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Phylogenetic Revision of *Eryphanis*
Boisduval, with a Description of a New
Species from Ecuador (Lepidoptera,
Nymphalidae)

Carla M. Penz
University of New Orleans, New Orleans, Louisiana,

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Carla M. Penz
Department of Biological Sciences
University of New Orleans
2000 Lakeshore Drive
New Orleans, Louisiana, 70148, USA
cpenz@uno.edu

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Phylogenetic revision of *Eryphanis* Boisduval, with a description of a new species from Ecuador (Lepidoptera, Nymphalidae)

Carla M. Penz

Department of Biological Sciences
University of New Orleans
2000 Lakeshore Drive
New Orleans, Louisiana, 70148, USA
cpenz@uno.edu

Abstract. This study provides a species-level phylogeny for the Neotropical brassoline genus *Eryphanis* Boisduval based on 43 morphological characters. A revised generic definition is given. Three subspecies are elevated to species status and a new species is described; *E. bubocula* (Butler, 1872), **status revised**; *E. lycomedon* (C. Felder and R. Felder, 1862), **status revised**; *E. opimus* (Staudinger, 1887), **status revised**; and *E. greeneyi* Penz and DeVries, **new species**. Diagnoses, annotated redescriptions, and illustrations of habitus and genitalia are provided for the nine *Eryphanis* species.

Key words. *polyxena*, *lycomedon*, *opimus*, *zolzivora*, status revised, Greeney

Introduction

The Neotropical genus *Eryphanis* Boisduval includes species with prominent blue or purple dorsal iridescence, a pair of ventral eye-spots in hindwing cells M3 and Cu1 that are distinctively fused, and male scent organs on the dorsal surface of hindwing cell Cu2 (Fig. 1-2). The earliest described taxa were placed in *Papilio* Linnaeus, and most others were either described under *Pavonia* Godart (a former name for *Caligo* Hübner, see Hemming 1967) or *Caligo*, indicating that *Eryphanis* has long been considered closely related to *Caligo* (e.g., Stichel 1909, Frühstorfer 1912, Blandin 1974). Stichel (1904, 1909) and Frühstorfer (1912) proposed sub-generic groups for *Eryphanis*, but they had conflicting species compositions. The ‘absence of a hairpencil in the anal region of the hindwing’ defined Stichel’s section *Psilocraspeda* that included *E. polyxena* (Meerburgh, 1780) only. Stichel defined section *Trichothamnodes* by the ‘presence of a brush-like hair-tuft close to the submedian of the hindwing’, which included *E. aesacus* (Herrich-Schäffer, 1850), *E. gerhardi* (Weeks, 1902), *E. reevesii* (Doubleday, 1849), *E. zolzivora* (Hewitson, 1877), and *E. seleucida* (Hewitson, 1877). Frühstorfer (1912) maintained the same characters, but organized his species groups as follows: (a) ‘absence of a hairpencil...’, including *E. polyxena*, *E. reevesii*, *E. zolzivora* and *E. seleucida*; and (b) ‘presence of a ... hair-tuft ...’, including *E. aesacus* and *E. gerhardi*.

Species richness assessments vary historically among authors. Godman and Salvin (1879) estimated eight or nine species, while Stichel (1909) and Frühstorfer (1912) recognized six. After the separation of *Caligopsis seleucida* from *Eryphanis* by Seydel (1924), the taxonomy of this group has been uneventful. Recently Casagrande (2004) recognized five species of *Eryphanis*: *E. aesacus*, *E. automedon* (Cramer, 1775) (type-species), *E. gerhardi*, *E. reevesii*, and *E. zolzivora*. Except for using the name ‘*automedon*’ instead of ‘*polyxena*’, Casagrande’s (2004) species list matches that of Stichel (1909).

Although most *Eryphanis* species have been reared, few have had their early stages described and illustrated in any detail (see Remarks in the Species Identification section). Nonetheless, some general characteristics are evident from the available natural history accounts. Members of *Eryphanis* have spherical, finely ribbed eggs. The first instar head capsule is densely covered with long setae that are plumose at the tips. Later instars show a characteristic “moustache” neighboring the stemmata that is composed of clusters of flat, ribbed setae of various lengths and widths (see Dias 1979). Mature larvae are cryptically colored, have three pairs of short head scoli, and typically rest with the head tilted back. The body is elongate, and bear five fleshy tubercles along the dorsal midline, and the caudae are notably long (ca. 25% of the total body length). The pupae are thin and elongated, light brown, and possess long head projections; characters that yield the appearance of a dried curled leaf (see Cubero 1985). The larvae feed at night on their Poaceae host plants (DeVries 1987, Penz et al. 2000 and references therein).

