forewing ground color straw, with few contrasting mark-

Table 1. Species diagnoses for the *S. nyx* complex based on male genitalia and secondary sexual characters. Format inspired by Ferguson (1992: 259).

	Thorax				
	Flattened hind tibial spur	Elongate hind tibial scales	Dark patch embedded within tibial scales	Epipleural setal tufts	Concavemeta-tarsal structure
themis	+	0/+	0/+	+	+
rasa	0	0	NA	0	0
nyx	+	+	0	0	+
clotho	+	+	+	+	+
lachesis	+	+	0/+	+	+
atropos	0	0	NA	0	0

	Abdomen	Genitalia			
	Coremata	Saccular bend or ulna	Ventro-medial setal comb	Distribution of ventro-marginal setae	Hook-shaped decumbent costal setal cluster
themis	Short	NA	0	0	0
rasa	NA	NA	0	0	0
nyx	Short	Round	+	Localized	0
clotho	Long	Round	+	Localized	+
lachesis	Short	Angled	0	Even	+
atropos	NA	Angled	0	Even	+

ings other than jagged chocolate-brown antemedial and postmedial lines, postmedial line outwardly bulging only slightly, towards costa. Medial area unicolorous with basal area and postmedial areas. Fringe darkened apically. *Hindwing*. Almost uniformly pale, shaded brown at subterminal area. **Abdomen** - Dorsal surface straw brown. Scales arranged in two terminal black dorsal spots in males. Lobe-like extensions resembling rudimentary coremata on 4th abdominal sternum. *Tympanal organs*. (Fig. 26). As for *yisticalis-themis* group, *vide supra*. **Male genitalia** (Figs 49, 50) - Tegumen divided into two obliquely opposed oval sections meeting caudally near base of uncus and diverging widely anteriorly towards valvae. Teguminal sulcus short, such that anterior margin of tegumen appears deeply invaginate, two oblong teguminal lobes joined obliquely. Uncus with prominent medial ridge; uncal tip hastate, trefoil-like; lateral edges of uncus swollen, appearing re-enforced and lending a shovel- or scoop-like appearance to uncus. Gnathal plate narrowed to a transverse band with arms at each corner and a small, nub-like process arising centrally; dorsal arms wrap around anal tube while a ventral pair extend to termini of vinculum. Vinculum variously U-shaped or horseshoe shaped with pronounced pockets or eyelets at each terminus. Juxta robust, V-shaped; valvae complex, robust costa arising near vincular terminus, extending almost length of valva, and taper-

ing to a point. A serrate, trigger-like ventral spine arises from ventral margin of sacculus; robust, spine-like setae at base of valva; saccular margin angled close to vinculum, not at saccular mid-point; ventro-marginal setae concentrated at venter or saccular ulna; valva with secondary fleshy subcostal setose lobe, setal plume recurved/decumbent. Elongate saccular process at outer saccular margin; saccular margin with several stout setae. Inner surface of valvae dorsal to saccular area with a small, circular setal cluster. Phallus moderately sclerotized; vesica with two large cornuti. **Female genitalia** (Fig. 51) - Papillae anales separate, not especially swollen; anterior and posterior apophyses threadlike, approximately equivalent in length; antrum/ductus bursae conspicuously sclerotized with a partial ventral collar or sleeve ventrally anterior to colliculum; a sharp constriction between ductus bursae and colliculum; colliculum a short sclerotized ring immediately posterior to corpus bursae with a narrow differentially sclerotized band around its center; corpus bursae membranous, more or less round, without signa or conspicuous appendices except single postero-dorsal lobe; ductus seminalis appears to originate from antrum.

Immature stages. Unknown.

Variation. This species varies most obviously in size (5.3 mm–10.0 mm in male forewing length), and based on the examination of several anomalous specimens from the British Virgin Islands, the presence of male secondary sexual characteristics (tibial hair pencils and abdominal coremata) do not perfectly covary: Hair-penciled males with and without coremata are noted from Guana Island, examples annotated and/or segregated in “Material examined” section above; see also Discussion.

Etymology. The specific epithet refers to the Greek Titaness and embodiment of divine order and is treated as a noun in apposition.

Biology. Possibly associated with Capparaceae. (<http://janzen.sas.upenn.edu/caterpillars/database.lasso>). Phenology, based on examined material: January–April, August in Costa Rica; March–April in Panama; April–May in Jamaica & Cayman Islands; July in Dominican Republic; June–July in Cuba; June, August in Puerto Rico; April–May in Venezuela; July–August in Brazil.

Distribution. Brazil, Cayman Islands, Costa Rica, Cuba, Dominican Republic, Florida (USA), Jamaica, Mexico, Panama, Puerto Rico, Venezuela. The Sanibel Island, Florida record represents the only known United States occurrence of any *Schacontia*.

Remarks. *Schacontia themis* is among the more widespread and collected species of *Schacontia*. It seems likely that more cryptic species (like *S. rasa*, below) exist.

***Schacontia rasa* Solis & Goldstein, sp. n.**

urn:lsid:zoobank.org:act:FDC54534-0A71-424E-9CFC-C48604E452F5

http://species-id.net/wiki/Schacontia_rasa

Figs 7, 27, 52–54

Material examined. (22♂, 32♀).

Type material. (3♂, 13♀), USNM. Holotype ♂ (Fig. 7). **Mexico:** Col. Becker 110514; Mexico: Tam San Fernando, 50 m, 28. vi. 1997, V. O. Becker Col.; USNM

genitalia slide “JAL 18” Paratypes (2♂, 13♀, 4 sex undet.). Same data as holotype (2♂, 4 sex undet., 13♀ incl. 1 with green USNM genitalia slide label “JAL 19.”

Other material examined. **Cuba** (3♂, 2♀): Col. Becker 72733, Cuba Gtnmo. Imias, 10 m, 17. vii. 1990, V.O. Becker, USNM ENT 00808543, DNA 2012 (1♂); Col. Becker 72409, Cuba: Holquin Mayari, 400 m, 12.vii.1990, V.O. Becker, USNM ENT 00808544, DNA 2012 (1♀); Santiago, Cuba, Collection Wm Schaus, Genitalia slide by DA ♂ USNM 108,096 (1♂); Col. Becker 73068, Cuba: Stgo. Siboney, 20 m, 23.vii.1990, V.O. Becker, genitalia slide by JAL, 16 (1♂, 1♀). **Dominican Republic** (15♂, 13♀) [CMNH]: Dominican Republic: Pedernales, 14.5 km N Cabo Rojo, 18-03N, 71-39W, 165 m, 19 July 1990, J. Rawlins, C.W. Young, S.A. Thompson (1♂, 7♀); Dominican Republic: Pedernales, 9.5 km N Cabo Rojo, 18-02N, 71-39W, 35 m, 19 July 1990, J. Rawlins, C.W. Young, S.A. Thompson (5♂, 3♀); Dominican Republic: Pedernales, 14.5 km N Cabo Rojo, 10 m, 17-55N, 71-39W 26–27 September 1991, C. Young, B. Thompson, R. Davidson, J. Rawlins Coastal desert (2♂, 1♀); Dominican Republic: Pedernales, 14.5 km N Cabo Rojo, 18-03N, 71-39W, 165 m, 26–27 September 1991, C. Young, S. Thompson, R. Davidson, J. Rawlins, Arid thornscrub (1♂); Dominican Republic: Pedernales, 1 km W Cabo Rojo, 17-55N, 71-39W, 10 m, 30 July 1990, C.W. Young, J.E. Rawlins, S. Thompson (4♂, 1♀); Dominican Republic: Pedernales, Cabo Rojo, Sea level, 17-55N 71-39W, 21 Oct 1991, J. Rawlins, R. Davidson, C. Young, S. Thompson, Edge of salt marsh (1♂); Dominican Republic: La Altagracia, Parque del Este, Caseta Guaraguo, 4.4 km SE Bayahibe, 18-19-59N, 68-48-42W, 3 m, 26–27 May 2004, C. Young, J. Rawlins, J. Fetzner, C. Nunez, semi-humid forest near sea, limestone, UV light. Sample 51114 (1♀); Dominican Republic: La Altagracia, 2 km N Bayahibe, 10-23N, 68-51W, 10 m, 3 July 1992, C. Young, R. Davidson, S. Thompson, J. Rawlins, Dry seasonal forest on limestone, USNM ENT 00808542, DNA 2012 [GenBank Accession #KC789514] (1♂). **British Virgin Islands** (1♂, 2♀): Virgin Gorda BVI Prickley Pear Id, Vixen Pt, 14.IV.56, J.F.G. Clarke, 33, Genitalia Slide ♂ by JAL USNM 108,872 (1♂); Col. Becker 66649, British Virgin Is., Guana I., 0–80 m. 9–23 vii 1987, V.O. Becker & S.E. Miller, #20, Genitalia Slide ♀ by JAL (1♀); British Virgin Is., Virgin Gorda Island, V. Gorda Peak, Ca. 400 m, 17–19 July 1986, S.E. Miller & M.G. Pogue, Black light trap in secondary moist forest, 37, Genitalia slide by JAL ♀ USNM 108,876 (1♀).

Diagnosis (Figs 7, 52–54). Very similar to *S. themis* (above), particularly with respect to the male genitalia, but lacking the secondary sexual characters enumerated above and the forewing ground color usually mouse gray instead of straw colored. Female hind tibia with a single pair of spurs (medial pair absent - diagnostic within the *ysticalis-themis* group).

Description. Male (Fig. 7). Forewing length: 7.0 mm–8.0 mm. **Head** - Ocelli present; proboscis normal; frons unmodified; labial palpi porrect, extending beyond clypeus. **Thorax** - *Forewing*. Medial area gray, unicolorous with basal area and postmedial areas; antemedial and postmedial lines jagged, darker gray. *Hindwing*. Postmedial line faint if present; outwardly tinged with bronze. **Abdomen** - Terga unicolorous with wings and thorax; scales arranged in two terminal black dorsal spots in males. *Tympanal organs*. (Fig. 27). As for *ysticalis-themis* group, *vide supra*. **Male genitalia** (Figs 52, 53) - Teguminal sulcus

short, anterior margin of tegumen appears deeply invaginate, two oblong teguminal lobes joined obliquely; uncus trefoil shaped, outermost tip hastate; lateral edges of uncus swollen, appearing re-enforced; uncus with raised, pronounced medial ridge; juxta robust, V-shaped; valvae complex, intrasaccular flange at latero-ventral edge and sclerotized to form a trigger-shaped process; robust, spine-like setae at base of valva; saccular margin angled close to vinculum, not at saccular mid-point; ventro-marginal setae concentrated at saccular ulna; valva with secondary outer, oblong lobe or process below costa; fleshy setose lobe and recurved/decumbent setal plume associated with terminus of costa. Phallus moderately sclerotized; vesica with two large cornuti. **Female genitalia** (Fig. 54) - Very similar to *S. themis* but posterior lobe of corpus bursae more pronounced, superficially rugose; both colliculum and sclerotized channel or sleeve of ductus more elongate than in *S. themis*.

Immature stages. Unknown.

Etymology. The specific epithet refers to the absence of male hind tibial and metatarsal structures and epipleural setal tufts (presumably secondary sexual characters) present in other *Schacontia* species (Table 1).

Biology. Unknown. Adults active June (Mexico), July (Cuba), and July, September (Dominican Republic).

Distribution. Mexico, Cuba, Dominican Republic (essentially, vic. Gulf of Mexico).

Remarks. *Schacontia rasa* is evidently the sister species of *S. themis*. Were it not for the characters associated with the forewing ground color, female hind tibia, and male genitalia and given the homoplastic nature of certain male secondary sexual characters comparable to the system described by Ohno (2000) [see discussion], *S. rasa* would be a more obvious candidate for conspecificity with *S. themis*. We have treated anomalous specimens with “chimeric” distributions of male secondary sexual characters under *S. themis* (above), and considered only those lacking both tibial hair pencils and abdominal coremata (in addition to genitalic features) to be unambiguously *S. rasa*, recognizing the need for future molecular work to evaluate the degree to which these character systems are functionally and genetically linked. DNA barcode data (meeting the Barcode Data Standard of Genbank, noted in Benson et al. 2012) are limited to three Dominican Republic specimens and do decisively unite two specimens of *S. themis* to the exclusion of *S. rasa*. Not enough specimens are sampled to test the variable sites as diagnostic characters and enable their use in the species’ diagnoses (Goldstein and DeSalle 2011), but the data corroborate (albeit by a distance measure of >7%) the reliability of the morphological characters as consistent with two distinct species.

It was suggested by V.O. Becker (pers. comm., following the submission of this work) that the name *Dichogama fernaldi* Möschler, 1890, the type material of which has apparently been lost from MNHU, might refer to this species (see Becker & Miller, in prep., for discussion) and that it should be placed in the now monotypic genus *Dichochroma*, whose description is, in turn, based on a single female (and only known specimen) of the type species, *D. muralis* Forbes, 1944. This attribution of the specimens we consider to fall within *S. themis* (or *S. rasa*, below) to *D. fernaldi* is, however, not well corroborated by any character identified in the original description by Möschler, but only by process of elimination and the report of its being reared on *Capparis* by Wolcott (1950-1951: 658, cited in Becker and Miller, in prep.). While eliminating a *nomen dubium* is

desirable and the process of elimination by which such an attribution might be reached intriguing, the recognition of two similar co-occurring species (*S. themis* and *S. rasa*) described here, corroborated at least indirectly by DNA barcode data, precludes any specific attribution. We therefore retain the description of *Schacontia themis* and *S. rasa* as such. Further, notwithstanding the superficial similarity of certain female *Schacontia* genitalia to those of the only known specimen *Dichochroma muralis*, both phylogenetic placement described in this work and priority of *Schacontia* would dictate that *Dichochroma* be sunk were it determined that these species were congeneric, even if male *Dichochroma muralis* were discovered and/or more compelling character data were brought to bear.

The *Schacontia nyx* complex: Some of these species are not readily diagnosed by a single character; each, rather, is characterized by either an absence of characters (as in *S. atropos*) or by combinations of characters, all of them male, both genitalic and external, the latter presumably secondary sexual features.

***Schacontia nyx* Solis & Goldstein, sp. n.**

urn:lsid:zoobank.org:act:B7C1FDB3-9A23-44BB-9CD4-8E1D8B8DBE78

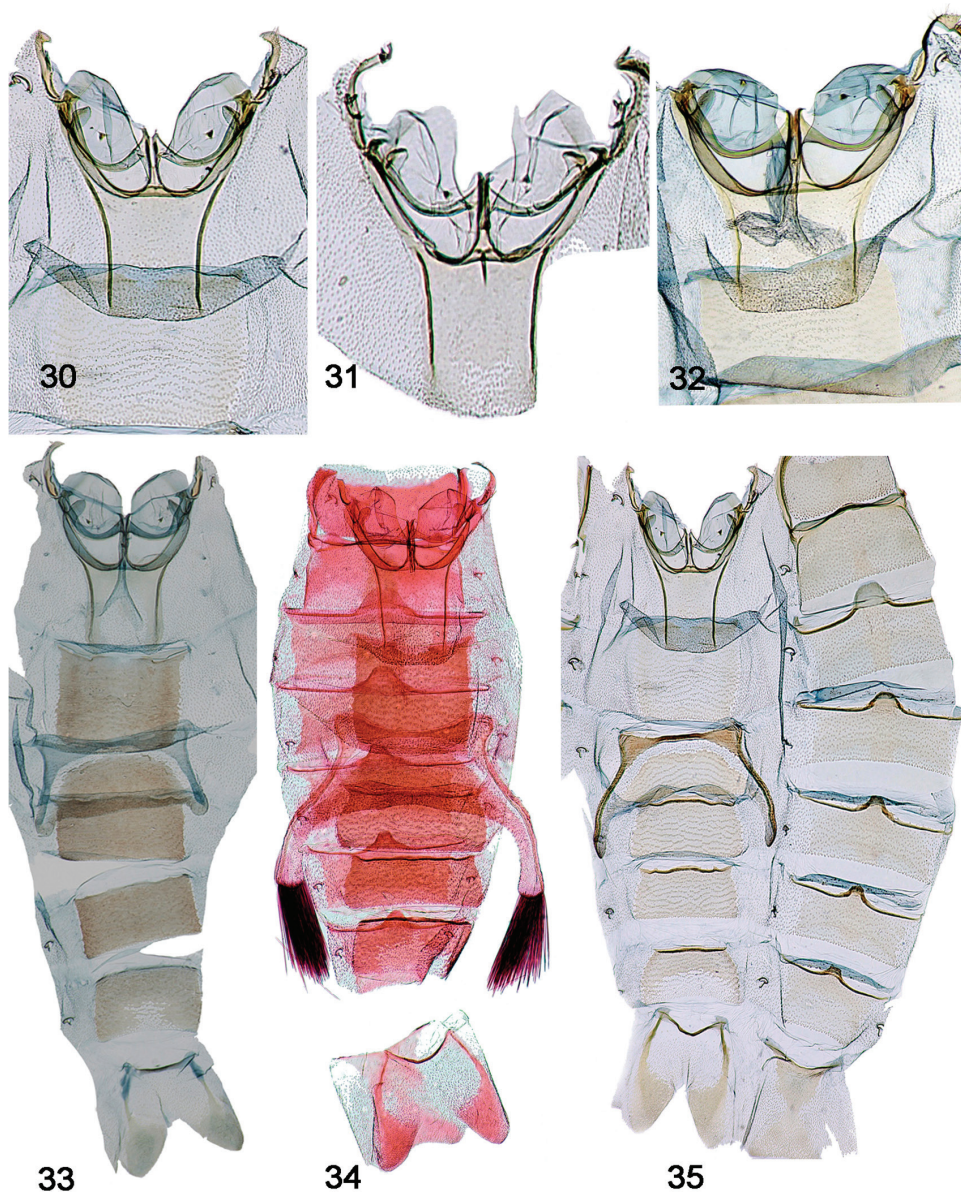
http://species-id.net/wiki/Schacontia_nyx

Figs 8, 28, 33, 55–57

Material examined. Type material. Holotype (♂, USNM): **Venezuela:** Guarico, Hato Masaguaral, 45 km S Calabozo 8.57N, 67.58W, Galry For #10, 75 m, 23–24 April 1988 uv lt. M. Epstein & R. Blahnik. Paratypes (4♂, 2♀), USNM: Venezuela: Same data as holotype (1♂, 1♀); Guarico, Hato Masaguaral, 45 km S Calabozo 8.57N, 67.58W, Galry Forest #20, 75 m, 13–16 May 1988 uv lt. M. Epstein & R. Blahnik (2♂, 1♀); Lara, 4 km NW of La Pastora 2–3 III 1978 riparian forest black-light, J.B. Heppner, Genitalia slide by DA ♂ USNM 108,101 (1♂)

Diagnosis. *Habitus* (Fig. 8). Although more readily diagnosed by the male genitalia, *nyx* can be differentiated on the basis of wing pattern. *Nyx* shares with other members of the genus (and in particular of the complex of sibling species to which it belongs) the configuration of the medial area, with its outward subcostal bulge, but its more mottled appearance and less uniformly contrasting ground coloration between the medial and both the antemedial and postmedial areas. Male *S. nyx* does not bear the epipleural setae shared by most other members of the complex; nor do they exhibit a dark patch embedded within the elongate hind tibial scales (Table 1). *Genitalia* (Figs 55, 56). Male specimens of *S. nyx* are most readily diagnosed by the obovate uncus, which is without pronounced medial ridges or lateral swellings. The subcostal processes are more conspicuous and elongate than in *S. themis* or *S. rasa*, but less narrow than in other species in the complex (*S. clotho*, *S. lachesis*, *S. atropos*, or *S. androgynae*).