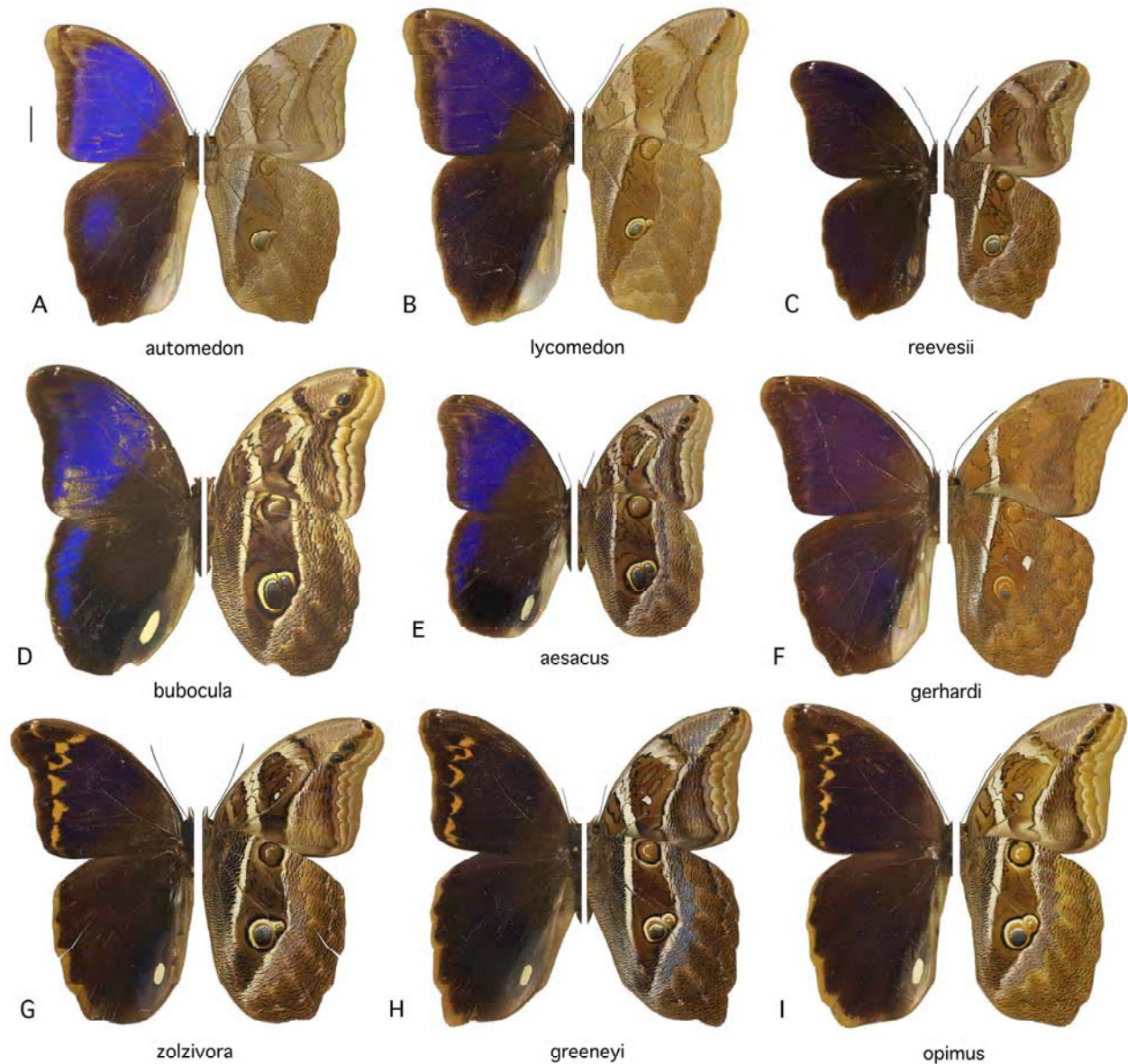


Figure 1. *Eryphanis* adult males, dorsal side on the left, ventral side on the right. Scale bar next to A = 1cm. **A)** *E. automedon*, Colombia, Cali. **B)** *E. lycomedon*, Colombia, Cali. **C)** *E. reevesii*, Brazil, São Paulo, Pinhal. **D)** *E. bubocula*, Costa Rica, Guanacaste, Rio San Lorenzo. **E)** *E. aesacus*, [Mexico], Catemaco. **F)** *E. gerhardi*, Bolivia. **G)** *E. zolzivora*, Bolivia. **H)** *E. greeneyi*, Ecuador, Napo, Yanayacu Biological Station, HOLOTYPE. **I)** *E. opimus*, Colombia, Cali.

Recent morphology-based cladistic analyses (Freitas and Brown 2004, Penz 2007) confirmed the close phylogenetic associations between *Eryphanis*, *Caligo* and *Caligopsis* Seydel. Although the work of Penz (2007) suggests that *Eryphanis* is a natural group, only two species were analyzed. This study uses comparative morphology to provide a phylogenetic analysis of all currently recognized species of *Eryphanis*, and provide illustrations of adults and genitalia. In the course of this investigation it became necessary to elevate three subspecies to species status, and describe a new species.

Material and methods

Species sampled. Appendix 1 lists the species included in the comparative morphology and phylogenetic analyses, and collection data for examined specimens. Criteria for sampling were as follows:

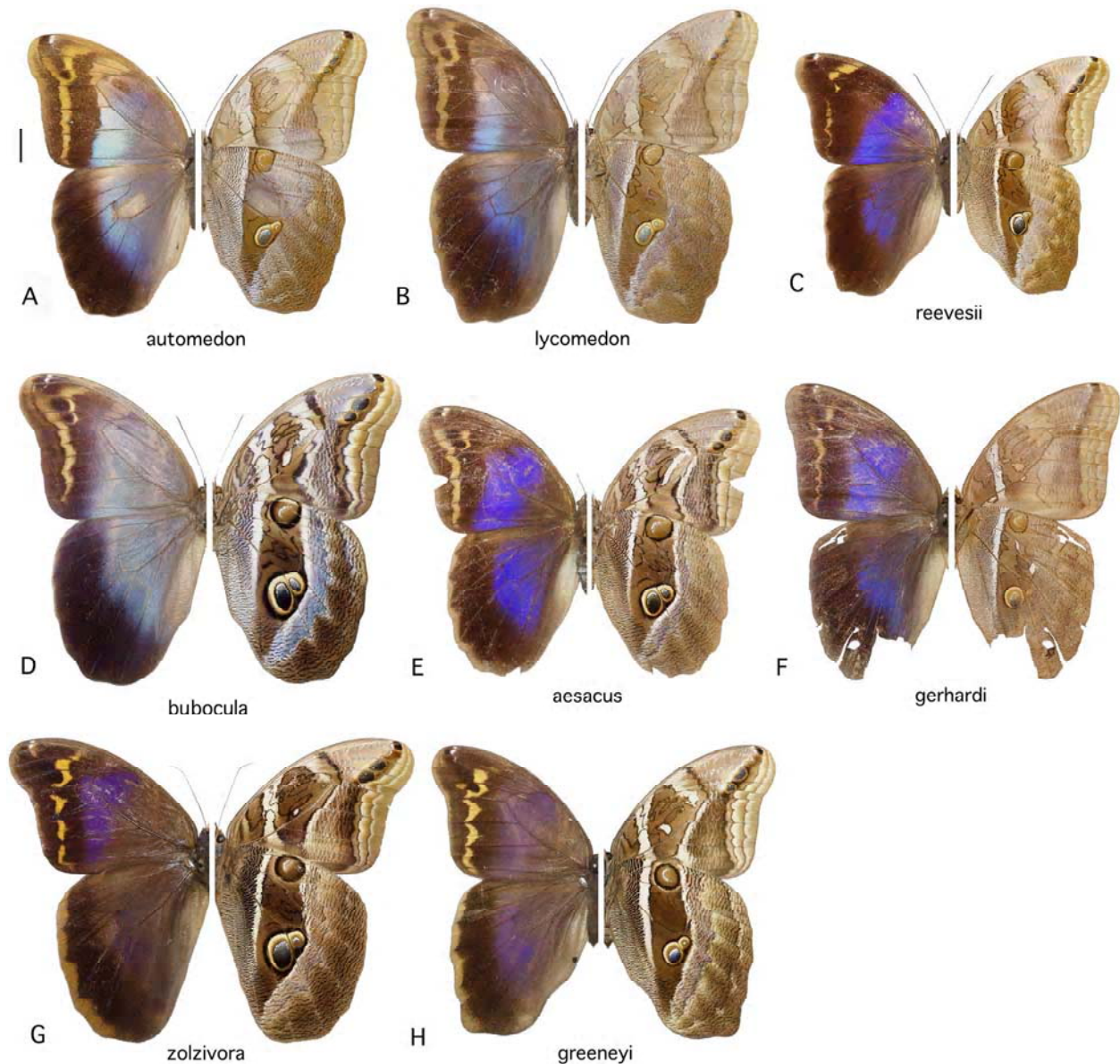


Figure 2. *Eryphanis* adult females, dorsal side on the left, ventral side on the right. Scale bar next to A = 1cm. **A)** *E. automedon*, Paraguay, Pedro Juan Caballero. **B)** *E. lycomedon*, Colombia, Cali. **C)** *E. reevesii*, Brazil, Rio de Janeiro, Nova Friburgo. **D)** *E. bubocula*, Costa Rica, Cartago, Tapanti. **E)** *E. aesacus*, Mexico, Oaxaca, Tuxtepec. **F)** *E. gerhardi*, Brazil, Rondonia, Jaru. **G)** *E. zolzivora*, Bolivia, Cochabamba. **H)** *E. greeneyi*, Ecuador, Napo, Yanayacu Biological Station, PARATYPE.

Outgroup: based on Freitas and Brown (2004) and Penz (2007), *Caligo illioneus* (Cramer, 1775), *C. idomeneus* (Linnaeus, 1758), and *Caligopsis seleucida* were selected as outgroups.

Ingroup: The ingroup included nine taxa; the five species listed by Casagrande (2004), three that are being elevated from subspecies to species, and one new species. The Species Identification section includes first hand morphological information on all taxa, and estimated geographical and altitudinal distributions based on published records and collection data (Appendix 1).

Characters and terminology. Pinned adults were used to examine external morphology. Abdomens and legs were prepared using a 10% solution of KOH, and subsequently stored in glycerol:70% ethanol solution (3:1). All structures were examined using an optical stereomicroscope with light and dark field

and magnification up to 130 X. Appendices 2 and 3 include a list of 43 characters and associated character matrix. Thirty-nine characters were structural, and nine refer to various aspects of wing color. Six uninformative characters (characters 1, 9, 32, 36, 37) were included because they may be useful for future analyses. Morphological terminology follows Kristensen (2004). Abbreviations used throughout the text are: FW, forewing; HW, hindwing; CI, consistency index; RI, retention index.

Phylogenetic analysis. Parsimony was used to infer phylogenetic relationships among species of *Eryphanis*. All characters had equal weight and multi-state characters were set as unordered. Heuristic searches in PAUP 4.0b10 (Swofford 2002) used stepwise addition with 500 tree-bisection-reconnection replicates starting from random trees. Implied weights analysis was used in the analysis that excluded wing color characters (Goloboff fit criterion $K=6$). Estimates of branch support were calculated from 1000 bootstrap replicates excluding uninformative characters and with 100 trees retained at each bootstrap run. MacClade 4 (Maddison and Maddison 2000) was used to assess the number of character changes per branch, character status, and to compare the number of steps of different topologies. Terms used to indicate character status (e.g., homoplasious above) follow MacClade 4.

Results

Parsimony analysis of the complete data set using equal weights yielded one most parsimonious tree 74 steps long (43 characters, CI excluding uninformative characters=0.6857, RI=0.7582; Fig. 3A). This tree indicates that *Eryphanis* is a monophyletic genus based on seven character changes, five of which are unique and universal. It also divided the nine *Eryphanis* species in two monophyletic groups; the automedon-group, including species that have iridescent blue dorsal coloration, and the zolzivora-group, containing the red-brown species with a well defined orange dorsal forewing submarginal band. The group-level arrangement in Fig. 3A suggests that prominent morphological changes occurred in the uncus and gnathos within the automedon-group (characters 29-33; Fig. 7D, F).