Description. Male (Fig. 8). Forewing length: 6.0–7.0 mm (n=3) (Female 7.3–7.7 mm; n=2). **Head** - Ocelli present; proboscis normal; frons of normal contour; labial and maxillary palpi drooping, extending beyond clypeus; vertex gray. **Thorax** - Tegulae uni-



Figures 30–35. Tympanal organs and male abdominal segments. **30–32.** Tympanal organs. **30** *S. lachesis* male, Bolivia, Cf. Fig. 11 **31** *S. lachesis* female, Bolivia, Cf. Fig. 11 **32** *S. atropos* male, Venezuela, Cf. Fig. 12 **33–35.** Male abdominal segments, illustrating coremata. **33** *S. nyx* Venezuela, Cf. Fig. 22 **34** *S. clotho* holotype, Catamayo, Ecuador, 1287, Cf. Fig. 9 **35** *S. lachesis* Bolivia, Cf. Fig. 24.

formly gray brown; flattened hind tibial spur, specialized hind tibial scales, and shallow concave metatarsal modification all present; female with two pair of hind tibial spurs (medial pair present). *Forewing.* Antemedial and postmedial lines darkened at medial area,

white towards basal and postmedial areas; white scales suffused both in basal area near anal margin and medial area, especially surrounding orbicular spot; patchy white scales in post-medial area; subterminal line unbroken; FW fringe dark brown, scales paler basad. *Hind-wing*. White, shaded grayish brown towards margin; postmedial line absent; subterminal line unbroken; HW fringe gray, scales paler basad. **Abdomen** - Scales arranged in two terminal black dorsal spots in males. Short coremata on 4th abdominal segment (Fig. 33). *Tympanal organs* (Fig. 28). As for *ysticalis-themis* group, *vide supra*. **Male genitalia** (Figs 55, 56) - Teguminal sulcus short, anterior margin of tegumen appears deeply invaginate, two oblong teguminal lobes joined obliquely; uncus trefoil-shaped tip reduced to a small, more or less rhomboid nipple, edges simple, undifferentiated; juxta U-shaped, tapered ventrally; valva complex, intrasaccular flange at latero-ventral edge and sclerotized to form a trigger-shaped process; robust, spine-like setae at base of valva; saccular margin rounded at saccular mid-point; prominent setal comb at ventro-medial margin of valva; ventro-marginal setae concentrated at saccular ulna; valva with pronounced, elongate secondary outer lobe or process below costa; recurved/decumbent setal plume associated with terminus of costa. Phallus moderately sclerotized; vesica with two large cornuti. **Female genitalia** (Fig. 57) - Papillae anales separate, not especially swollen; antrum/ductus bursae present, diffusely sclerotized ventrally anterior to colliculum; colliculum present, short, sclerotized, immediately posterior to corpus bursae, with narrow differentially sclerotized band around center; ductus seminalis attached posterior of corpus bursae; corpus bursae round; small accessory bursa present; ductus seminalis originates at posterior end of corpus.

Immature stages. Unknown

Etymology. *Nyx*, the primordial goddess of the night who according to myth stood at the beginning of creation, refers to the first of five closely related species in this complex. The specific epithet is treated as a noun in apposition.

Biology. Unknown. Adults March–May.

Distribution. Northern Venezuela.

***Schacontia clotho* Solis & Goldstein, sp. n.**

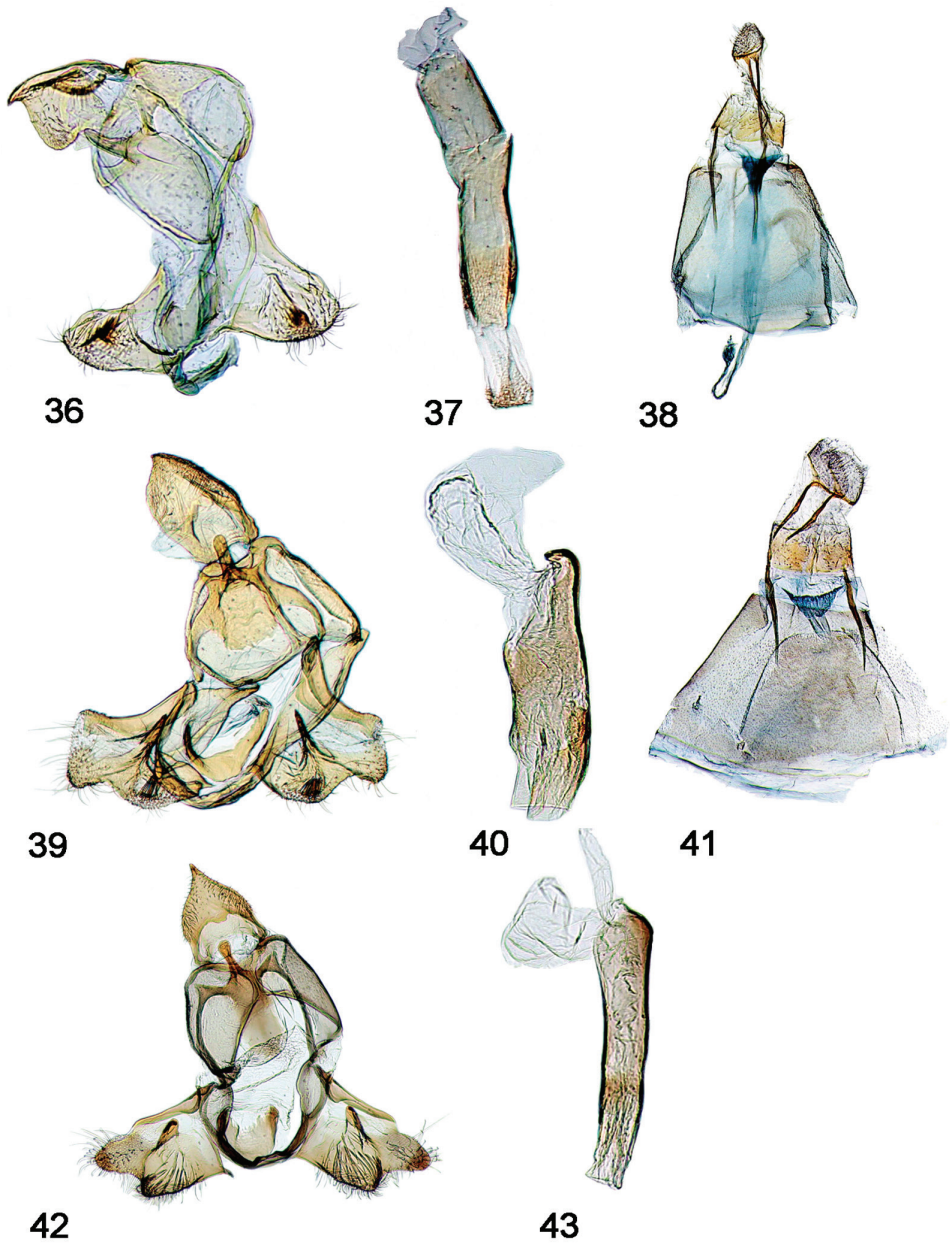
urn:lsid:zoobank.org:act:55C68C29-D157-4838-8F52-F277B9E1CA66

http://species-id.net/wiki/Schacontia_clotho

Figs 9, 29, 34, 58–60

Material examined. Type material. Holotype (♂, USNM) (Fig. 9): **Ecuador:** Loja Catamayo, 1300 m, 20. xii 1992, V.O. Becker Col., Col. Becker 102660, Genitalia 1287. Paratypes (1♂, 1♀), USNM. Ecuador: Same data as holotype (1♂, 1♀), the latter accompanied by “Genitalia Slide ♀ by JAL.”

Diagnosis. *Habitus* (Fig. 9). This species superficially resembles *S. rasa* in coloration and maculation; it is smaller and the male bears all of the secondary sexual characters, including coremata, known to occur within *Schacontia* (Table 1). *Genitalia* (Figs 58–60). The male genitalia of *S. clotho* place it unambiguously within the *S. nyx* complex as opposed to with *S. themis* or *S. rasa*. Moreover the subcostal lobe of the valva is elongate.



Figures 36–43. Male, female genitalia. **36** *S. medalba* male, Brazil 107887 **37** *S. medalba* phallus, data as above **38** *S. medalba* female, Brazil, Castro, Parana, Collection Wm Schaus, Genitalia slide by MAS ♀ USNM 107,011 **39** *S. chanesalis* male, Guatemala USNM 107,891m, Cf. Fig. 22 **40** *S. chanesalis* phallus, data as above **41** *S. chanesalis* female, Guatemala, Quirigua Guat., Schaus and Barnes coll, Genitalia slide by DA ♀ USNM 107,892 **42** *S. umbra* male, Ecuador VOB 100504, Cf. Fig. 3 **43** *S. umbra* phallus, data as above.

Description. Male. (Fig. 9). Forewing length: 6.9–7.0 mm (n=3) (Female 6.8 mm). **Head** - Ocelli present; proboscis normal; frons of normal contour; labial palpi porrect, extending beyond clypeus. **Thorax** - Prothoracic collar and tegulae an admixture of brown and mouse-gray scales. Flattened hind tibial spur, specialized hind tibial scales, epipleural setae present, and dark patch amidst male hind tibial scales all present. Female with two pairs of hind tibial spurs (medial pair present); shallow concave metatarsal modification present. **Forewing.** More lanceolate than in other *Schacontia* species. More or less uniform mouse gray, with very light dusting of very pale gray in medial and postmedial areas; medial area more darkly shaded than basal area and postmedial areas; FW fringe brown; subterminal line unbroken. **Hindwing.** Nearly translucent; postmedial line absent; fringe pale yellowish; subterminal line unbroken. **Abdomen** - Scales arranged in two terminal black dorsal spots in males; elongate coremata on 4th abdominal segment (Fig. 34). **Tympanal organs** (Fig. 29). As for *ysticalis-themis* group, *vide supra*. **Male genitalia** (Figs 58, 59) - Uncus trefoil-shaped tip reduced to a small, more or less rhomboid nipple; lateral edges of uncus simple, undifferentiated; juxta broadly V-shaped, comparable in shape to an avian furcula, arms not robust; valvae complex, intrasaccular flange at latero-ventral edge and sclerotized to form a trigger-shaped process; robust, spine-like setae at base of valva; saccular margin rounded at mid-point; prominent setal comb at ventro-medial margin of valva; ventro-marginal setae concentrated at saccular ulna; costal bar diverges from subcostal lobe towards base of costa (isolation of costa >75% along length, character 49); valva with pronounced, elongate secondary outer lobe or process below costa; recurved/decumbent setal plume associated with terminus of costa; sharply hooked setal cluster prominent. Phallus moderately sclerotized; vesica with two large cornuti. **Female genitalia** (Fig. 60) - Papillae anales separate, not swollen; antrum/ductus bursae elongate (not chalice-like), faintly sclerotized posterior to colliculum, separated from colliculum by a sharp constriction; colliculum a short ring (not an elongate collar), with faintly sclerotized band, immediately posterior to corpus bursae; corpus more or less globular, surface complex; ductus seminalis originates at posterior end of corpus bursae.

Immature stages. Unknown.

Etymology. The specific epithet refers to the youngest of the three fates in Greek mythology, responsible for spinning the thread of human life, and is treated as a noun in apposition.

Biology. Unknown. Adults December.

Distribution. Southern Ecuador.

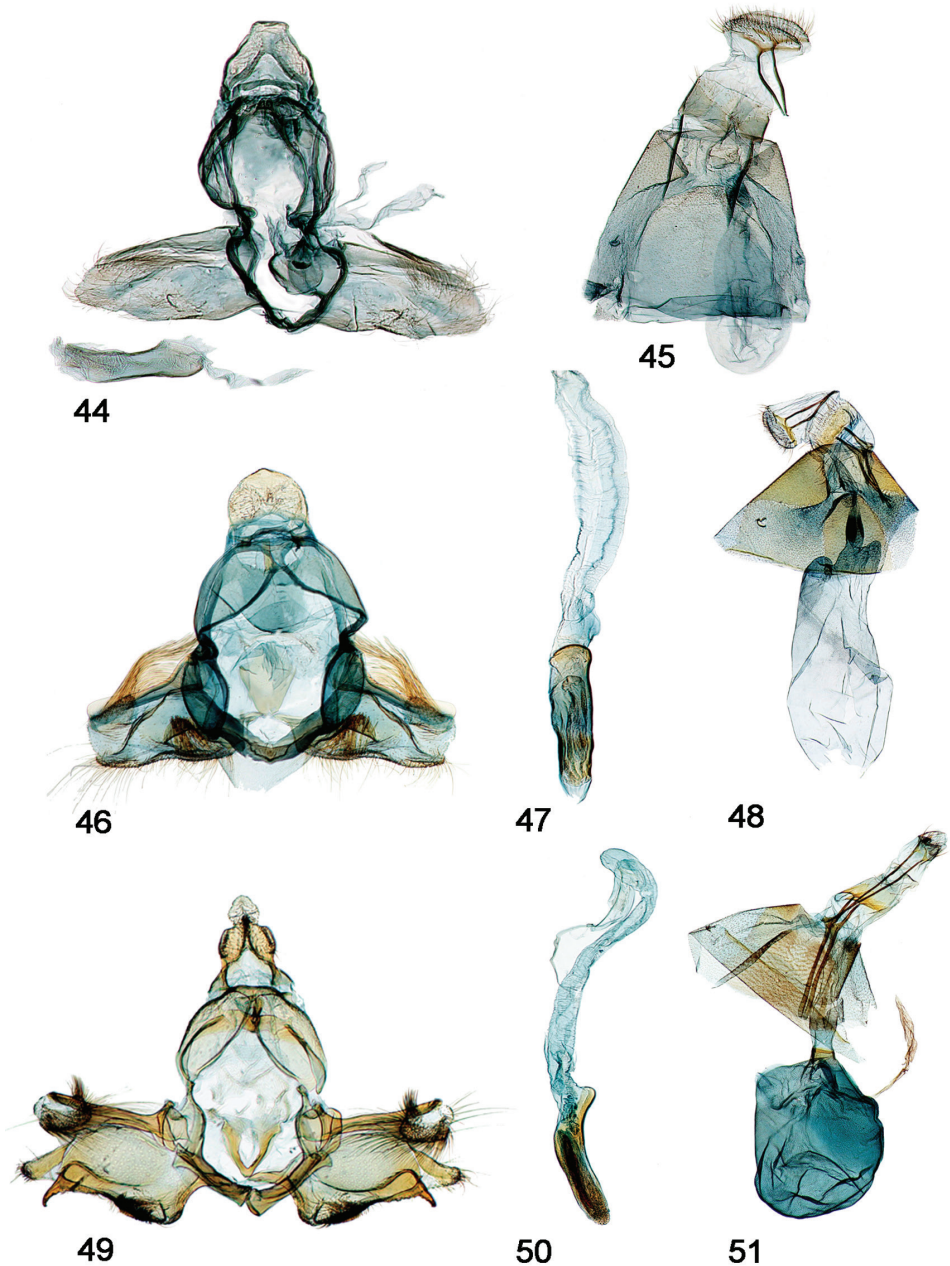
***Schacontia lachesis* Solis & Goldstein, sp. n.**

urn:lsid:zoobank.org:act:886A4F51-EA8A-4D43-9C58-FA7A1743BA1A

http://species-id.net/wiki/Schacontia_lachesis

Figs 10, 11, 30, 35, 61–63

Material examined. Type material. Holotype (♂, USNM) (Fig. 10): **Brazil:** Col. Becker 55439, Brasil: RJ Arrai al do Cabo, 50 m, 29.i.1985, V.O. Becker col. Paratypes