When nine wing color characters are excluded from the analysis (characters 1-6, 10-12) a different result is obtained. The strict consensus of 21

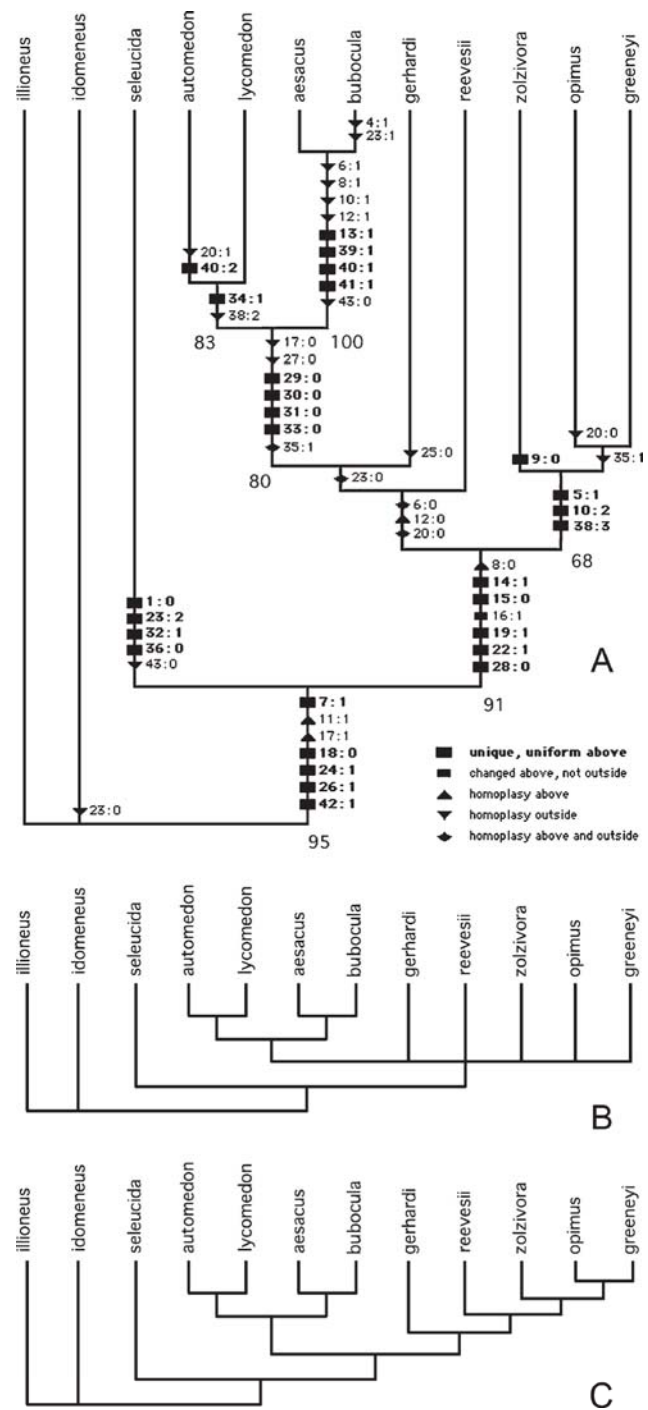


Figure 3. Trees resulting from cladistic analyses. Character numbers on branches correspond to list in Appendix 2. Legend for character status follows MacClade 4. Numbers below branches are bootstrap values. **A)** Single, most parsimonious tree from the analysis of 43 morphological characters. **B)** Strict consensus tree from the equal-weights analysis of 34 structural characters only (color characters omitted). **C)** Tree from the implied weights analysis of 34 structural characters only (color characters omitted).

equally parsimonious trees from an equal-weights analysis showed poor resolution within *Eryphanis* (Fig. 3B), and an implied weights analysis grouped *E. gerhardi* and *E. reevesii* with *E. zolzivora* and relatives (Fig. 3C). In this analysis species with a straight uncus and modified gnathos are grouped apart from the remainder taxa (characters 29-33; Fig. 3B, 7D, F), and this arrangement suggests that dorsal color changes occurred in the ancestor of *E. zolzivora* and its two closest relatives within a larger assemblage that includes 'blue' species.

Character support for the placement of *E. gerhardi* and *E. reevesii* is weak in both circumstances described above (Fig. 3A, C). When both 'color' and 'uninformative' characters are omitted, topologies in Fig. 3A and C imply the same number of steps (57 steps; characters 9, 32, 36, 37 are uninformative). However, when all 43 characters are considered, the topologies in Fig. 3A is five steps shorter than that in Fig. 3C (74 and 79 steps, respectively). Here I tentatively divide the nine species of *Eryphanis* in two species groups based on Fig. 3A because this topology incorporates more information (43 characters instead of 34, but see Discussion). Accordingly, and starting with *Eryphanis*, the main groups resulting from my analyses are listed below.

GENUS *Eryphanis* Boisduval, 1870

Eryphanis butterflies can be recognized by their dorsal wing coloration with various iridescent tones. Depending on the species the iridescence can form patches; i.e., sections of the wing that have well defined borders that separate them from non-iridescent sections (e.g., *E. automedon*, Fig. 1A). In contrast, other species have an iridescent sheen (e.g., *E. gerhardi*, Fig. 1F); i.e., a diffuse gloss that can be best seen when the butterfly is examined at an oblique angle. This genus ranges from Mexico to southern South America, and from lowland to Andean forests. Adults are crepuscular and feed on rotten fruits and sap.

The genus *Eryphanis* can be identified by the combination of six unique characters from adult morphology (Fig. 3, character numbers listed in parenthesis correspond to those in Appendix 2). In both sexes, iridescence not extended to the postmedial-basal areas of both wings (except for *E. bubocula* female) (character 2:1, Fig. 1-2). In males, presence of a scent organ in cell Cu2 (14:1, Fig. 1). This scent organ is an oval shaped depression on the wing membrane that is densely packed with elongate scales that are pale yellow to light brown, depending on the species. An area covered by shiny scales encircles this scent organ. This shiny halo reaches vein Cu2, where the scales become very dark. It is possible that the broad, black androconial patch found near the HW tornus in *E. aesacus* and *E. bubocula* (Fig. 1) might represent an extension of these dark scales. In males, absence of dorsal hindwing hairpencil in cell 1A (15:0, Fig. 7A). Instead, all males have a sparse coating of long hairs in cells 1A and 2A, which is particularly well developed in *E. reevesii*. Note that the hairpencil in cell 1A is also absent in some species of *Caligo*, a genus that is closely related to *Eryphanis* (e.g., Frühstorfer 1912, Blandin 1974, Penz 2007). In males, presence of a thin, sclerotized, setae-bearing flange associated with the dorsal, basal region of valva (19:1, Fig. 4, 7D). In males, spines along dorsal edge of valva generally organized in one single row (22:1, Fig. 4, 7F). In males, distal end of phallus projected as a hollow prong beyond opening (28:0, Fig. 4, 7E). Mature larvae are recognizable by their elongated tails, which can be ca. 25% of the total body length and are proportionately longer than those of other brassolines but similar in length to the closely related *Caligopsis* (see Furtado and Campos-Neto 2004).

SPECIES GROUPS within *Eryphanis*

automedon-group

Eryphanis automedon, *E. lycomedon* (C. Felder and R. Felder, 1862), *E. aesacus* and *E. bubocula* form a strongly supported assemblage within the automedon-group. This assemblage is supported by seven character changes, all from male genitalia (Fig. 3A, Fig. 4A-B, D-E). Here, males lack a hairpencil on the posterior portion of tegumen (17:0, Fig. 7F); the phallus prong is adjacent to distal opening (27:0, Fig. 7E); the uncus is straight in lateral view (29:0, Fig. 7D), having reduced lateral wings basally (30:0, Fig. 7D) and distally (31:0, Fig. 7D); the gnathos lacks a prong (33:0, Fig. 7F) and generally has small spines in the posterior ventral region (35:1, also present in species of the zolzivora-group, Fig. 7F).

The sister relationships of *E. gerhardi* and *E. reevesii* with the four species above is supported by three character changes, two of which pertain to wing color, and one to male genitalia. None of these character states are unique to this group as a whole. Character states that support the automedon-group are: males lack ventral FW postmedial white band (6:0, except for *E. aesacus* and *E. bubocula*; Fig. 1D-

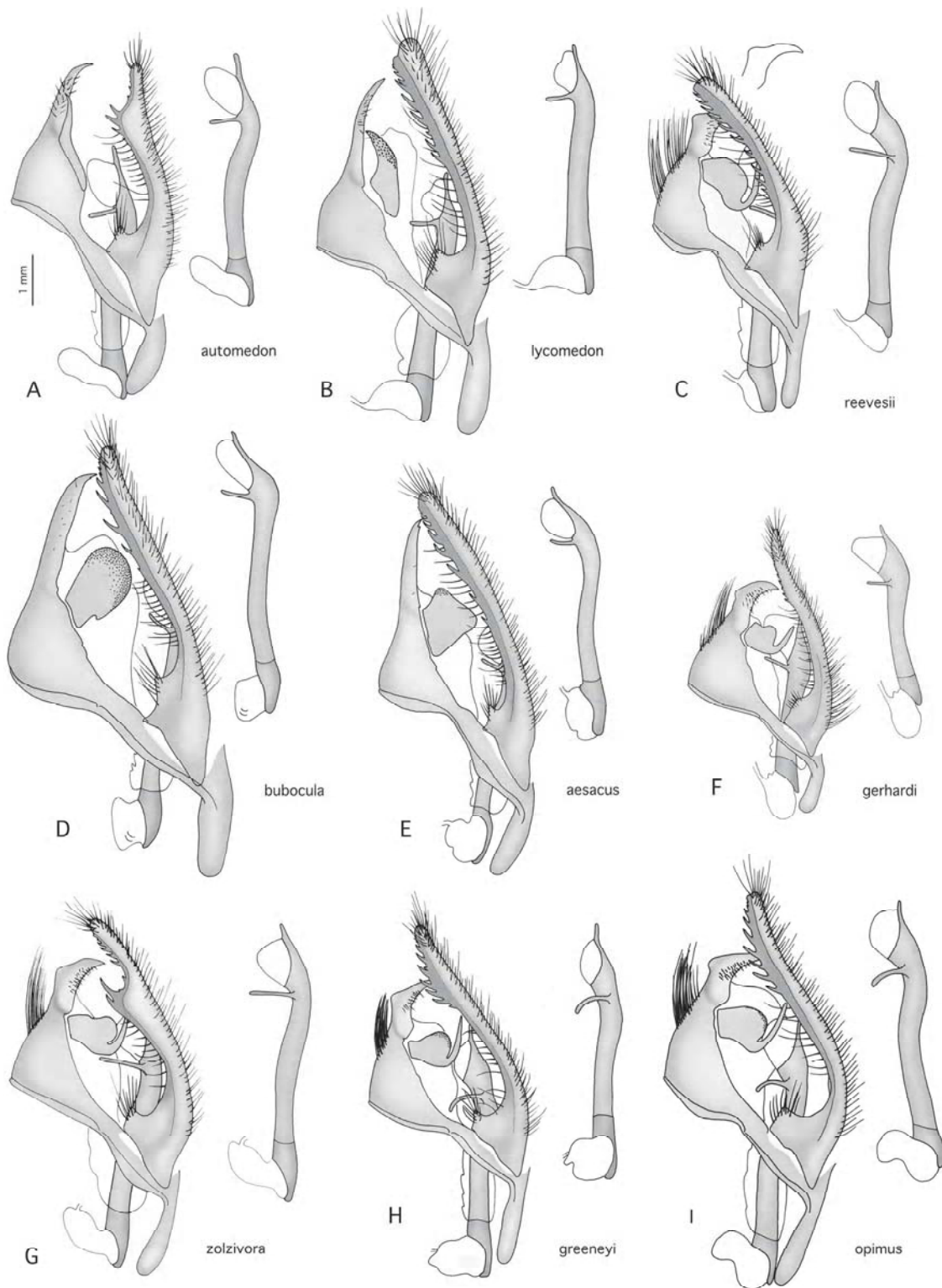


Figure 4. *Eryphanis* male genitalia in lateral view, with separate drawings of the phallus. Scale bar next to A = 1mm. Note that the phallus was not removed from the genitalic capsule, and the drawing angles are thus not homogeneous across species. **A)** *E. automedon*, Colombia, Cali. **B)** *E. lycomedon*, Colombia, Cali. **C)** *E. reevesii*, Brazil, São Paulo, Pinhal. **D)** *E. bubocula*, Costa Rica, Guanacaste, Rio San Lorenzo. **E)** *E. aesacus*, Mexico, San Luis Potosi. **F)** *E. gerhardi*, Bolivia, Cochabamba. **G)** *E. zolzivora*, Bolivia, Cochabamba. **H)** *E. greeneyi*, Ecuador, near Baños, PARATYPE. **I)** *E. opimus*, Colombia, Cali.