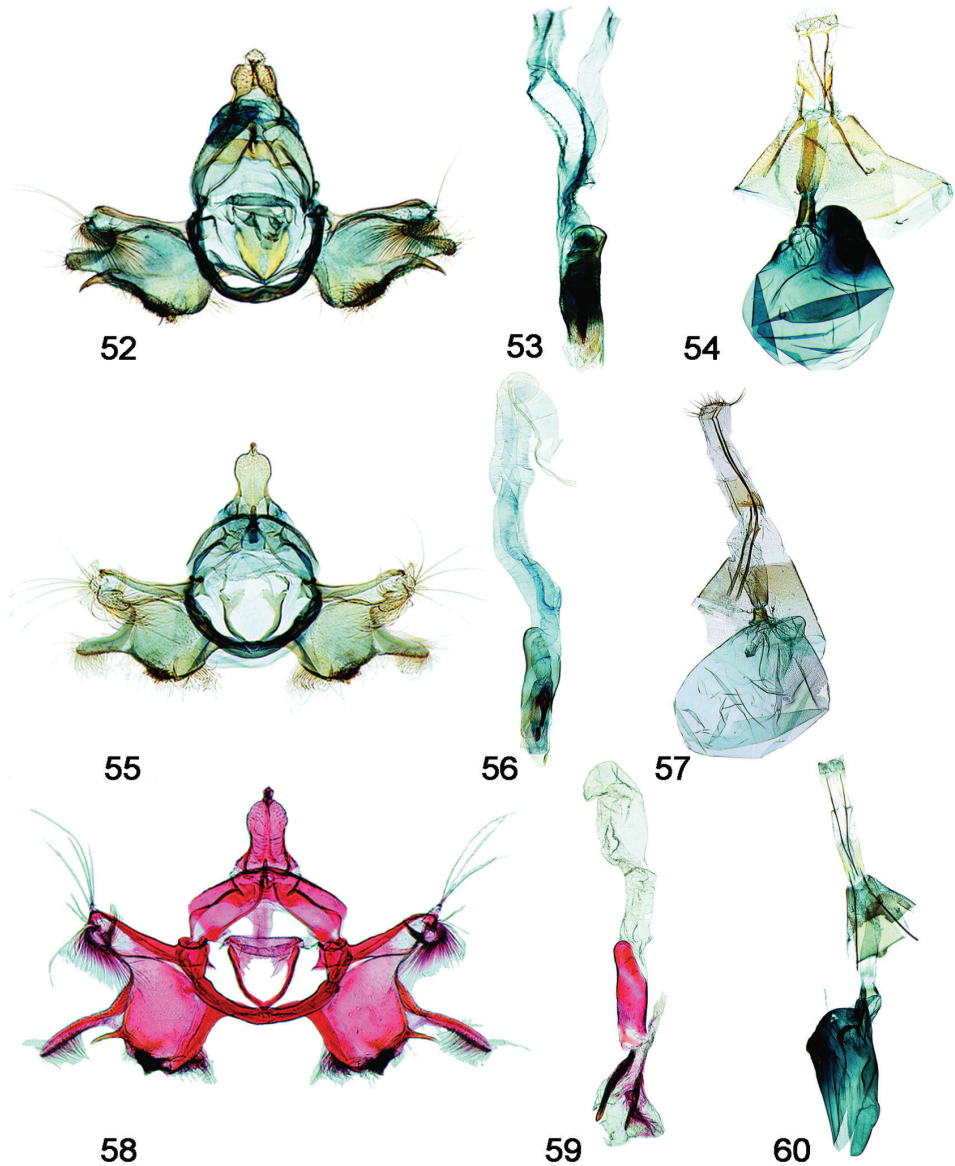


Figures 44–51. Male, female genitalia. **44** *S. speciosa* male, paratype, Brasil, VOB 65271, Cf. Fig. 4 zzz**45** Female, Brasil: BA Jequié, 600–750m; Col. Becker 105714 **46** *S. ysticalis* (a) male, Venezuela: Guarico, Huato Masaguaral , 45km S Calabozo 8.57°N, 67.58°W, Galry For#4 75m, 13-16May1988, uv light M. Epstein R. Blahnik; green label Genitalic Slide by DA ♂ USNM 108,100 **47** Phallus, data as above **48** Female, Venezuela Guarico, Huato Masaguaral , 45km S Calabozo Slide by DA ♀ USNM 107,896 **49** *S. themis* (a) male, Costa Rica, Cf. Fig. 20 **50** Phallus, data as above **51** Female, Costa Rica, Guanacaste: Santa Rosa Nat'l Pk. 97 SRNP 2354.2 JAL 2 May 2003 #6.

14 males, 11 females, USNM: **Brazil:** Same data as holotype (1♂, 1♀); Col. Becker 91635, Brasil: CE Pacatuba, 250 m, 6. iv. 1994, V.O. Becker Col. (1♂); Col. Becker 111257, Brasil: MT 60 km, S Poconé, 1–7.xii.1997, V.O. Becker Col. (1♀); Col. Becker 88540, Brasil: RO Cacaúlândia, 140 m, 15–18.x.1993, V. O. Becker Col. (1♀); Col. Becker 93888, Brasil: MT Chapada dos Guimarães, 800 m, 20.xi.1994, V. O. Becker Col. (1♀); Col. Becker 105713, Brasil: BA Jequié, 600–750 m, 11–22. xi.1995, V.O. Becker Col. (4♂, 1 ♀ and a disassociated male genitalic slide); Col. Becker 54553 Brasil: RJ Maricá, 5 m, 12–15.i.1995, V.O. Becker Col. (3♂, incl. 1 male w/white tag “Genitalia 1259”, 1♀). **Bolivia:** Santa Cruz, Puerto Suarez, 150 m, Nov 1908, J. Steinbach, CMNH Acc. 3758 (3♂, 1 abd. detached, prob. ♀); Santa Cruz, Provincia del Sara, 350 m, October 1911, Jose Steinbach, CMNH Acc. 5038 (2♀); Santa Cruz, Provincia del Sara, 350 m, Dec 1912, Jose Steinbach, CMNH Acc. 5038 (1♀); Santa Cruz, Puerto Suarez, 150 m, Dec 1908, J. Steinbach, CMNH Acc. 3758 (2♂, 1♀, dissection).

Diagnosis. *Habitus* (Figs 10–11). A polymorphic species, some specimens resembling *S. rasa* and *S. clotho* in showing little to no ground color contrast between the variably mouse-gray or straw-colored medial area and the rest of the forewing; other specimens display a sharper contrast, with the medial area primarily gray and the antemedial and postmedial areas straw colored, very similar to some specimens of *S. atropos* (below). Like most members of the genus (other than *S. rasa*; Table 1), *S. lachesis* males bear specialized hind tibial scales, but like *S. nyx* some specimens lack the dark patch embedded within them. *Genitalia* (Figs 61–63). Like those of *S. themis*, *S. rasa*, and *S. atropos*, male genitalia of *S. lachesis* have the uncus with raised or swollen edges, but do not share the other synapomorphies of the *S. themis-rasa* pair and strongly resemble other members of the *S. nyx* complex in bearing more elongate subcostal processes and ornate costae. Males of *S. lachesis* are distinguished from those of *S. atropos* (below), which they most closely resemble, by a combination of short coremata (Fig. 35), angled as opposed to rounded saccular bend (ulna), absence of a ventro-medial setal comb, and a more even distribution of ventro-marginal setae (Table 1).

Description. (Figs 10, 11). Male. Forewing length: 5.0–7.5 mm. **Head** - Ocelli present; proboscis normal; frons of normal convex contour; labial palpi porrect, extending beyond clypeus. **Thorax** - Flattened hind tibial spur, specialized hind tibial scales, and epipleural setae present; female with two pair of hind tibial spurs (medial pair present); shallow concave metatarsal modification. *Forewing*. Prothoracic scaling tan gray, straw or yellowish. Forewing coloration equally variable, medial area polymorphic, exhibiting a range of contrast not known from other *Schacontia*, ranging from light to dark brown in both sexes, dusted with white; basal and postmedial areas straw colored; antemedial and postmedial lines jagged; orbicular spot faint but apparent; fringe scales darker at base; subterminal line unbroken. *Hindwing*. Postmedial line absent; fringe scales darker at base; subterminal line unbroken. **Abdomen** - Coremata on 4th abdominal segment (Fig. 35); scales arranged in two terminal black dorsal spots in males. *Tympanal organs* (Figs 30, 31). As for *yisticalis-themis* group, *vide supra*. **Male genitalia** (Figs 61, 62) - Teguminal sulcus short, such that anterior margin of tegumen appears deeply invaginate, two oblong teguminal lobes joined obliquely; lateral edges of uncus swollen, appearing reinforced; un-



Figures 52–60. Male, female genitalia. **52** *S. rasa* (a) male, Mexico; f. Fig. 21 **53** Phallus, data as above **54** Female, Mexico JAL 19 (same data) **55** *S. nyx* (a) male, Venezuela, Cf. Fig. 22 **56** Phallus, data as above **57** Female, Venezuela; Cf. Fig. 8 **58** *S. clotho* (a) male, HOLOTYPE, Ecuador; Cf. Fig. 9 **59** Phallus, data as above **60** Female, Ecuador: Loja, Catamayo, 1300 m, 20 XII 1992, V.O. Becker JAL 5 May 2003 #24.

cus trefoil-shaped tip reduced to a small, more or less rhomboid nipple; juxta U-shaped, tapered ventrally; valvae complex, intrasaccular flange transposed towards latero-ventral edge and sclerotized to form a trigger-shaped process; robust, spine-like setae at base of valva; saccular margin sharply angled at saccular mid-point; ventro-marginal setae distrib-

uted along length of outer margin of sacculus; valva with pronounced, elongate secondary outer lobe or process below costa; fleshy setose lobe and recurved/decumbent setal plume associated with terminus of costa; sharply hooked setal cluster prominent. Phallus moderately sclerotized; vesica with two large cornuti. **Female genitalia** (Fig. 63) - Papillae anales separate, unswollen; colliculum present, short, sclerotized, immediately posterior to corpus bursae, with narrow sclerotized band around center, sometimes separated from bursa by a sharp constriction; ductus bursae present, conspicuously sclerotized ventrally, entering corpus bursae dorsally; appendix bursae ventral, superficially complex; ductus seminalis attached at posterior end of ventral corpular out-pocketing.

Immature stages. Unknown.

Etymology. In Greek mythology, *Lachesis* is the middle sister of the three fates, the personification of destiny responsible for measuring the duration of human life. The specific epithet is treated as a noun in apposition.

Biology. Unknown. Adults in Brazil active January, April, November, December; adults in Bolivia active October–December.

Distribution. Central Brazil (Rondonia east to Bahia, Ceara and Rio de Janeiro), Bolivia (Santa Cruz).

***Schacontia atropos* Solis & Goldstein, sp. n.**

urn:lsid:zoobank.org:act:D7D8AE98-0E23-4C74-8813-79F0B16CBF62

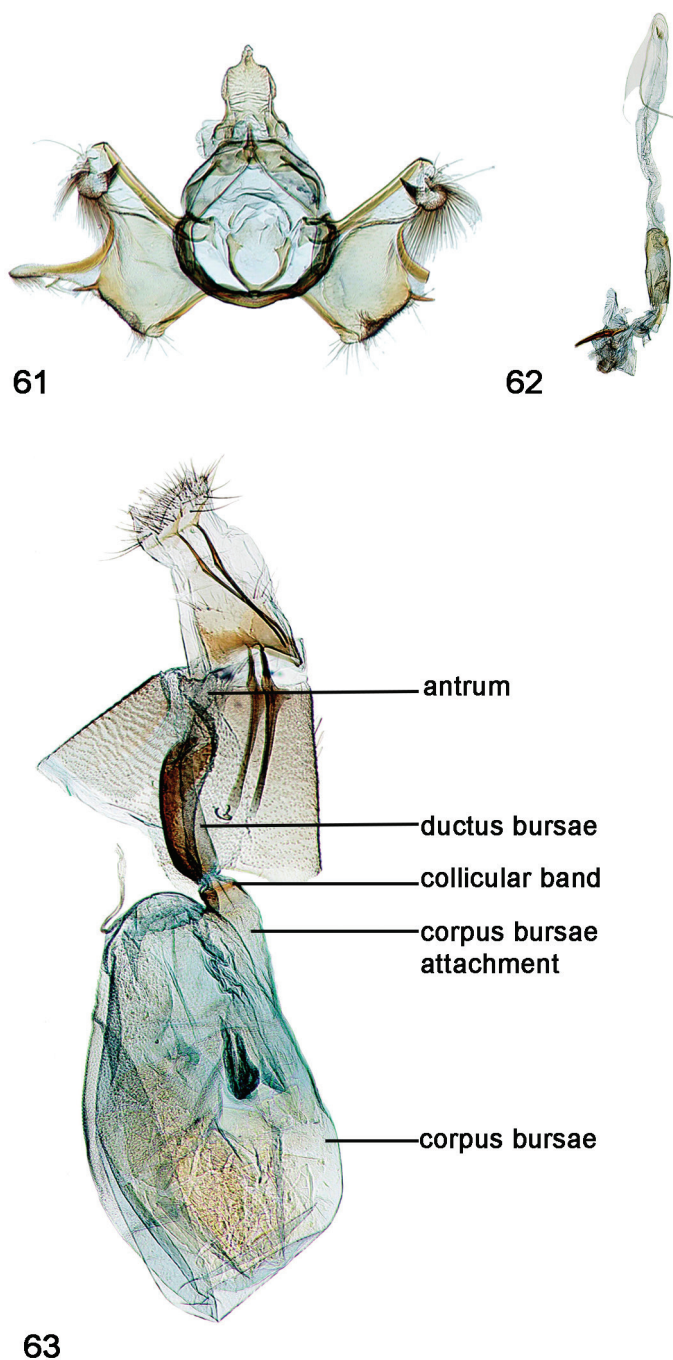
http://species-id.net/wiki/Schacontia_atropos

Figs 12, 32, 64, 65

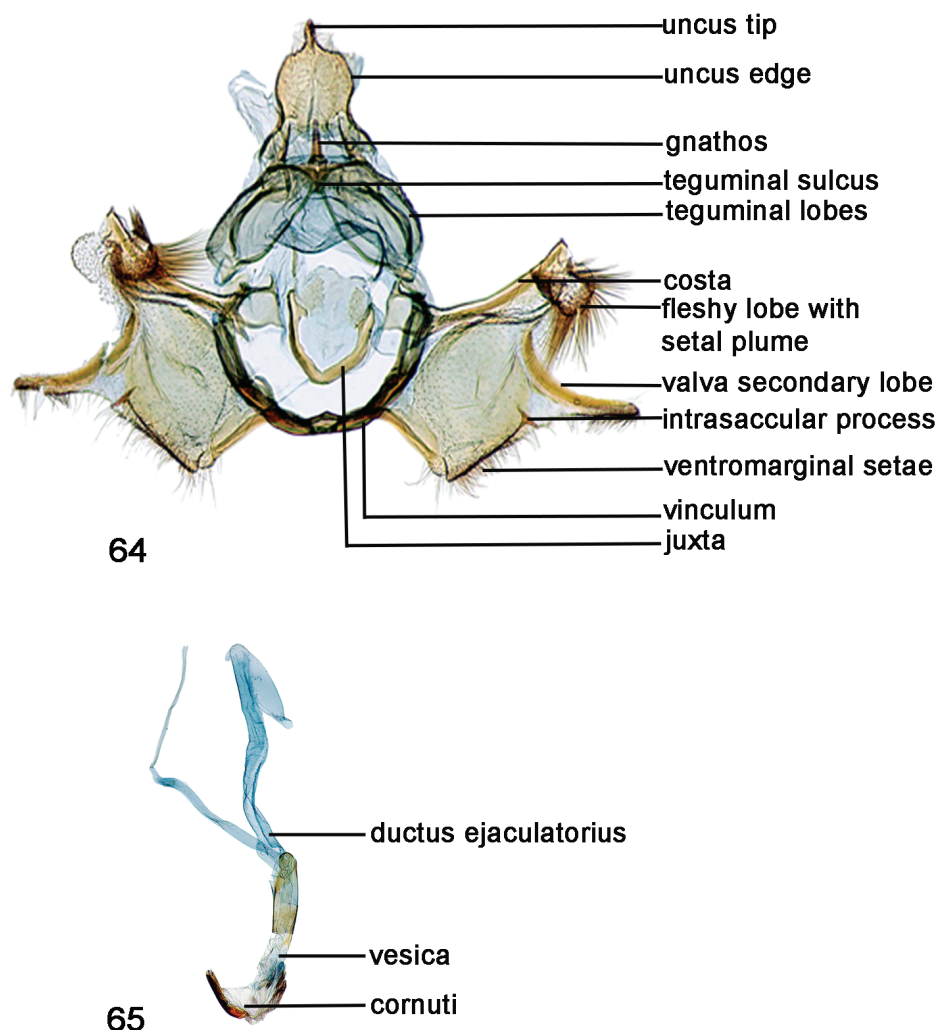
Material examined. Type material. Holotype (♂, USNM) (Fig. 12): **Venezuela:** San Estaban Carabobo, Venez., Dec. 1–20 1939, Pablo J. Anduse. Paratypes (2♂), USNM. **Venezuela:** Same data as holotype (1♂); Lara, 4 km NW of La Pastora, 2–3 III 1978 riparian forest blacklight, J.B. Heppner (1♂).

Diagnosis. *Habitus* (Fig. 12). Overlaps in appearance with *S. lachesis*, but males lack all secondary sexual features; hindwing uniformly pale throughout. *Genitalia* (Figs 64, 65). Male genitalic features place it squarely in the *nyx* complex, from whose other member species it may be distinguished by the combination of the angled ventral edge of the saccus (ulna) and unmodified edges of the uncus.

Description. (Fig. 12). Male. Forewing length: 5.4–5.5 mm (n = 2). **Head** - Ocelli present; proboscis normal; frons of normal contour; labial palpi porrect, extending beyond clypeus. **Thorax** - Prothoracic scaling light straw yellow. Female with two pair of hind tibial spurs (medial pair present). *Forewing*. Ground color straw yellow; medial area brown gray, heavily suffused with white scales, orbicular spot present. *Hindwing*. Pale overall, nearly translucent, not more darkly tinged subterminally as in other members of *S. nyx* complex; postmedial line faint if present. **Abdomen** - Scales arranged in two terminal black dorsal spots in males. *Tympanal organs* (Fig. 32). As for *ysticalis-themis* group, *vide supra*. **Male genitalia** (Figs 64, 65) - Teguminal sulcus



Figures 61–63. Male, female genitalia. **61** *S. lachesis* (a) male, HOLOTYPE, Bolivia, CMNH; Cf. Fig. 11 **62** Phallus, data as above **63** Female, Brasil: MT 60 km S Pocone. Pantanal 100m 1-7.xii. 1997; V.O. Becker Col.; Col Becker 111257.



Figures 64–65. 64 *S. atropos*, male, Venezuela; Cf. Fig. 12 65 Phallus, data as above.

short, such that anterior margin of tegumen appears deeply invaginate, the two oblong teguminal lobes joined obliquely; uncus trefoil-shaped tip reduced to a small, more or less rhomboid nipple; juxta U-shaped, tapered ventrally; valvae complex, intrasaccular flange transposed towards latero-ventral edge and sclerotized to form a trigger-shaped process; robust, spine-like setae at base of valva; saccular margin sharply angled at saccular mid-point; ventro-marginal setae distributed along length of outer margin of sacculus; valva with pronounced, elongate secondary outer lobe or process below costa; fleshy setose lobe and recurved/decumbent setal plume associated with terminus of costa; sharply hooked setal cluster prominent. Phallus moderately sclerotized; vesica with two large cornuti. **Female genitalia** - Unknown.

Immature stages. Unknown.

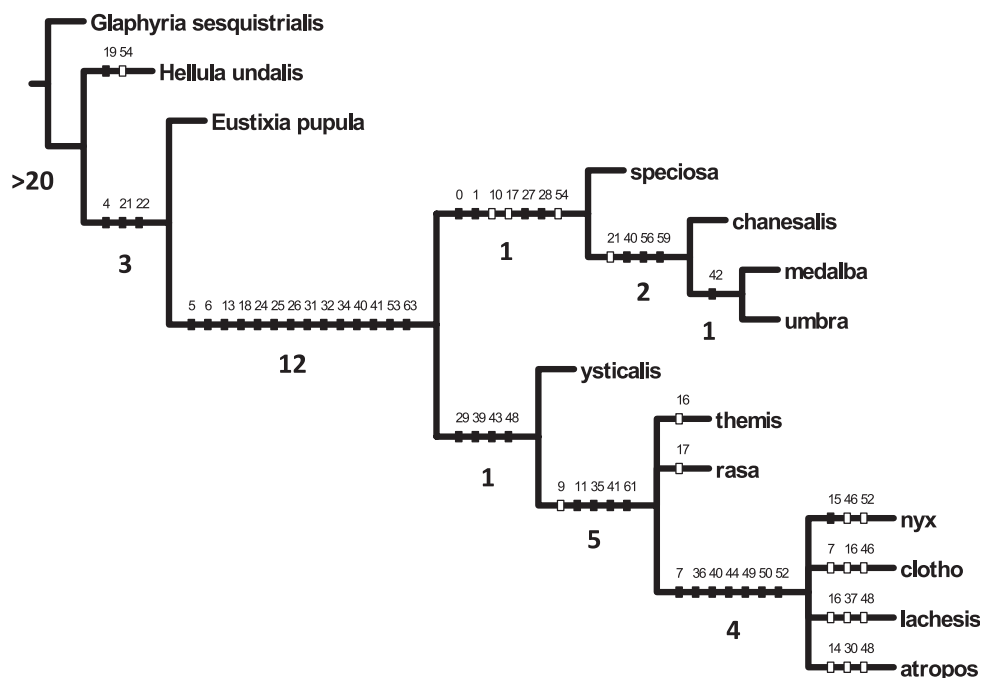


Figure 66. Strict consensus (L=108, CI=67, RI=81) of eight most parsimonious trees (L=102, CI=71, RI=84) obtained from a cladistic analysis of morphological data with unambiguous character state transformations indicated. Numbered hatch marks on nodes refer to characters undergoing forward changes (solid=unreversed; hollow=reversed). Bremer values are indicated below relevant branches.

Etymology. The specific epithet refers to the third of the three fates. Treated as a noun in apposition.

Biology. Unknown.

Distribution. Northern Venezuela.

Remarks. Given the phenomenon described by Ohno (2000) it is well within the realm of possibility that this species represents a synonym of *S. lachesis*.

Discussion

The moths treated in this paper comprise a range of geographically widespread and potentially localized cryptic species united by a range of synapomorphies. It is not possible to infer an unambiguous center of origin for *Schacontia*; members of both the typical *medalba* group and the *ysticalis*-*themis* group are distributed from Mexico to South America. While we note at least three trans-isthmian species (*S. chanesalis*, *S. ysticalis*, and *S. themis*), several species - including the entire *S. nyx* complex - are restricted to South America, while *Schacontia rasa* is known only from Mexico and the Caribbean. Among the more intriguing features of *Schacontia* that warrant further study is their

gall-forming habits in association with capparaceous plants, and the enormous variation in size, which may be a function of indeterminate instar number.

There likely exist undiscovered *Schacontia* species, cryptic and otherwise. *Schacontia chanesalis* in particular may represent a complex of Mayrian species that are difficult to diagnose without more extensive molecular data. However, available data are such that obvious breaks in the continuum of variation are not obvious, and rather than allowing the weakly articulated epithet *S. replica* to persist as valid we have elected to synonymize it, along with *S. pfeifferi*. Although its presumptive range differs geographically from that of *S. chanesalis*, we saw little point in retaining *S. pfeifferi* given a lack of apparent distinguishing characters. Although its presumptive range differs geographically from that of *S. chanesalis*, we saw little point in retaining *S. pfeifferi* given a lack of apparent distinguishing characters. We took a less conservative approach within the *S. nyx* complex, nominating species on the basis of characters we suspect may be more labile than our limited collection of specimens suggests. We attribute the lack of phylogenetic decisiveness, particularly in the *nyx* complex, to homoplasy among characters associated with the male secondary sexual features.

By far the richest source of phylogenetic signal in our matrix are the male genitalia, accounting for almost half the characters included in our analysis. This is not unusual for species-level studies of Lepidoptera (or insects generally), and there may be a growing consensus that despite their likely being subjected to sexual selection and thus potentially evolving quite rapidly (Fisherian runaway), male genitalic characters nonetheless contain valuable information at multiple hierarchic levels (Simonsen and Roe 2009; Song and Bucheli 2010), a situation analogous to that of third positions or transitions in molecular phylogenetics (e.g. Källersjö et al. 1998). A noteworthy exception is the work of Solis and Maes (2002), who concluded that male genitalic characters were not especially useful at the subfamily level within the Crambidae.

In contrast, it is of particular relevance to the taxonomy of *Schacontia* that relatively little complex variation is observed in the female genitalia, particularly given that four of the five species described prior to this work - two of which are synonymized herein - have female holotypes.

Solis et al. (2009) discussed the roles of secondary sexual structures, including scent-producing structures and their associated modified scales (reviewed by Hallberg and Poppy 2003), in lepidopteran diversification broadly and in Pyraloidea specifically. They highlighted the historical differences of opinion between taxonomists who discounted the importance of such structures and those who viewed them as invaluable in lepidopteran classification (e.g., Janse 1931) and, following Solis (1993) and Simonsen and Roe (2009), in phylogenetic reconstruction in spite of empirical demonstrations of homoplasy. Based on the present work, male secondary sexual characters were among the more homoplastic we analyzed, at least insofar as their removal contributes resolution to the phylogenetic hypothesis generated. The intraspecific lability of characters such as hind tibial hair pencils or the abdominal coremata remains to be studied in detail. Other pyraloid examples of this kind have been discussed by Solis et al. (2009), and Hayden (2010, 2011) has since added examples of independently derived

and readily reversed structures from the odontine crambids: some species of *Cliniodes* bearing tufts on the prothoracic femora and 7th sternite have sister species in which these structures are reduced or absent. In the genus *Dicepolia*, the two most commonly encountered species share a prothoracic tibial tuft but are otherwise unrelated; meanwhile an S7 tuft is an unreversed synapomorphy of Neotropical members of the genus.

Apropos of species diagnosis, we recall that as compelling as are the raw diversity of secondary sexual characters and the demonstrations of their phylogenetic lability, there have been suggestions that the expression of such structures may be underlain by rather simple genetic systems. Following Ohno's (2000) observation of within-brood polymorphism with respect to mid-tibial tufts in *Ostrinia* (Crambidae), Frolov et al. (2007) suggested that this polymorphism may depend on two di-allelic loci unrelated to reproductive isolation. Although Frolov et al. speculated somewhat with respect to the putative roles of such structures in sympatric speciation, it is clear that even seemingly complex structures may be subject to the simple rules of Mendelian inheritance, character fixation and extinction. If such is the case, then even "important" characters such those involved in courtship, lekking, or mate recognition might be polymorphic, locally fixed, or even frequency-dependent, and might not necessarily serve to diagnose species. Apparent polymorphism in features such as tibial hair pencils (as in *S. lachesis*) or abdominal coremata (as in *S. themis*) speak to the possibility that species pairs such as *S. lachesis-atropos* or *S. themis-rasa* might be conspecific. Our limited DNA barcode data suggest otherwise for the latter species pair, but can not corroborate the diagnostic power of the morphological characters themselves without more extensive sampling.

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References

- Amsel HG (1956) Microlepidoptera Venezuela I. Boletín de Entomología Venezolana 10(1/2): 1–337. [110 pls]
- Benson DA, Karsch-Mizrachi I, Clark K, Lipman DJ, Ostell J, Sayers EW (2012) Nucleic Acids Research 40. doi: 10.1093/nar/gkr1202
- Borror DJ, Triplehorn CA, Johnson NF (1989) An Introduction to the Study of Insects. Sixth Edition. Holt, Rinehart and Wilson Inc, Orlando, 875 pp.
- Bremer K (1988) The limites of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42(4): 795–803.
- Clarke JFG (1941) The preparation of the slides of the genitalia of Lepidoptera. Bulletin of the Brooklyn Entomological Society 36: 149–161.
- Cuignet M, Windsor D, Reardon J, Hance T (2008). The diversity and specificity of parasitoids attacking Neotropical tortoise beetles (Chrysomelidae, Cassidinae). In: Jolivet P, Santiago-Blay J, Schmitt M (Eds) Research on Chrysomelidae, 1. Brill Publishers, Leiden, 345–367.
- Druce H (1899) Biologia Centrali-americana. Insecta. Lepidoptera – Heterocera. Vol. 2. 622 pp.
- Dyar HG (1914) Descriptions of New Species and Genera of Lepidoptera from Mexico. Proceedings United States National Museum 47(2054): 365–409.
- Dyar HG (1925) Some new American moths (Lepidoptera). Insecutor Inscitiae Menstruus 13(1/3): 1–19.
- Ferguson DC (1992) *Franclemontia interrogans* (Walker), a new genus for an old species (Lepidoptera: Noctuidae: Amphipyridae). Journal of the New York Entomological Society 100(2): 257–266.
- Frolov AN, Bourguet D, Ponsaard S (2007) Reconsidering the taxonomy of several Ostrinia species in the light of reproductive isolation: a tale for Ernst Mayr. Biological Journal of the Linnean Society 91: 49–72.
- Goldstein PZ, DeSalle R (2011) Integrating DNA barcode data and taxonomic practice: Determination, discovery, and description. Bioessays 33(2): 135–147.
- Goloboff PA, Farris JS, Nixon KC (2008) TNT, a free program for phylogenetic analysis. Cladistics 24(5): 774–786.
- Hallberg E, Poppy G (2003) Exocrine glands: chemical communication and chemical defense. In: Kristensen NP (Ed.) Lepidoptera, Moths and Butterflies. Vol. 2. Berlin: Walter de Gruyter, 361–375.
- Hayden JE (2010) Phylogeny, distribution, and description of a Caribbean species of *Dicepolia* (Lepidoptera: Crambidae). Tropical Lepidoptera Research 20(2): 77–84.

- Hayden JE (2011) Revision of *Cliniodes* Guenee (Lepidoptera: Crambidae: Odontiinae). *Annals of Carnegie Museum* 79(4): 231–347.
- Hrcek J, Miller SE, Quicke DLJ and Smith MA (2011) Molecular detection of trophic links in a complex insect host-parasitoid food web. *Molecular Ecology Resources* 11: 786–794.
- Janse AJT (1931) Contribution towards the study of the genera of the Epipaschiinae. *Transactions of the Entomology Society London* 79: 439–492.
- Källersjö M, Farris JS, Chase MW, Bremer B, Fay MF, Humphries CJ, Petersen G, Seberg O, Bremer K (1998) Simultaneous parsimony jackknife analysis of 2538 *rbcL* DNA sequences reveals support for major clades of green plants, land plants, seed plants and flowering plants. *Plant Systematics and Evolution* 213: 259–287.
- Luquet GC, Minet J (1982) Découverte dans le Vaucluse d'une nouvelle espèce de Pyrale et désignation de l'espèce-type du genre *Krombia* Chrétien (Lepidoptera, Crambidae, Cybalomiinae). *Alexanor* 12(7): 317–326.
- Klots AB (1970) Lepidoptera. In: Tuxen SL (Ed.) *Taxonomist's glossary of genitalia in insects*. Munksgaard, Copenhagen, 115–130.
- Maes KVN (1985) A comparative study of the abdominal tympanal organs in Pyralidae (Lepidoptera). I. Description, terminology, preparation technique. *Nota Lepidopterologica* 8: 341–350.
- Maes KVN (1995) A comparative morphological study of the adult Crambidae (Lepidoptera: Pyraloidea). *Bulletin et Annales de la Societe Royale Belge d'Entomologie* 131: 383–434.
- Mally R, Nuss M (2011) Molecular and morphological phylogeny of European *Udea* moths (Insecta: Lepidoptera: Pyraloidea). *Arthropod Systematics & Phylogeny* 69(1): 55–71.
- Minet J (1985) Etude morphologie et phylogenetique des organes tympaniques des Pyraloidea 2 – Pyralidae, Crambidae, premiere partie (Lepidoptera: Glossata). *Annals de la Societe Entomologique de France* 21: 69–86.
- Mithen R, Marquez J (2010) Glucosinolate biochemical diversity and innovation in the Brassicales. *Phytochemistry* 71(17/18): 2074–2086.
- Munroe E (1958) Hampson's Schoenobiinae (Lepidoptera: Pyralidae). *Proceedings of the Tenth International Congress of Entomology* 1: 301–302.
- Munroe E (1995) Cybalomiinae. In: Heppner JB (Ed.) *Checklist: Atlas of Neotropical Lepidoptera*. Association for Neotropical Lepidoptera. Gainesville, Florida, 42.
- Nixon KC (1999–2002) WinClada v. 1.00.08 Published by the author, Ithaca, New York. Available from <http://www.cladistics.com/wincDownload.htm>
- Ohno S (2000) Emergence of two nominal species, *Ostrinia scapularis* and *O. orientalis*, from a single brood (Lepidoptera: Crambidae). *Entomological Science* 3(4): 635–637.
- Phillips RE, Solis MA (1996) *Neurophyseta* (Lepidoptera: Crambidae) de Costa Rica. *Revista de Biologia. Tropical* 44: 693–717.
- Schaus W (1904) New species of American Heterocera. *Transactions American Entomological Society* 30: 135–178.
- Simonsen TJ, Roe AD (2009) Phylogenetic utility and comparative morphology of the composite scale brushes in male phycitine moths (Lepidoptera, Pyralidae). *Zoologischer Anzeiger* 248: 119–136.

- Solis MA (1993) A phylogenetic analysis and reclassification of the genera of the *Pococera* complex. *Journal of the New York Entomological Society* 101(1): 1–83.
- Solis, MA (2009) Transfer of all Western Hemisphere Cybalomiinae to other subfamilies (Crambidae: Pyraloidea: Lepidoptera): *Elusia* Schaus, *Dichochroma* Forbes, *Schacontia* Dyar, *Cybalomia extorris* Warren, and *C. lojanalis* (Dognin). *Proceedings of the Entomological Society of Washington* 111(2): 493–504.
- Solis MA, Maes KVN (2002) Preliminary phylogenetic analysis of the subfamilies of Crambidae (Pyraloidea Lepidoptera). *Belgian Journal Of Entomology* 4: 53–95.
- Solis MA, Metz MA, Janzen DH (2009) Phylogenetic analysis of *Cosmopterosis* (Lepidoptera: Crambidae: Glaphyriinae) with discussions on male secondary sexual characters and larval feeding on *Capparis* (Capparaceae) in the Pyraloidea and Lepidoptera (Insecta). *Annals of the Entomological Society of America* 102(5): 766–784.
- Song H, Bucheli SR (2010) Comparison of phylogenetic signal between male genitalia and non-genitalic characters in insect systematics. *Cladistics* 26: 23–35.
- Wilson JJ (2012) DNA barcodes for insects. In: Kress WJ, Erickson DL (Eds) *DNA Barcodes: Methods and Protocols, Methods in Molecular Biology*, Vol. 858, 17–46.
- Wolcott GN (1950–1951) The insects of Puerto Rico. *Journal of Agriculture of the University of Puerto Rico* 32 (1/4): 1–975.
- Wooton RJ (1979) Function, homology and terminology in insect wings. *Systematic Entomology* 4: 81–93.
- Yoshiyasu Y (1985) A systematic study of the Nymphulinae and the Musotiminae of Japan (Lepidoptera: Pyralidae). *Scientific Report Kyoto Prefectural University, Agriculture* 37: 1–162.