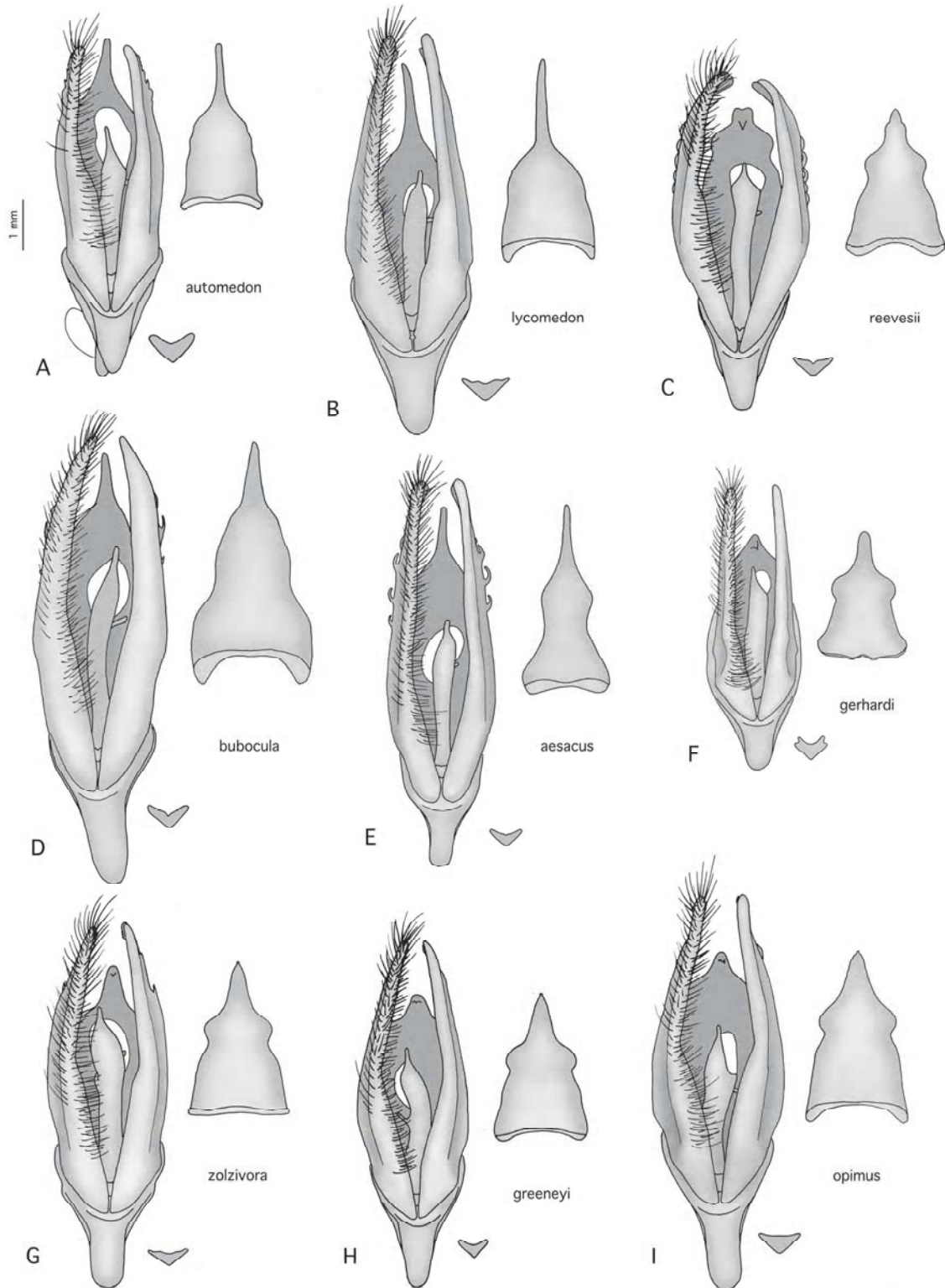


Figure 5. *Eryphanis* male genitalia in ventral view, with separate drawings of the juxta and dorsal view of tegumen+uncus. Scale bar next to A = 1mm. **A)** *E. automedon*, Colombia, Cali. **B)** *E. lycomedon*, Colombia, Cali. **C)** *E. reevesii*, Brazil, São Paulo, Pinhal. **D)** *E. bubocula*, Costa Rica, Guanacaste, Rio San Lorenzo. **E)** *E. aesacus*, Mexico, San Luis Potosi. **F)** *E. gerhardi*, Bolivia, Cochabamba. **G)** *E. zolzivora*, Bolivia, Cochabamba. **H)** *E. greeneyi*, Ecuador, near Baños, PARATYPE. **I)** *E. opimus*, Colombia, Cali.

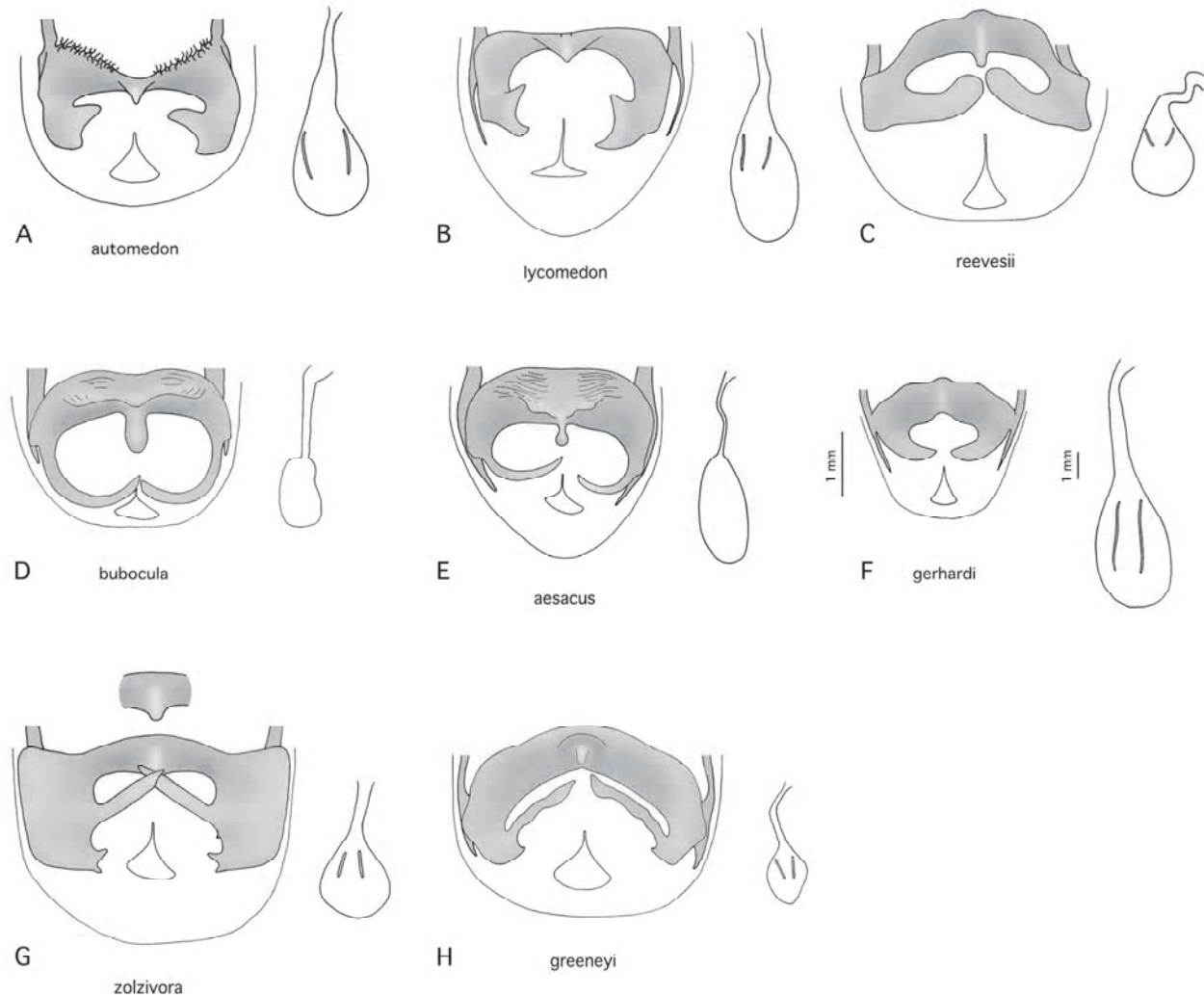


Figure 6. *Eryphanis* female sterigma and corpus bursa. Ribs of the intersegmental sac were omitted. Scale bars next to F = 1mm, note that sterigma and corpus bursa are in different magnifications. **A)** *E. automedon*, Peru, Puerto Maldonado. **B)** *E. lycomedon*, Costa Rica, Puntarenas. **C)** *E. reevesii*, Brazil, São Paulo, Pinhal. **D)** *E. bubocula*, Costa Rica, Cartago, Tapanti. **E)** *E. aesacus*, Mexico. **F)** *E. gerhardi*, Brazil, Rondonia, Jaru. **G)** *E. zolzivora*, Bolivia, Cochabamba. **H)** *E. greeneyi*, Ecuador, Napo, Yanayacu Biological Station, PARATYPE.

E, 7A), the ventral HW eyespot in cell Cu1 is contained inside this cell (12:0, except for *E. aesacus* and *E. bubocula*, Fig. 1D-E, 7A), and the valva lacks subterminal swelling (20:0, except for *E. automedon*; Fig. 4A-B, D-E, 7D).

zolzivora-group

Eryphanis zolzivora, *E. opimus* (Staudinger, 1887) and *E. greeneyi*, **new species** were grouped by three character changes, two from wing color and one from female genitalia (Fig. 1G-I, 3A, 6G-H). In males of this group, the distal branch of the dorsal FW submarginal band does not form a line across cells M2 and M3 (5:1, Fig. 7A), and the dorsal HW orange marginal edge is well developed (10:2, Fig. 7A). In females, the sterigma has one elongated projection plus smaller points (38:3, Fig. 7J).

Association between *Eryphanis* and *Caligopsis*

Penz (2007) listed three characters supporting sister relationships between *Eryphanis* and *Caligopsis*, one of which is unique (character 26:1 in this study). Four additional character changes are given here (Fig. 3A, Appendices 2 and 3), and the most important are the presence of a partly sclerotized setae-

bearing region in the diaphragma around the male phallus (24:1, Fig. 7B), and the female ductus seminalis joining a channel in the body wall that is dorsal to the antrum (42:1, Fig. 7C).

SPECIES IDENTIFICATION

Below I provide a diagnosis and annotated redescription for previously recognized *Eryphanis* species, plus the description of a new species. This information is intended as an update to the checklist by Casagrande (2004), and discussion of subspecific taxa were kept intentionally brief. References to the original descriptions of all taxa listed here can be found in Lamas et al. (1995).

Eryphanis automedon (Cramer, 1775) (Fig. 1A, 2A, 4A, 5A, 6A)

Type species of *Eryphanis* Boisduval by original designation.

Type locality. Surinam.

Diagnosis. Both sexes similar to *E. lycomedon*. Males can be distinguished from *E. lycomedon* by the localized dorsal night blue to purple iridescent patches on both FW and HD, and HW margin usually lacking a pale brown outline dorsally, plus the valva with a narrow tip and subterminal swelling. The narrow valva tip can be often seen in pinned specimens without preparation, thus facilitating identification. Females nearly indistinguishable from *E. lycomedon*, but the following trend was observed. In *E. automedon* females the dorsal FW iridescence sometimes forms a pale blue sheen that extends into discal cell, the dorsal HW pale brown outline is vestigial or absent. The HW iridescence is usually more extended distally within the Cu1 and Cu2 cells, and the projection at vein Cu1 is sometimes less pronounced than in *E. lycomedon*. Old, faded *E. automedon* females from locations overlapping with *E. lycomedon* can only be confidently distinguished from the latter by the sterigma through dissection.