Appendix I

Matrix

	0	10	20	30	40	50	60	
medalba	0011011-01	10110-0001	0001101000	011210-000	1110--010-	-0-10-00-0	-001	
chanesalis	0011011-01	10110-0001	0001101000	011210-000	1100--010-	-0-10-0100	-001	
umbra	0011011-01	10110-0-01	0001101000	011210-000	1110--010-	-0-?-0-----	---1	
speciosa	0022011-01	10110-0002	1102101000	011210-000	2100--000-	-1010-1101	0001	
ysticalis	1122011-11	00110-0102	1102101111	011110-001	21010-0120	0101101101	0011	
themis	1102011010	0101111102	1102101111	1111111111	22010-0120	0101111111	1111	
rasa	1102011010	01010-0002	1102101111	0111111111	22010-0120	0101111101	1111	
nyx	1102011110	0101100102	1102101111	1111110001	3201111121	1101111111	1111	
clotho	1102011010	0101111102	1102101111	1111110001	3201111121	1111111101	1111	
lachesis	1102011110	01011*1102	1102101111	1111110101	3201100111	1111111111	1111	
atropos	1102011110	01010-0-02	1102101111	0111110001	3201100111	111111-----	---1	
Glaphyria	1100100010	10000-0111	0010010110	000000-000	00?0--000-	-0-0111?-1	1010	
Hellula	1100100-01	00000-0110	0010010110	000000-000	00?0--000-	?0-00-10-1	1010	
Eustixia	1111000--1	00-00-0111	0101010110	000000-000	00?0--000-	-0-0101101	1000	

Descriptions of eleven Opatrini pupae (Coleoptera, Tenebrionidae) from China

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Abstract

The pupal stage of eleven Opatrini species occurring in the northern China are described and a key for their identification is provided. The species are *Scleropatrum horridum horridum* Reitter, *Gonocephalum reticulatum* Motschulsky, *Opatrum (Opatrum) subaratum* Faldermann, *Eumylada potanini* (Reitter), *E. punctifera* (Reitter), *Penthicus (Myladion) alashanicus* (Reichardt), *P. (Myladion) nojonicus* (Kaszab), *Myladina unguiculina* Reitter, *Melanesthes (Opatronesthes) rugipennis* Reitter, *M. (Melanesthes) maxima maxima* Ménétriers and *M. (Melanesthes) jintaiensis* Ren.

Keywords

Tenebrionidae, Opatrini, pupa, taxonomy, China

Introduction

Studies of immatures stages of the insect are needed and important due to the fact, that the results are useful for phylogenetic analysis of particular groups which has already been shown many times (e.g. Böving and Craighead 1931; Beutel and Friedrich 2005). However, taxonomic studies on immature stages of the family Tenebrionidae are rather sporadic and therefore our knowledge of such developmental stages is very limited. This especially holds true for tenebrionid pupae, descriptions of which are rather extremely rare. So this is the primary aim for the present study.

For the tenebrionid pupae, several workers have made their contributions (St-George 1924; Daggy 1946; Ho 1960, 1969; Abdulla 1964; Spilman 1966, 1969, 1979, 1984; Watt 1974; Wei et al. 1989; Ren and Ye 1990; Steiner 1995; Bouchard and Steiner 2004; Yu and Yang 2004; Cherney 2006; Gosik 2007; Dunford and Steiner 2007; Simões et al. 2009; Matthews et al. 2010; Purchart and Nabozhenko 2012), but a few involved the tribe Opatrini, including Ogloblin and Kolobova (1927), Wu and Gao (1978), Yu et al. (1993), Yu et al. (1999), Cherney (2005) and Cherney and Fedorenko (2006).

In this study, the pupal stage of eleven Opatrini species occurring in the northern China are described in detail based on the material at our disposal. The species are *Scleropatrum horridum horridum* Reitter, *Gonocephalum reticulatum* Motschulsky, *Opatrum* (*Opatrum*) *subaratum* Faldermann, *Eumylada potanini* (Reitter), *E. punctifera* (Reitter), *Penthicus* (*Myladion*) *alashanicus* (Reichardt), *P. (Myladion) nojonicus* (Kaszab), *Myladina unguiculina* Reitter, *Melanesthes* (*Opatronesthes*) *rugipennis* Reitter, *M. (Melanesthes) maxima maxima* Ménétriès and *M. (Melanesthes) jintaiensis* Ren. Each species is provided with photos of habitus, head, pronotum, lateral processes of abdominal tergites V and VII and urogomphi. Also, a key for their identification is provided. Besides, the diagnosis of tribe is summarized.

Materials and methods

The study was based on the examination of 26 pupal specimens of Opatrini, which were identified as 11 species belonging to 7 genera. All of them were obtained by breeding from adults in the lab. All pupae are preserved in the glycerine and alcohol solution (1: 20) and deposited in the School of Agriculture of Ningxia University, Yinchuan, China.

Terminology of morphological features followed that of Bouchard and Steiner (2004) and Gosik (2007). Abbreviations are used as follows: BL: body length (from the posterior border of abdominal tergite IX to head); PL: pronotal length (from anterior to posterior border); PW: pronotal width (from one lateral border to the other at the maximal point); MSL: mesonotal length (from anterior to posterior border); MTL: metanotal length (from anterior to posterior border); UL: urogomphus length (from the base to apex of urogomphus); BUL: distance between urogomphi (from one apex to the other of urogomphus).

The measurements and photographing were carried out under the Free Angle Observation System VHX-100 (Keyence international trade company limited, Japan). When more than one pupa for a taxon was used, the range of values is given. The figures of lateral processes of abdominal tergites in this study are photographed in dorsal view and with the head towards the right. Lateral processes of abdominal tergites I–VII each has 2 large setose tubercles along outer border, of which the anterior one is named as large setose tubercle I (Fig. 1: t), the posterior one as large setose tubercle II (Fig. 1: u).

Description

Pupal characteristics of Opatrini The body white to light yellow (light brown before emergence of imago). Head bent to pronotum (Fig. 1: 2). Anterior border of clypeus emarginated in middle (Fig. 1: 5). Dorsomeson distinct. Pronotal shape as that of adult. Mesonotum slightly convex in middle of posterior part (Fig. 1: 4). Elytral sheath shroud metathoracic wing sheath (Fig. 1: 1–3) completely or not (Fig. 1: 10–12, Fig. 3: 10–12). Apices of elytral sheath acute (Fig. 1: 2–3). Abdominal tergites I–VII each with a pair of lateral processes in middle of lateral borders. Lateral processes dorsoventrally flattened and lune platform in lateral view, with anterior and posterior borders strongly sclerotized and densely dentated (Fig. 1: 8–9), except weakly sclerotized at anterior borders of those of abdominal tergite I and posterior borders of VII (Fig. 1: 1, Fig. 1: 9). Abdominal tergites I–VI each with a pair of spiracles in front of lateral processes, the spiracles of abdominal tergites II–VI visible in lateral view. Posterior borders of abdominal tergites I–VI straight or broadly emarginated, VII–VIII broadly protuberant. Abdominal tergites I–VIII slightly narrowed posteriorly (Fig. 1: 1), IX with a pair of well-developed urogomphi (Fig. 1: 6–7).

Key to the known pupae of the tribe Opatrini from China

- 1 Posterior border of the pronotum bisinuate (Fig. 1: 4, 13; Fig. 2: 4, 13; Fig. 3: 4)..... **2**
- Posterior border of the pronotum broadly protuberant **6**
- 2 Urogomphi diverging from each other (Fig. 1: 6–7, 15–16; Fig. 2: 6–7) **3**
- Urogomphi parallel to each other (Fig. 2: 15–16; Fig. 3: 6–7) (*Eumylada* Reitter, 1889) **5**
- 3 Lateral borders of pronotum flattened and stretched laterally (Fig. 1: 13–14; Fig. 2: 4–5)..... **4**
- Lateral borders of pronotum unlike above (Fig. 1: 4–5) (*Scleropatrum* Reitter, 1887)..... ***Scleropatrum horridum horridum* Reitter, 1898**
- 4 Metathoracic wing sheath incompletely shrouded by elytral sheath (Fig. 1: 10–12) (*Gonocephalum* Solier, 1834) ***Gonocephalum reticulatum* Motschulsky, 1854**
- Metathoracic wing sheath completely shrouded by elytral sheath (Fig. 2: 1–3) (*Opatrum* Fabricius, 1775) ***Opatrum (Opatrum) subaratum* Faldermann, 1835**
- 5 Anterior border of pronotum broadly emarginated and the emargination straight in middle, posterior angles prominent (Fig. 2: 13) ***Eumylada potanini* (Reitter, 1889)**
- Anterior border of pronotum broadly emarginated and the emargination protuberant in middle, posterior angles not prominent (Fig. 3: 4) ***Eumylada punctifera* (Reitter, 1889)**

- 6 BUL longer than UL. (Fig. 3: 15–16; Fig. 4: 6–7) (*Penthicus* Faldermann, 1836).....7
- BUL shorter than UL.(Fig. 4: 15–16; Fig. 5: 6–7, 15–16; Fig. 6: 6–7).....8
- 7 Anterior border of pronotum broadly emarginated and the emargination distinctly protuberant in middle (Fig. 3: 13)
.....*Penthicus (Myladion) alashanicus* (Reichardt, 1936)
- Anterior border of pronotum broadly emarginated and the emargination straight in middle (Fig. 4: 4)
.....*Penthicus (Myladion) nojonicus* (Kaszab, 1968)
- 8 Pronotum nearly oval, with lateral borders broadly protuberant. (Fig. 5: 4, 13; Fig. 6: 4) (*Melanesthes* Lacordaire, 1859)9
- Pronotum subquadrate, with lateral borders nearly straight (Fig. 4: 13) (*Myladina* Reitter, 1889)*Myladina unguiculina* Reitter, 1889
- 9 Urogomphi parallel to and slightly separated from each other (Fig. 5: 15–16; Fig. 6: 6–7).....10
- Urogomphi diverging posteriorly and distinctly separated from each other (Fig. 5: 6–7)*Melanesthes (Opatronesthes) rugipennis* Reitter, 1889
- 10 Urogomphi with apices leaning against each other (Fig. 5: 15–16)
.....*Melanesthes (Melanesthes) maxima maxima* Ménétriers, 1854
- Urogomphi with apices slightly separated from each other (Fig. 6: 6–7)
.....*Melanesthes (Melanesthes) jintaiensis* Ren, 1992

(1) Genus *Scleropatrum* Reitter, 1887

Scleropatrum horridum horridum Reitter, 1898

http://species-id.net/wiki/Scleropatrum_horridum_horridum

Fig. 1: 1–9

Redescription. Male. Body covered with short setae on surface; the total number of setose tubercles and setae on vertex, mandibles, the last segment of maxillary palpus, pronotal borders and hypomeron about 40–50 and 40–48, respectively.

Head bent at right angle to pronotum. Labrum covered with short setae along anterior and lateral borders, anterior border straight. Oculus reniform.

Pronotum: transverse, widest near middle, with the anterior part distinctly narrowed and the posterior part slightly narrowed, anterior border broadly emarginated and the emargination slightly protuberant in middle, lateral borders broadly protuberant; posterior border of pronotum bisinuate (Fig. 1: 4); anterior angles acute, posterior angles nearly right-angled; disc flat, sparsely covered with setae, with short and narrow furrows.

Mesonotum slightly convex in middle of posterior part, posterior border protuberant. Posterior border of metanotum straight.

Elytral sheath striped and sparsely setose. Metathoracic wing sheath completely shrouded by elytral sheath (Fig. 1: 1–3).

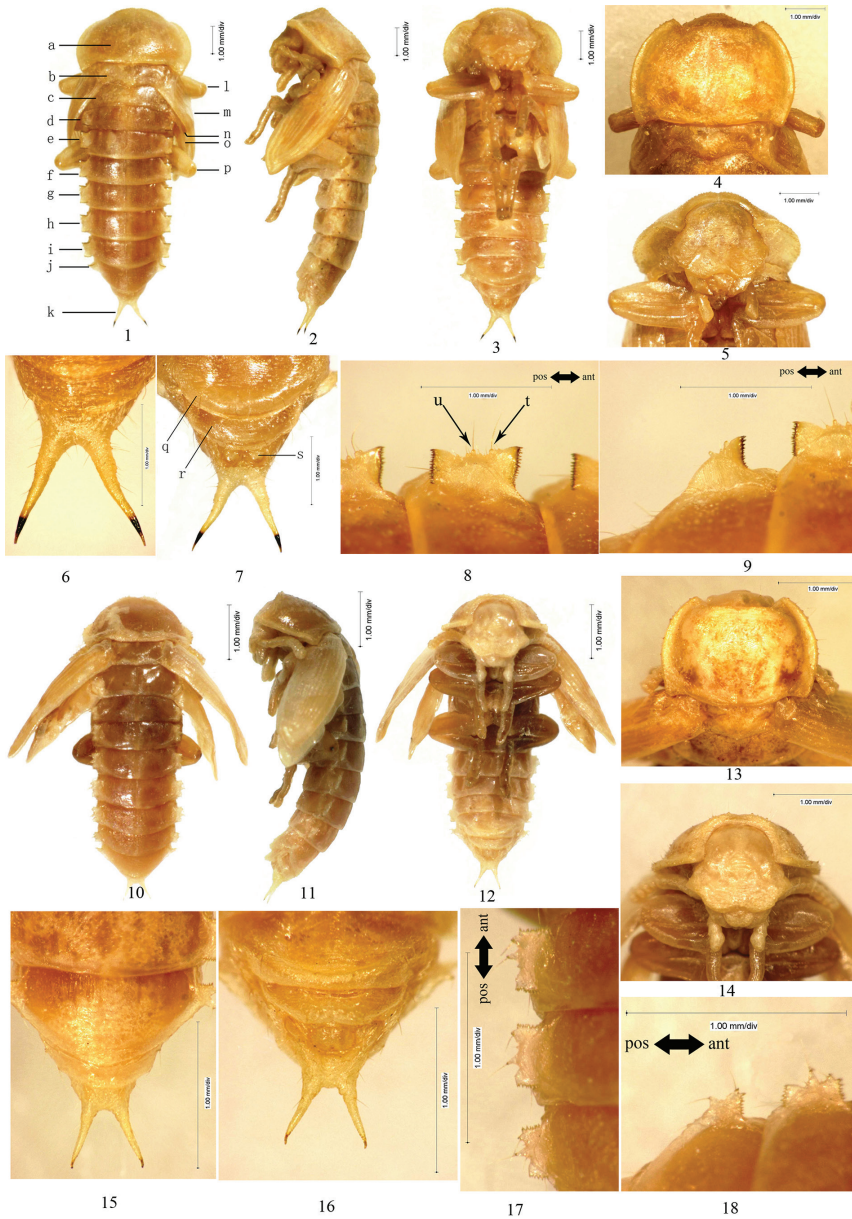


Figure 1. 1–9 *Scleropatrum horridum horridum* Reitter, 1898 1 Pupal habitus in dorsal view 2 Pupal habitus in lateral view 3 Pupal habitus in ventral view 4 Pronotum 5 Head 6 Urogomphi in dorsal view 7 Urogomphi in ventral view 8 Lateral process of abdominal tergite V 9 Lateral process of abdominal tergite VII 10–18 *Gonocephalum reticulatum* Motschulsky, 1854 10 Pupal habitus in dorsal view 11 Pupal habitus in lateral view 12 Pupal habitus in ventral view 13 Pronotum 14 Head 15 Urogomphi in dorsal view 16 Urogomphi in ventral view 17 Lateral process of abdominal tergite V 18 Lateral process of abdominal tergite VII. a Pronotum b Mesonotum c Metanotum d Abdominal segment I e Abdominal segment II f Abdominal segment III g Abdominal segment IV h Abdominal segment V i Abdominal segment VI j Abdominal segment VII k Urogomphi l Profoot m Elytral sheath n Mesofoot o Metathoracic wing sheath p Metafoot q Abdominal sternite VII r Abdominal sternite VIII s Gonotheca t large setose tubercle u large setose tubercle II.

Abdominal segments I–IX curved ventrally. The width of abdominal segments I–VII gradually narrowed posteriorly. Posterior border of abdominal sternite VIII emarginated in middle, each side of the emargination with a long seta. Posterior border of abdominal tergite IX emarginated in middle; urogomphi diverging from each other, BUL subequal to UL (Fig. 1: 6–7). Abdominal tergites I–VII each with a concaveness between its lateral process and lateral border in middle, lateral processes each with 2 large and several minute setose tubercles along outer border, of which 1–2 minute setose tubercles present in front of large setose tubercle I, 2–4 minute setose tubercles between large setose tubercles I and II, 3–4 minute setose tubercles behind large setose tubercle II (Fig. 1: 8–9). Outer borders of lateral processes of abdominal tergites I–VI straight. Spiracles of abdominal tergites I–VI oval, slightly convex.

Gonotheca without apophysis.

Female. Similar to the male, but posterior border of abdominal sternite VIII broadly protuberant; gonotheca with an obtusely rounded apophysis on the anterior part and a conical apophysis on the posterior part.

Measurements. BL: 10–13 mm; PL: 2.7–3.5 mm; PW: 3.8–4.4 mm; MSL: 0.8–0.9 mm; MTL: 0.6–0.8 mm; UL: 0.8–1.3 mm; BUL: 1.1–1.3 mm.

Material examined. adults collected information: 1 May 2002, Shutai Town, Haiyuan County, Ningxia, China; pupation date: 17 May 2003; adults collected information: 10 July 2001, Suyukou, Helan Mountain, Ningxia, China; pupation date: 28 June 2002.

Remarks. This species was included in the key of tenebrionid pupae by Yu et al. (1999), but only mentioned with some characters for identification. Here its morphological characters are described in detail and provided with the photos for the first time.

(2) Genus *Gonocephalum* Solier, 1834

Gonocephalum reticulatum Motschulsky

http://species-id.net/wiki/Gonocephalum_reticulatum

Fig. 1: 10–18

Redescription. Male. Body sparsely covered with short setae; the total number of setose tubercles and setae on pronotal borders, hypomeron, vertex, mandibles and the last segment of maxillary palpus about 14–18 and 22–28, respectively.

Head bent at acute angle to pronotum, each side with a longitudinal, shallow groove between clypeus and gena. Labrum without setae, anterior border rounded. Oculus oval.

Pronotum: transverse, widest near middle, with the anterior part distinctly narrowed and the posterior part slightly narrowed; anterior border broadly emarginated and the emargination straight in middle; lateral borders broadly protuberant, flattened and stretched laterally; posterior border of pronotum bisinuate (Fig. 1: 13); anterior angles acute, posterior angles obtuse; disc flat, without setae, with short and narrow furrows.

Mesonotum slightly convex in middle of posterior part, posterior border protuberant. Posterior border of metanotum straight.

Elytral sheath striped and sparsely setose. Metathoracic wing sheath incompletely shrouded by elytral sheath (Fig. 1: 10–12).

Abdominal segments III–IX curved ventrally. The width of abdominal segments I–VII subequal to each other. Posterior border of abdominal sternite VIII slightly emarginated in middle, each side of the emargination with a long seta. Posterior border of abdominal tergite IX emarginated in middle; urogomphi diverging from each other, BUL subequal to UL (Fig. 1: 15–16). Abdominal tergites I–VII each with a concaveness between its lateral process and lateral border in middle, lateral processes each with 2 equally large and several minute setose tubercles along outer border, of which no minute setose tubercle presents in front of large setose tubercles I, 1 minute setose tubercle between large setose tubercles I and II and behind II, respectively (Fig. 1: 17–18). Outer borders of lateral processes of abdominal tergites I–VI straight. Spiracles of abdominal tergites I–VI nearly rounded, slightly convex.

Gonotheca without apophysis.

Female. Similar to the male, but posterior border of abdominal sternite VIII broadly protuberant; gonotheca without apophysis on the anterior part but with a conical apophysis on the posterior part.

Measurements. BL: 5–5.5 mm; PL: 1.4–1.5 mm; PW: 2–2.1 mm; MSL: 0.9–1.0 mm; MTL: 1.1–1.2 mm; UL: 0.5 mm; BUL: 0.5 mm.

Material examined. 3, adults collected information: 6 April 1999, Ningxia Agriculture College, Yinchuan City, Ningxia, China; pupation date: 20 June 1999.

Remarks. This species was included in the key of tenebrionid pupae by Yu et al. (1999), but only mentioned with some characters for identification. Here its morphological characters are described in detail and provided with the photos for the first time.

(3) Genus *Opatrum* Fabricius, 1775

Opatrum (Opatrum) subaratum Faldermann, 1835

http://species-id.net/wiki/Opatrum_subaratum

Fig. 2: 1–9

Redescription. Male. Body nearly glabrous. Pronotal borders with 8–10 setose tubercles.

Head bent at acute angle to pronotum. Anterior border of labrum slightly emarginated in middle. Vertex with a central apophysis, in front of the apophysis with a pair of pits, behind the apophysis with a transverse, shallow groove. Oculus oval.

Pronotum: transverse, widest near middle, with the anterior part distinctly narrowed and the posterior part slightly narrowed; anterior border broadly emarginated and the emargination straight in middle; lateral borders broadly protuberant, flattened and stretched laterally (Fig. 2: 4–5); posterior border bisinuate (Fig. 2: 4); a longitudinal groove extended along dorsomeson from middle to posterior border; anterior angles obtuse, posterior angles acute; disc convex, glabrous, with short and narrow furrows.

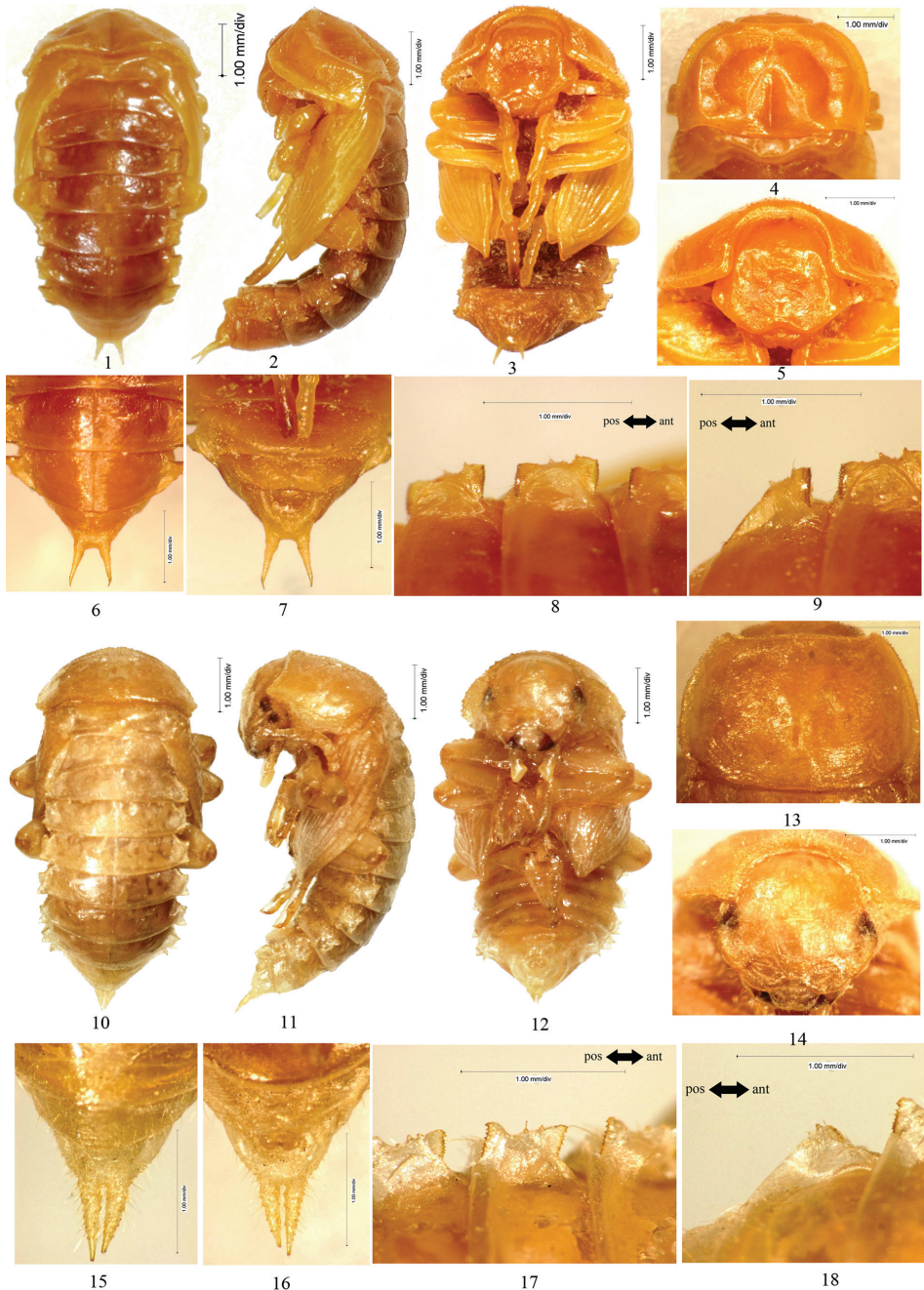


Figure 2. 1–9 *Opatrum (Opatrum) subaratum* Faldermann, 1835 1 Pupal habitus in dorsal view 2 Pupal habitus in lateral view 3 Pupal habitus in ventral view 4 Pronotum 5 Head 6 Urogomphi in dorsal view 7 Urogomphi in ventral view 8 Lateral process of abdominal tergite V 9 Lateral process of abdominal tergite VII 10–18 *Eumylada potanini* (Reitter, 1889) 10 Pupal habitus in dorsal view 11 Pupal habitus in lateral view 12 Pupal habitus in ventral view 13 Pronotum 14 Head 15 Urogomphi in dorsal view 16 Urogomphi in ventral view 17 Lateral process of abdominal tergite V 18 Lateral process of abdominal tergite VII.

Mesonotum slightly convex in middle of posterior part, posterior border protuberant. Posterior border of metanotum straight.

Elytral sheath striped and sparsely setose. Metathoracic wing sheath completely shrouded by elytral sheath (Fig. 2: 1–3).

Abdominal segments III–IX curved ventrally. The width of abdominal segments I–VII gradually narrowed posteriorly. Posterior border of abdominal sternite VIII slightly emarginated in middle, each side of the emargination with a long seta. Posterior borders of abdominal tergite IX straight; urogomphi diverging from each other, BUL shorter than UL (Fig. 2: 6–7). Abdominal tergites I–VII each with a concaveness between its lateral process and lateral border in middle, lateral processes each with 2 equally large and several minute setose tubercles along outer border, of which no minute setose tubercle presents in front of large setose tubercles I, 1–2 minute setose tubercles between large setose tubercles I and II and behind II, respectively (Fig. 2: 8–9). Lateral processes with anterior and posterior borders slightly sclerotized, outer borders of lateral processes of abdominal tergites I–VI slightly protuberant. Spiracles of abdominal tergites I–VI oval.

Gonotheca without apophysis.

Female. Unknown.

Measurements. BL: 6.7 mm; PL: 2.2 mm; PW: 3.5 mm; MSL: 0.5 mm; MTL: 0.6 mm; UL: 0.7 mm; BUL: 0.6 mm.

Material examined. 2, adults collected information: 30 June 1998, Xuanhua County, Hebei, China; pupation date: 22–26 September 2000.

Remarks. This species was included in the key of tenebrionid pupae by Yu et al. (1999), but only mentioned with some characters for identification. Here its morphological characters are described in detail and provided with the photos for the first time.

(4) Genus *Eumylada* Reitter, 1889

Eumylada potanini (Reitter, 1889)

http://species-id.net/wiki/Eumylada_potanini

Fig. 2: 10–18

Description. Male. Body covered with setae on surface. Pronotal borders, hypomeron, vertex, labrum, mandibles, the last segment of maxillary palpus and abdominal sternite with dense, short setae.

Head bent at right angle to pronotum. Anterior border of labrum slightly emarginated in middle. Oculus reniform, densely covered with setae on posterior part.

Pronotum: transverse, widest at posterior one-fourth, with the anterior part distinctly narrowed and the posterior part slightly narrowed; anterior border broadly emarginated and the emargination straight in middle, lateral borders broadly protuberant, posterior border bisinuate (Fig. 2: 13); anterior angles acute, posterior angles

slightly obtuse, protruding; disc slightly convex, sparsely covered with setae, with short and narrow furrows.

Mesonotum slightly convex in middle of posterior part, posterior border slightly protuberant. Posterior border of metanotum straight.

Elytral sheath striped, setose. Each elytral sheath with an apophysis near base. Metathoracic wing sheath completely shrouded by elytral sheath (Fig. 2: 10–12).

Abdominal segments I–IX curved ventrally. The width of abdominal segments I–VII gradually narrowed posteriorly. Abdominal tergites I–III each with 2 pits near anterior border and placed on both sides of dorsomeson, the pits of tergite I obscure, those of tergites II and III distinct. Posterior border of abdominal sternite VIII distinctly emarginated in middle, each side of the emargination with a long seta. Urogomphi parallel to and distinctly separated from each other, BUL shorter than UL (Fig. 2: 15–16). Abdominal segment IX and urogomphi densely covered with long setae. Abdominal tergites I–VII each with a concaveness between its lateral process and lateral border in middle, lateral processes thin, nearly transparent, each with 2 large setose tubercles and 0–2 setae along outer border, without minute setose tubercle (Fig. 2: 17–18). Outer borders of lateral processes of abdominal tergites I–VI slightly emarginated in middle. Spiracles of abdominal tergites I–VI oval.

Gonotheca without apophysis.

Female. Unknown.

Measurements. BL: 6.9 mm, PL: 2.2 mm; PW: 3.4 mm; MSL: 0.7 mm; MTL: 0.7 mm; UL: 0.7 mm; BUL: 0.1 mm.

Material examined. adults collected information: 19 April 2002, Baijitan, Lingwu County, Ningxia, China; pupation date: 22 May 2003.

Eumylada punctifera (Reitter, 1889)

http://species-id.net/wiki/Eumylada_punctifera

Fig. 3: 1–9

Redescription. Female. Body densely covered with fine setae on surface, except sparsely on vertex, pronotum, tibiae and tarsus; the total number of setose tubercles and setae on pronotal borders, hypomeron, vertex, mandibles and the last segment of maxillary palpus about 56 and 82, respectively.

Head bent at right angle to pronotum. Anterior border of labrum rounded. Oculi reniform.

Pronotum: transverse, widest near middle, with the anterior part distinctly narrowed and the posterior part slightly narrowed; anterior border broadly emarginated and the emargination straight in middle, lateral borders broadly protuberant, posterior border bisinuate (Fig. 3: 4); both anterior and posterior angles acute; disc slightly convex, with short and narrow furrows.

Mesonotum slightly convex in middle of posterior part, posterior border protuberant. Posterior border of metanotum slightly protuberant.

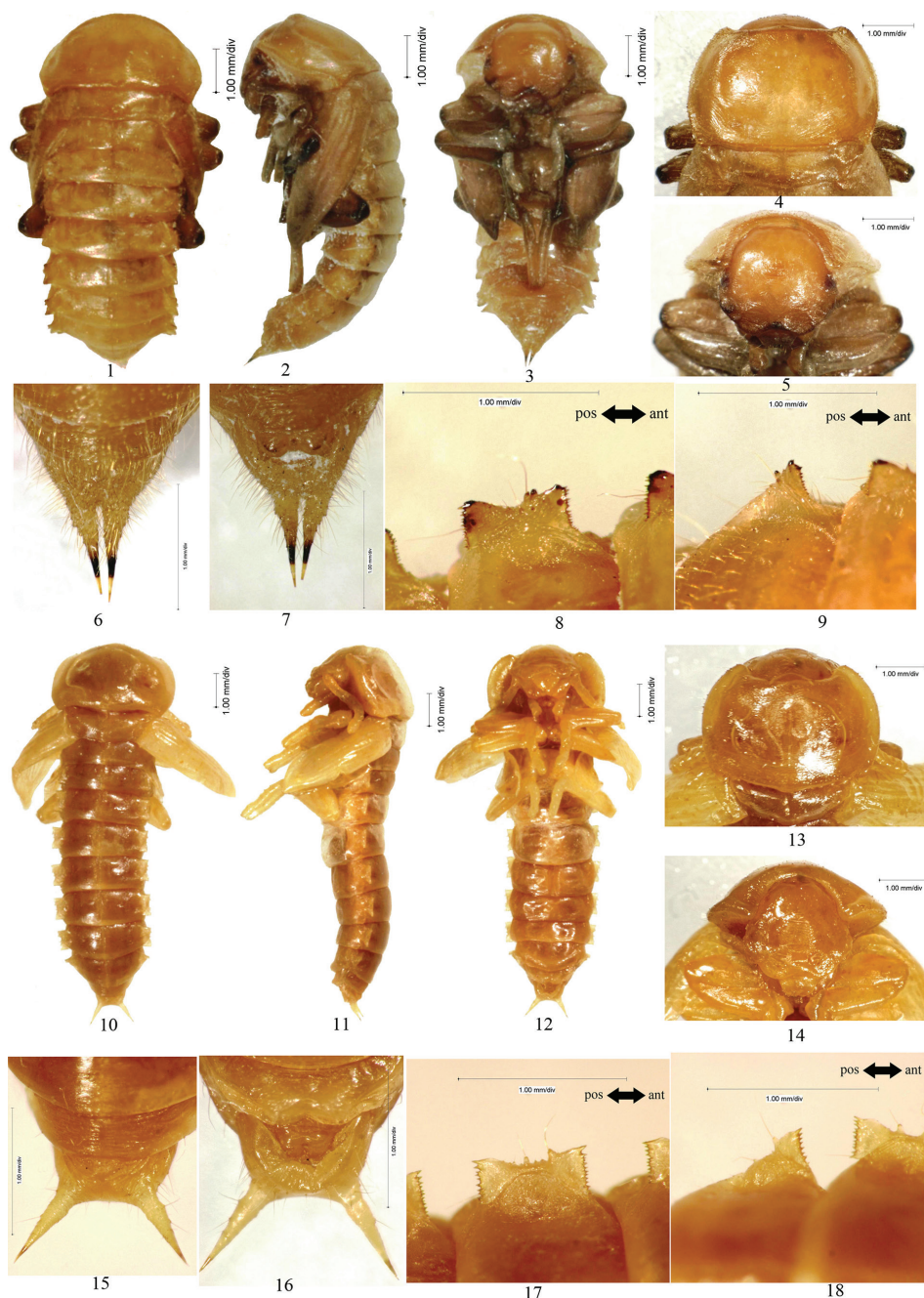


Figure 3. 1–9 *Eumylada punctifera* (Reitter, 1889) 1 Pupal habitus in dorsal view 2 Pupal habitus in lateral view 3 Pupal habitus in ventral view 4 Pronotum 5 Head 6 Urogomphi in dorsal view 7 Urogomphi in ventral view 8 Lateral process of abdominal tergite V 9 Lateral process of abdominal tergite VII 10–18 *Penthicus (Myladion) alashanicus* (Reichardt, 1936) 10 Pupal habitus in dorsal view 11 Pupal habitus in lateral view 12 Pupal habitus in ventral view 13 Pronotum 14 Head 15 Urogomphi in dorsal view 16 Urogomphi in ventral view 17 Lateral process of abdominal tergite V 18 Lateral process of abdominal tergite VII.

Elytral sheath striped and sparsely setose. Metathoracic wing sheath completely shrouded by elytral sheath (Fig. 3: 1–3).

Abdominal segments III–IX curved ventrally. The width of abdominal segments I–VII gradually narrowed posteriorly. Posterior border of abdominal sternite VIII broadly protuberant; abdominal segment IX and urogomphi densely covered with long setae. Urogomphi parallel to and distinctly separated from each other, BUL shorter than UL (Fig. 3: 6–7). Abdominal tergites I–VII each with a concaveness between its lateral process and lateral border in middle, lateral processes each with 3 large setose tubercles and 6–10 setae along outer border, without minute setose tubercle (Fig. 3: 8–9). Outer borders of lateral processes of abdominal tergites I–VI slightly emarginated in middle. Spiracles of abdominal tergites I–VI oval.

Gonotheca with an obtusely rounded apophysis on the anterior part and a conical apophysis on the posterior part.

Male. Unknown.

Measurements. BL: 7.9 mm; PL: 2.4 mm; PW: 3.8 mm; MSL: 0.7 mm; MTL: 0.7 mm; UL: 0.5 mm; BUL shorter than 0.1 mm.

Material examined. adults collected information: 2 May 2000, Shijiazhi Village, Gulang County, Gansu, China; pupation date: 14 June 2001.

Remarks. This species was included in the key of tenebrionid pupae by Yu et al. (1999), but only mentioned with some characters for identification. Here its morphological characters are described in detail and provided with the photos for the first time.

(5) Genus *Penthicus* Faldermann, 1836

Penthicus (*Myladion*) *alashanicus* (Reichardt, 1936)

http://species-id.net/wiki/Penthicus_alashanicus

Fig. 3: 10–18

Redescription. Male. Body sparsely covered with short setae on surface of pronotum, abdominal segments and elytral sheath. The total number of setose tubercles and setae on pronotal borders, hypomeron, vertex, mandibles and the last segment of maxillary palpus about 26–30 and 24–32, respectively.

Head bent at acute angle to pronotum, each side with an obscure groove between clypeus and gena. Anterior border of labrum distinctly emarginated in middle. Oculus oval.

Pronotum: transverse, widest near middle, with the anterior part distinctly narrowed and the posterior part slightly narrowed; anterior border broadly emarginated and the emargination distinctly protuberant in middle; lateral borders broadly protuberant, posterior border broadly protuberant (Fig. 3: 13); anterior angles acutely rounded, posterior angles obtusely sharp; disc flat, with short and narrow furrows.

Mesonotum slightly convex in middle of posterior part, posterior border protuberant. Posterior border of metanotum straight.

Elytral sheath striped and sparsely setose. Metathoracic wing sheath incompletely shrouded by elytral sheath (Fig. 3: 10–12).

Abdominal segments VI–IX curved ventrally. The width of abdominal segments I–VI subequal to each other. Posterior border of abdominal sternite VIII emarginated in middle, each side of the emargination with a long seta. Posterior border of abdominal tergite IX broadly emarginated in middle; urogomphi diverging from each other, BUL longer than UL (Fig. 3: 15–16). Abdominal tergites I–VII each with a concaveness between its lateral process and lateral border in middle, lateral processes each with 2 equally large and several minute setose tubercles along outer border, of which 0–1 minute setose tubercle presents in front of large setose tubercle I, 2 minute setose tubercles between large setose tubercles I and II, 3 minute setose tubercles behind large setose tubercle II (Fig. 3: 17–18). Outer borders of lateral processes of abdominal tergites I–VI slightly emarginated in middle. Spiracles of abdominal tergites I–VI nearly rounded, slightly convex.

Gonothea without apophysis.

Female. Unknown.

Measurements. BL: 11.0 mm; PL: 2.7 mm; PW: 3.7 mm; MSL: 0.9 mm; MTL: 0.7 mm; UL: 0.7 mm; BUL: 1.4 mm.

Material examined. adults collected information: 7 June 1999, Longshou Mountain, Shandan County, Gansu, China; pupation date: 31 August 1999.

Remarks. This species was included in the key of tenebrionid pupae by Yu et al. (1999), but only mentioned with some characters for identification. Here its morphological characters are described in detail and provided with the photos for the first time.

***Penthicus (Myladion) nojonicus* (Kaszab, 1968)**

http://species-id.net/wiki/Penthicus_nojonicus

Fig. 4: 1–9

Redescription. Female. Body covered with short setae on surface, of which slightly densely on head, pronotum and abdominal sternite; the total number of setose tubercles and setae on pronotal borders, hypomeron, vertex, mandibles and the last segment of maxillary palpus about 30–34 and 40–50, respectively.

Head bent at acute angle to pronotum. Labrum sparsely covered with short setae along anterior and lateral borders, anterior border slightly emarginated in middle. Oculus reniform.

Pronotum: transverse, widest near middle, the anterior part narrowed almost the same as the posterior part; anterior border broadly emarginated and the emargination straight in middle, lateral and posterior borders broadly protuberant, posterior border slightly emarginated in middle (Fig. 4: 4); anterior angles acute, posterior angles obtusely acute; disc flat, glabrous, with short and narrow furrows.

Mesonotum slightly convex in middle of posterior part, posterior border slightly protuberant. Posterior border of metanotum straight.

Elytral sheath striped and sparsely setose. Metathoracic wing sheath completely shrouded by elytral sheath (Fig. 4: 1–3).

Abdominal segments I–IX curved ventrally. The width of abdominal segments I–VII gradually narrowed posteriorly. Posterior border of abdominal sternite VIII broadly protuberant. Posterior border of abdominal tergite IX straight; urogomphi diverging from each other, BUL longer than UL (Fig. 4: 6–7). Abdominal tergites I–VII each with a concaveness between its lateral process and lateral border in middle, lateral processes each with 2 large setose tubercles and several minute setose tubercles along outer border, of which no minute setose tubercle presents in front of large setose tubercles I, 1–2 minute setose tubercles between large setose tubercles I and II, 2–3 minute setose tubercles behind large setose tubercle II (Fig. 4: 8–9). Outer borders of lateral processes of abdominal tergites I–VI emarginated in middle. Spiracles of abdominal tergites I–VI oval, slightly convex.

Gonotheca with an obtusely rounded apophysis on the anterior part and a conical apophysis on the posterior part.

Male. Unknown.

Measurements. BL: 11.0 mm; PL: 3.4 mm; PW: 4.6 mm; MSL: 0.9 mm; MTL: 0.9 mm; UL: 0.8 mm; BUL: 1.3 mm.

Material examined. adults collected information: 14 July 2000, Fanjiayao Village, Baiyin City, Gansu, China; pupation date: 14 June 2001.

Remarks. This species was included in the key of tenebrionid pupae by Yu et al. (1999), but only mentioned with some characters for identification. Here its morphological characters are described in detail and provided with the photos for the first time.

(6) Genus *Myladina* Reitter, 1889

Myladina unguiculina Reitter, 1889

http://species-id.net/wiki/Myladina_unguiculina

Fig. 4: 10–18

Redescription. Male. Body covered with setae on surface, of which slightly densely on elytral sheath and abdominal segments; the total number of setose tubercles and setae on pronotal borders, hypomeron, vertex, mandibles and the last segment of maxillary palpus about 14–20 and 40–60, respectively.

Head bent at right angle to pronotum. Labrum sparsely covered with setae along anterior and lateral borders, anterior border distinctly emarginated in middle. Oculus reniform.

Pronotum: subquadrate, widest near middle, with the anterior part distinctly narrowed and the posterior part slightly narrowed; anterior border broadly emarginated and the emargination slightly protuberant in middle, lateral borders nearly straight, posterior border straight (Fig. 4: 13); anterior angles acutely rounded, posterior angles acute; disc flat, glabrous, with short and narrow furrows.

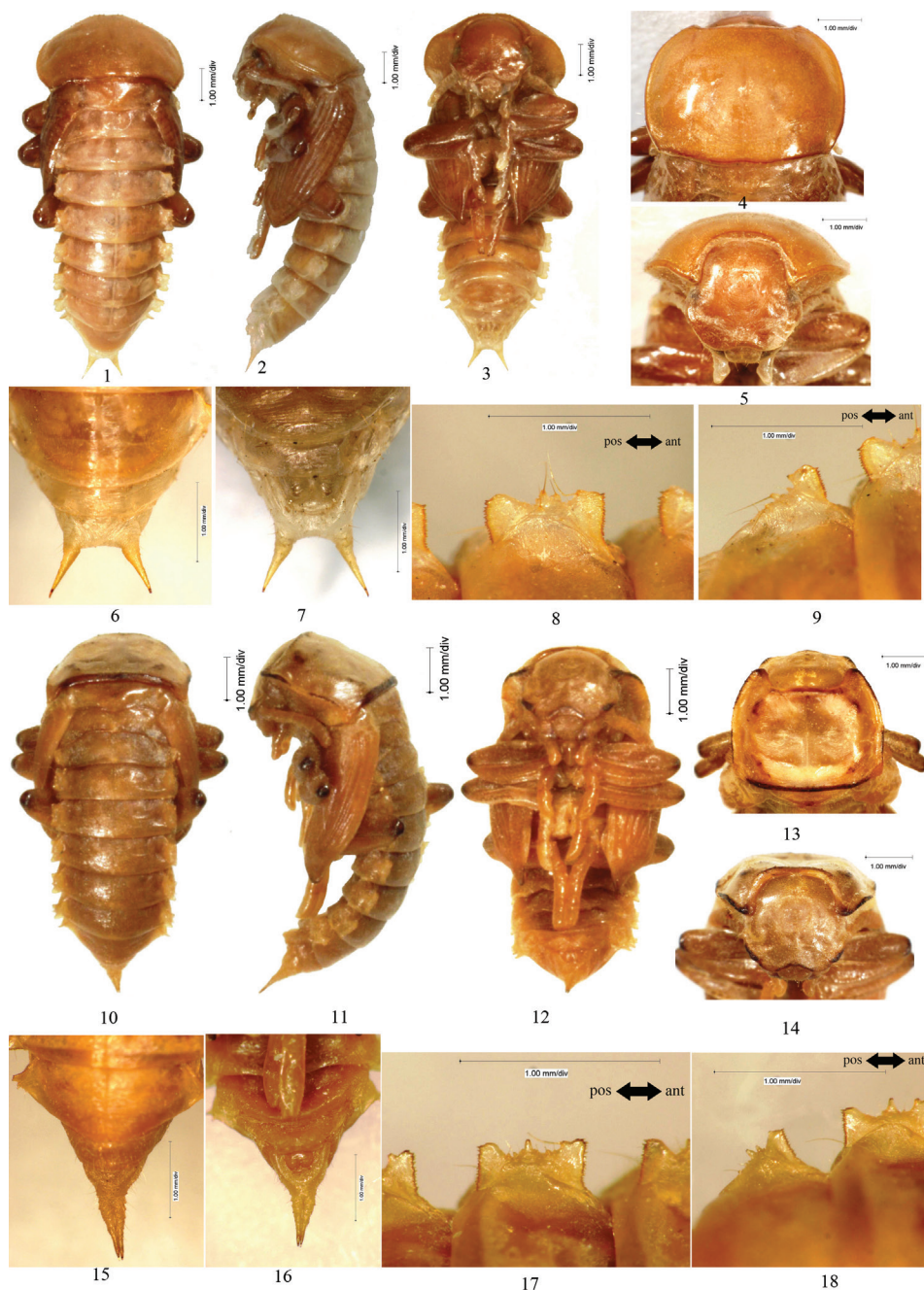


Figure 4. 1–9 *Penthicus (Myladion) nojonicus* (Kaszab, 1968) 1 Pupal habitus in dorsal view 2 Pupal habitus in lateral view 3 Pupal habitus in ventral view 4 Pronotum 5 Head 6 Urogomphi in dorsal view 7 Urogomphi in ventral view 8 Lateral process of abdominal tergite V 9 Lateral process of abdominal tergite VII 10–18 *Myladina unguiculina* Reitter, 1889 10 Pupal habitus in dorsal view 11 Pupal habitus in lateral view 12 Pupal habitus in ventral view 13 Pronotum 14 Head 15 Urogomphi in dorsal view 16 Urogomphi in ventral view 17 Lateral process of abdominal tergite V 18 Lateral process of abdominal tergite VII.

Mesonotum slightly convex in middle of posterior part, posterior border protuberant. Posterior border of metanotum straight.

Elytral sheath striped and densely setose. Metathoracic wing sheath completely shrouded by elytral sheath (Fig. 4: 10–12).

Abdominal segments I–IX curved ventrally. The width of abdominal segments I–VII gradually narrowed posteriorly. Posterior border of abdominal sternite VIII emarginated in middle, each side of the emargination with a long seta. Abdominal segment IX, urogomphi and gonotheca densely covered with setae. Urogomphi broad at base, parallel to each other, with apices slightly separated, BUL much shorter than UL (Fig. 4: 15–16). Abdominal tergites I–VII each with a concaveness between its lateral process and lateral border in middle, lateral processes each with 2 large and several minute setose tubercles along outer border, large setose tubercles II distinctly larger than I, no minute setose tubercle presents in front of large setose tubercles I, 2–3 minute setose tubercles between large setose tubercles I and II and behind II, respectively (Fig. 4: 17–18). Outer borders of lateral processes of abdominal tergites I–VI slightly protuberant in middle. Spiracles of abdominal tergites I–VI oval.

Gonotheca without apophysis.

Female. Similar to the male, but posterior border of abdominal sternite VIII broadly protuberant; gonotheca with an obtusely rounded apophysis on the anterior part and a conical apophysis on the posterior part.

Measurements. BL: 7.5–7.7 mm; PL: 2.6–2.7 mm; PW: 3.3–3.5 mm; MSL: 0.8 mm; MTL: 0.5 mm; UL: 0.8–0.9 mm; BUL: 0.1 mm.

Material examined. 10, Adults collected information: 24 June 2001, Gaoshawo Town, Yanchi County, Ningxia, China; pupation date: 2–10 September 2001.

Remarks. This species was included in the key of tenebrionid pupae by Yu et al. (1999), but only mentioned with some characters for identification. Here its morphological characters are described in detail and provided with the photos for the first time.

(7) Genus *Melanesthes* Lacordaire, 1859

Melanesthes (*Opatronesthes*) *rugipennis* Reitter, 1889

http://species-id.net/wiki/Melanesthes_rugipennis

Fig. 5: 1–9

Description. Male. Body covered with setae on surface, of which slightly dense on abdominal sternite, head and pronotum; the total number of setose tubercles and setae on pronotal borders, hypomeron, vertex, mandibles and the last segment of maxillary palpus about 22–26 and 10–16, respectively.

Head bent at acute angle to pronotum, densely covered with setae between oculus and pronotum. Labrum covered with short setae along anterior border, anterior border distinctly emarginated in middle. Oculus reniform.



Figure 5. 1–9 *Melanesthes (Opatronesthes) rugipennis* Reitter, 1889 1 Pupal habitus in dorsal view 2 Pupal habitus in lateral view 3 Pupal habitus in ventral view 4 Pronotum 5 Head 6 Urogomphi in dorsal view 7 Urogomphi in ventral view 8 Lateral process of abdominal tergite V 9 Lateral process of abdominal tergite VII 10–18 *Melanesthes (Melanesthes) maxima maxima* Ménétriers, 1854 10 Pupal habitus in dorsal view 11 Pupal habitus in lateral view 12 Pupal habitus in ventral view 13 Pronotum 14 Head 15 Urogomphi in dorsal view 16 Urogomphi in ventral view 17 Lateral process of abdominal tergite V 18 Lateral process of abdominal tergite VII.

Pronotum: transverse, widest at posterior one-fourth, with the anterior part distinctly narrowed and the posterior part slightly narrowed; anterior border broadly emarginated and the emargination protuberant in middle, lateral borders broadly protuberant, posterior border straight (Fig. 5: 4); anterior angles acute, posterior angles nearly right-angled, acute; disc flat, sparsely covered with setae, with short and narrow furrows.

Mesonotum slightly convex in middle of posterior part, posterior border straight. Posterior border of metanotum slightly protuberant.

Elytral sheath striped and glabrous. Metathoracic wing sheath completely shrouded by elytral sheath (Fig. 5: 1–3).

Abdominal segments I–IX curved ventrally. The width of abdominal segments I–VII gradually narrowed posteriorly. Posterior border of abdominal sternite VIII emarginated in middle, each side of the emargination with a long seta. Abdominal sternite IX with 8–10 setae. Posterior border of abdominal tergite IX emarginated in middle. Urogomphi diverging from each other, each with a long seta on outer border, BUL shorter than UL (Fig. 5: 6–7). Abdominal tergites I–VII each with a concaveness between its lateral process and lateral border in middle, lateral processes each with 2 large and several minute setose tubercles along outer border, of which no minute setose tubercle presents in front of large setose tubercles I, 1 minute setose tubercle between large setose tubercles I and II, 1–2 minute setose tubercles behind large setose tubercle II (Fig. 5: 8–9). Outer borders of lateral processes of abdominal tergites I–VI slightly emarginated in middle. Spiracles of abdominal tergites I–VI oval, slightly convex.

Gonotheca without apophysis.

Female. Similar to the male, but posterior border of abdominal sternite VIII broadly protuberant; gonotheca with an obtusely rounded apophysis on the anterior part and a conical apophysis on the posterior part.

Measurements. BL: 8.5–8.6 mm; PL: 3.0–3.1 mm; PW: 4.3–4.4 mm; MSL: 0.9 mm; MTL: 0.8 mm; UL: 0.7–0.8 mm; BUL: 0.6–0.7 mm.

Material examined. 3, adults collected information: 1 May 2002, Shutai Town, Haiyuan County, Ningxia, China; pupation date: 25–27 May 2003.

Melanesthes (Melanesthes) maxima maxima Ménétériès, 1854

http://species-id.net/wiki/Melanesthes_maxima_maxima

Fig. 5: 10–18

Redescription. Female. Body covered with setae on surface; setae on abdominal tergites and urogomphi more; the total number of setose tubercles and setae on pronotal borders, hypomeron, vertex, mandibles and the last segment of maxillary palpus about 16–20 and 50–58, respectively.

Head bent at acute angle to pronotum. Labrum covered with sparsely short setae along anterior and lateral borders, anterior border distinctly emarginated in middle. Oculus oval.

Pronotum: transverse, widest near middle, with the anterior part distinctly narrowed and the posterior part slightly narrowed; anterior border broadly emarginated

and the emargination protuberant in middle, lateral borders broadly protuberant, posterior border straight (Fig. 5: 13); anterior angles rounded, posterior angles obtusely rounded; disc flat, glabrous, with short and narrow furrows, each side with a apophysis before the posterior border.

Mesonotum slightly convex in middle of posterior part, posterior border protuberant. Metanotum slightly convex in middle of anterior part, posterior border straight.

Elytral sheath obscurely striped and finely setose; with a distinct groove between elytral sheath and mesonotum. Metathoracic wing sheath completely shrouded by elytral sheath (Fig. 5: 10–12).

Abdominal segments III–IX curved ventrally. The width of abdominal segments I–VII gradually narrowed posteriorly. Posterior border of abdominal sternite VIII broadly protuberant. Abdominal segment IX and urogomphi densely covered with, brown, long setae. Urogomphi parallel to each other, with apices of urogomphi leaning against each other, BUL much shorter than UL (Fig. 5: 15–16). Abdominal tergites I–VII each with a concaveness between its lateral process and lateral border in middle, lateral processes each with 2–3 large setose tubercles and about 5–7 minute setose tubercles along outer border (Fig. 5: 17–18). Outer borders of lateral processes of abdominal tergites I–VI protuberant in middle. Spiracles of abdominal tergites I–VI oval.

Gonotheca with an obtusely rounded apophysis on the anterior part and a conical apophysis on the posterior part, a brown apophysis between gonothecas.

Male. Unknown.

Measurements. BL: 11.8 mm; PL: 3.2 mm; PW: 5.4 mm; MSL: 0.3 mm; MTL: 0.2 mm; UL: 1.0 mm; BUL shorter than 0.1 mm.

Material examined. adults collected information: 22 April 2001, Yaoba Town, Alxa Left Banner, Neimenggu, China; pupation date: 22 June 2001.

Remarks. This species was included in the key of tenebrionid pupae by Yu et al. (1999), but only mentioned with some characters for identification. Here its morphological characters are described in detail and provided with the photos for the first time.

Melanesthes (Melanesthes) jintaiensis Ren, 1992

http://species-id.net/wiki/Melanesthes_jintaiensis

Fig. 6: 1–9

Description. Female. Body densely covered with setae on surface, of which distinctly long on mandibles and oculus; the total number of setose tubercles and setae on pronotal borders, hypomeron, vertex, mandibles and the last segment of maxillary palpus about 40–42 and 300–350, respectively.

Head bent at acute angle to pronotum, densely covered with setae between oculus and pronotum. Labrum densely covered with short setae along anterior and lateral borders, anterior border rounded. The suture between labrum and clypeus indistinct. Oculus reniform.

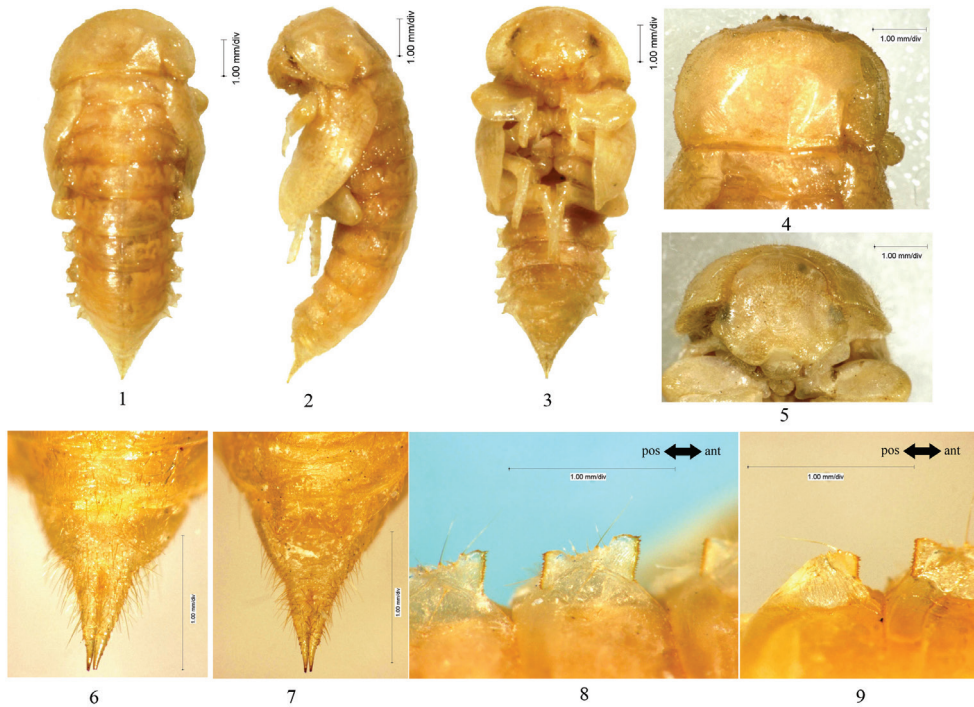


Figure 6. 1–9 *Melanesthes (Melanesthes) jintaiensis* Ren, 1992 1 Pupal habitus in dorsal view 2 Pupal habitus in lateral view 3 Pupal habitus in ventral view 4 Pronotum 5 Head 6 Urogomphi in dorsal view 7 Urogomphi in ventral view 8 Lateral process of abdominal tergite V 9 Lateral process of abdominal tergite VII.

Pronotum: transverse, widest near middle, with the anterior part distinctly narrowed and the posterior part slightly narrowed; anterior border broadly emarginated and the emargination protuberant in middle, lateral borders broadly protuberant, posterior border straight (Fig. 6: 4); anterior angles acute, posterior angles rounded; disc flat, densely covered with setae, with short and narrow furrows.

Mesonotum slightly convex in middle of posterior part, posterior border slightly protuberant. Metanotum slightly convex in middle of anterior part, posterior border straight.

Elytral sheath striped and densely setose. Metathoracic wing sheath completely shrouded by elytral sheath (Fig. 6: 1–3).

Abdominal segments I–IX curved ventrally. The width of abdominal segments I–VII gradually narrowed posteriorly. Posterior border of abdominal sternite VIII broadly protuberant. Abdominal segment IX and urogomphi densely covered with brown, long setae. Urogomphi parallel to each other, with apices slightly separated from each other, BUL shorter than UL (Fig. 6: 6–7). Abdominal tergites I–VII each with a concaveness between its lateral process and lateral border in middle, lateral processes each with 2 large and several minute setose tubercles along outer border, of which no minute setose tubercle presents in front of large setose tubercles I, 1 minute setose tubercle between large setose tubercles I and II, 3–4 minute setose tubercles behind large setose tubercle II (Fig. 6: 8–9). Outer borders of lateral processes of

abdominal tergites I–VI emarginated in middle. Spiracles of abdominal tergites I–VI oval, slightly convex.

Gonotheca with 6–8 setae, an obtusely rounded apophysis on the anterior part and a conical apophysis on the posterior part.

Male. Unknown.

Measurements. BL: 9.5 mm; PL: 2.4 mm; PW: 4.1 mm; MSL: 0.9 mm; MTL: 0.8 mm; UL: 0.9 mm; BUL shorter than 0.1 mm.

Material examined. adults collected information: 31 May 2002, Zhengshaqu Village, Yongning County, Ningxia, China; pupation date: 29 August 2002.

Results and discussion

After describing in detail the eleven pupae from China, we studied and characterized the morphology of *Opatrini* pupae. This was carried out by examining all available material as well as drawings and descriptions provided in the literature. The results indicate that all known *Opatrini* pupae have a pair of urogomphi on abdominal tergite IX, the abdominal lateral processes are dorsoventrally flattened and bear strongly sclerotized, densely dentated anterior and posterior borders each.

Two main types of urogomphi can be identified in the pupae described in this paper, which may be a useful taxonomic character for distinguishing the genera. The urogomphi in *Scleropatrum horridum horridum*, *Gonocephalum reticulatum*, *Opatrum* (*Opatrum*) *subaratum*, *Penthicus* (*Myladion*) *alashanicus*, *P.* (*Myladion*) *nojonicus*, *Melanesthes* (*Opatronesthes*) *rugipennis* are identical. In these species, the urogomphi are diverging from each other, but can be distinguished by the the relative value of length and distance between urogomphi. Comparatively, the urogomphi in *Eumylada potanini*, *E. punctifera*, *Melanesthes* (*Melanesthes*) *maxima maxima*, *M.* (*Melanesthes*) *jintaiensis*, *Myladina unguiculina* are parallel to each other, but the species are different in if there is a space between them or not. Also, the pronotum is a good character to differentiate the species.

More taxonomic studies are needed in order to assess the value of different morphological characters, but the data presented here demonstrate that abdominal lateral processes, urogomphi and pronotum can be useful for the taxonomy of the pupal stages at generic and specific levels within *Opatrini*.

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We are grateful to Dr. Patrice Bouchard (Canadian National Collection of Insects, Arachnids and Nematodes) providing valuable suggestions, literature and especially for his critical review of the manuscript. We are grateful to Prof. Zhang Feng, Associate Prof. Yang Yu-Xia (College of Life Sciences of Hebei University, Baoding, China) and Prof. Wang Xin-Pu (School of Agriculture of Ningxia University, Yinchuan, China) for

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References

- Abdulla M (1964) The immature stages of a south Indian *Cryphaeus* (Coleoptera: Tenebrionidae). Proceedings of the Royal Entomological Society of London 39: 153–156.
- Beutel RG, Friedrich F (2005) Comparative study of larvae of Tenebrionoidea (Cucujiformia, Coleoptera). European Journal of Entomology 102: 241–264.
- Bouchard P, Steiner W (2004) First descriptions of Coelometopini pupae (Coleoptera: Tenebrionidae) from Australia, Southeast Asia and the Pacific region, with comments on phylogenetic relationships and antipredator adaptations. Systematic Entomology 29: 101–114. doi: 10.1111/j.1365-3113.2004.00230.x
- Böving AG, Craighead FC (1931) An illustrated synopsis of the principal larval forms of the order Coleoptera. Entomologica America (NS) 11: 1–351.
- Cherney LS (2005) Darkling-beetles (Coleoptera, Tenebrionidae). Fauna of Ukraine. Vol. 19. Beetles. Issue 10. Kiev, Naukova Dumka, 431 pp. [In Russian]
- Cherney LS (2006) Morphology of Preimaginal Stages of Some Species of Beetles (Coleoptera, Tenebrionidae) Darkling of the Fauna of Ukraine. Vestnik zoologii 40(4): 351–358. [In Russian]
- Cherney LS, Fedorenko LV (2006) Keys to darkling beetles (Coleoptera, Tenebrionidae) of Fauna of Ukraine (imago, larvae, pupae). Kiev, Kolobig, 247 pp. [In Russian]
- Daggy T (1946) Notes on the ecology and taxonomy of certain pupae of the family Tenebrionidae (Coleoptera). Proceedings of the Indiana Academy of Sciences 56: 253–260.
- Dunford JC, Steiner WE (2007) Madagascar Beetle, *Leichenum canaliculatum variegatum* (King) (Insecta: Coleoptera: Tenebrionidae). University of Florida. IFAS extension EENY-399 (IN723): 1–7.
- Gosik R (2007) Description of the pupa of *Mycetochara axillaris* (Paykull, 1799) (Coleoptera, Tenebrionidae). Baltic Journal of Coleopterology 7: 179–184.
- Ho FK (1960) Discrimination between the pupae of *Tribolium confusum* Duv. and *T. castaneum* (Hbst.) (Coleoptera: Tenebrionidae). Annals of the Entomological Society of America 53: 280–281.
- Ho FK (1969) Identification of pupae of six species of *Tribolium* (Coleoptera: Tenebrionidae). Annals of the Entomological Society of America 62: 1232–1237.
- Matthews EG, Lawrence JF, Bouchard P, Steiner WE, Ślipiński SA (2010) 11.14 Tenebrionidae Latreille, 1802. In: Leschen RAB, Beutel RG, Lawrence JF (Eds) Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom. Volume IV- Arthropoda: Insecta. Part 38. Coleoptera, Beetles. Volume 2: Systematics (Part 2). Walter de Gruyter, Berlin, 574–659.
- Ogloblin DA, Kolobova AN (1927) Darkling beetles (Tenebrionidae) and their larvae, harmful to agriculture. Trudy Poltavskoy selskochozyaistvennoy opytnoy stanzii 61: 1–60. [In Russian]

- Purchart L, Nabozhenko MV (2012) Description of larva and pupa of the genus *Deretus* (Coleoptera: Tenebrionidae) with key to the larvae of the tribe Helopini. In: Hájek J, Bezděk J (Eds) Insect biodiversity of Socotra Archipelago. Acta Entomologica Musei Nationalis Pragae 52 (2): 295–302.
- Ren GD, Ye JH (1990) A preliminary study on the *Microdera elegans* Reitter. Plant Protection 16: 15–16. [In Chinese]
- Simões MVP, Quintino HYS, Monné ML (2009) Larva and pupa of *Nilio* (*Linio*) *lanatus* Germar, 1824 (Coleoptera: Tenebrionidae). Zootaxa 2175: 51–56.
- Spilman TJ (1966) Larva and Pupa of *Amarygmus morio* from Hawaii (Coleoptera: Tenebrionidae). Proceedings of the Hawaiian Entomological Society, XIX: 297–301.
- Spilman TJ (1969) Larva and Pupa of *Pyanisia tristis* from Alabama (Coleoptera: Tenebrionidae). The Coleopterists Bulletin 23(3): 57–61.
- Spilman TJ (1979) Larvae and pupae of *Centronopus calcaratus* and *Centronopus suppressus* (Coleoptera: Tenebrionidae) with an essay on wing development in pupae. Proceedings of the Entomological Society of Washington 81: 513–521.
- Spilman TJ (1984) Identification of larvae and pupae of the larger grain borer, *Prostephanus truncatus* (Coleoptera: Bostrichidae), and the larger black flour beetle, *Cynaues angustus* (Coleoptera: Tenebrionidae). In: Mills RB, Wright VF, Pedersen JR, McGaughey WH, Beeman RW, Kramer KJ, Speirs RD, Storey CL (Eds) Proceedings of the 3rd International Working Conference on Stored-Product Entomology, 23-28 October, 1983. Manhattan Kansas, 44–53.
- Steiner WEJ (1995) Structures, behavior and diversity of the pupae of Tenebrionidae (Coleoptera). In: Pakaluk J, Slipinski SA (Eds) Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson. Muzeum i Instytut Zoologii PAN, Warszawa, 503–539.
- St-George RA (1924) Studies on the larvae of North American beetles of the subfamily Tenebrioninae with a description of the larva and pupa of *Merinus laevis* (Oliver). Proceedings of the United States National Museum, Washington 65: 1–32.
- Watt JC (1974) A revised subfamily classification of Tenebrionidae (Coleoptera). New Zealand Journal of Zoology 1: 381–452. doi: 10.1080/03014223.1974.9517846
- Wei JH, Zhang ZL, WANG MC (1989) Soil pests of China. Shanghai Science and Technology Press, Shanghai, 400–414. [In Chinese]
- Wu FZ, Gao ZN (1978) Diagrams and Explanations in Agriculture insect of Ningxia (a revised edition). Agriculture Press, Beijing, 260–261. [In Chinese]
- Yu YZ, Ren GD, Dai JX (1999) Identification on the pupae of Tenebrionidae (Coleoptera) from North China. Journal of Ningxia University (Natural Science Edition) 20: 364–367. [In Chinese]
- Yu YZ, Ren GD, Ma F (1993) Record and narration on six species pupae in soil of family Tenebrionidae (Coleoptera). Journal of Ningxia Agricultural College, Supplementum 14: 79–84. [In Chinese]
- Yu YZ, Yang GJ (2004) Pupa identification of Pimeliinae-insects from North China. Entomological knowledge 41: 354–357. [In Chinese]

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When describing the new species *Unixenus corringlensis* Short & Huynh, sp. n., the latitude given for the single collecting event of this species in Corringale state forest is incorrect and should be 33°40'00"S not 33°22'12"S.

The correct wording in the species description for the holotype, a male paratype and two specimens included as other material is as follows:

Holotype. Female, Corringale State Forest, NSW, 33°40'00"S, 147°15'00"E (±1 km) (incorrectly recorded on label and in AM database as 33°22'12"S, 147°15'00"E, new latitude estimated with google earth), 21–26 March 1996, collected by D. Smith, AM KS.119541. Specimen mounted on slides, deposited in AM.

Paratypes. 1 male, same collection as holotype, AM KS.119540.

Other material. 2 immature specimens, (sex and stadia not determined), same collection as holotype, AM KS.53604, preserved in ethanol.

The Table of localities included as an appendix also requires the same correction. Portion of the table is shown below with corrections highlighted in yellow.

Acknowledgement

We thank Dr Robert Mesibov for alerting us to the presence of the incorrect latitude in our paper.

Table of localities- part only, showing all entries for *U. corringlensis* sp. n. Corrections highlighted in yellow.

Repository	Registration	Type status	Genus	Species	Specimens	Location	State	LatDS	LatMS	LatSS	LongDE	LongME	LongSE	Lar/long-source
AM	KS.119541	holotype	Unixenus	corringlensis	1F	Corringale State forest	NSW	33	40	00	147	15	0	Google earth estimate
AM	KS.119540	paratype	Unixenus	corringlensis	1M	Corringale State forest	NSW	33	40	00	147	15	0	Google earth estimate
AM	KS.87406	paratype	Unixenus	corringlensis	1M	Sewern State forest, Atholwood Loop Rd	NSW	29	4	28	151	0	53	AM database
AM	KS.119542	paratype	Unixenus	corringlensis	1F	Sewern State forest, Atholwood Loop Rd	NSW	29	4	28	151	0	53	AM database
AM	KS.119543	paratype	Unixenus	corringlensis	1F	Newnes State forest, Birds Rock Flora reserve, 0.6 km from Sunnyside Ridge Rd	NSW	33	19	43	150	11	23	AM database
AM	KS.87400		Unixenus	corringlensis	4	Sewern State forest, Atholwood Loop Rd	NSW	29	4	28	151	0	53	AM database
AM	KS.87410		Unixenus	corringlensis	2	Sewern State forest, Atholwood Loop Rd	NSW	29	4	28	151	0	53	AM database
AM	KS.53604		Unixenus	corringlensis	2 imm.	Corringale State forest	NSW	33	40	00	147	15	0	Google earth estimate
AM	KS.119544		Unixenus	corringlensis	1M, stadium VII	Newnes State forest, Birds Rock Flora reserve, 0.6 km from Sunnyside Ridge Rd	NSW	33	19	43	150	11	23	AM database