Annotated redescription. Male. FW length 55-59 mm (n=8). Dorsal FW and HW with conspicuous and localized night blue to purple iridescent patches, depending on the locality. FW iridescent patches extend from submedial to postmedial areas. HW always with an iridescent patch (variable in size, and subtle in old specimens), never a sheen. Dorsal FW submarginal line faint, diffuse, continuous. Dorsal HW marginal outline absent. HW with a projection at vein Cu1 that extends beyond anal margin. FW and HW main ventral color varying from faded brown in Brazilian and Peruvian specimens, to faded caramel color in Colombian, Bolivian, and Paraguayan specimens. Ventral HW white postmedial transverse band vestigial or absent. Ventral HW eyespot in cell Cu1 contained within cell. Uncus elongate, slender; valva with subterminal swelling; and gnathos slender, sharply pointed, with few or no spines.

Female. FW length 59-60 mm (n=3). Wing color pattern different from male. Dorsal sky-blue iridescent patches on medial areas of FW and HW, slightly larger on HW. Dorsal FW iridescent patch expanded inside discal cell in some specimens. Dorsal FW discal cell often with a pair of faint brown stripes near the distal end. FW submarginal line faded orange, conspicuous, continuous, nearly straight. Submarginal branch of FW submarginal line starts at M1, and postmedial branch starts at wing margin or below the R stem and joins the submarginal branch in cell M2. Dorsal HW iridescence more extended distally than in *E. lycomedon*, and marginal outline absent or vestigial. Ventral surface of wings as in male. Posterior edge of sterigma with conspicuous oblique ribs, and sterigma projections with two blunt points.

Distribution. Venezuela to the Guianas and Brazil (northern and eastern), and Colombia to Paraguay; ranging from sea level (e.g., Obidos, Brazil) to ca. 1,000 m (e.g., Cali, Colombia) (Casagrande 2004, Appendix 1).

Remarks. Six dissected males from five countries (Appendix 1) show consistent genitalic morphology, but varied in their iridescence hue (more purple or more blue), and the size of the HW iridescent patch (extremely small in a male from Bolivia, and some males from Trinidad, French Guiana, and Brazil; not

illustrated). Casagrande (2004) recognized seven subspecies, but here I elevate *E. lycomedon* C. Felder and R. Felder, 1862 to full species (see below). The subspecies of *E. automedon* should be reassessed by examination of type specimens (see comments below on *E. automedon novicia* Stichel, 1904). In females of both *E. automedon* and *E. lycomedon* the HW projection at vein Cu1 varies in size (e.g., it is short in Paraguayan specimens, Fig. 2A; it is long in Peruvian specimens, not illustrated). The life history of *E. automedon* has been described by Dias (1979) based on specimens from Minas Gerais, Brazil [as *E. polyxena*].

***Eryphanis lycomedon* (C. Felder and R. Felder, 1862), status revised
(Fig. 1B, 2B, 4B, 5B, 6B)**

Type locality. Colombia.

Diagnosis. Both sexes similar to *E. automedon*. Males can be distinguished from *E. automedon* by having a purple iridescent sheen on HW (glossy when specimen is tilted), and HW margin usually with a pale brown outline dorsally, plus the valva with an even width and slightly wider at tip. The widened valva tip can be often seen in pinned specimens without dissection, thus facilitating identification. Females nearly indistinguishable from *E. automedon*, but the following trend was observed. In females of *E. lycomedon* the dorsal FW iridescence forms a pale blue sheen barely extended into discal cell, the dorsal HW pale brown outline is usually well developed. The HW iridescence is usually less extended distally within the Cu1 and Cu2 cells, and the projection at vein Cu1 is usually more pronounced than in *E. automedon*. Old, faded females from locations overlapping with *E. automedon* can only be confidently distinguished from the latter by the sterigma through dissection.

Annotated redescription. Male. FW length 55-60 mm (n=5). Dorsal FW and HW with purple iridescent sheen extended from submedial to postmedial areas of the FW. In some specimens the FW iridescence can be sufficiently strong to form an iridescent patch. Iridescence of the HW usually a sheen and not forming a discrete patch, but in some specimens HW iridescence can be sufficiently strong to approximate an iridescent patch. Dorsal FW submarginal line faint, diffuse, continuous. Dorsal HW marginal outline thin to vestigial or absent. HW with a projection at vein Cu1 that extends beyond anal margin. Ventral FW and HW faded caramel color. Ventral HW white postmedial transverse band vestigial or absent. Ventral HW eyespot in cell Cu1 contained within cell. Uncus elongate and slender, valva nearly uniform in width and slightly widened at tip, gnathos broad, sharp-pointed and with small terminal spines.

Female. FW length 57-66 mm (n=5). Wing color pattern different from male. Dorsal FW and HW with sky-blue iridescent patches. Iridescent patches on medial areas of both wings, slightly larger on the HW. FW iridescent patch barely extends into cell Cu1 and discal cell, but is conspicuous across cell Cu2. Dorsal FW submarginal line faded orange, conspicuous, continuous, nearly straight. Submarginal branch of FW submarginal line starts at M1, and postmedial branch starts at wing margin or below the R stem, and joins the submarginal branch in cell M2. Dorsal HW iridescence less extended distally than in *E. automedon*. Dorsal HW marginal outline vestigial to moderately developed, depending on the locality. Ventral surface of wings as in male. Posterior edge of sterigma with delicate transverse ribs, sterigma projection with two blunt points.

Distribution. Guatemala to Colombia (DeVries 1987), expanded here to Ecuador, Bolivia and Southern Brazil (Santa Catarina), with an estimated altitudinal range of 0-1,200 m (DeVries 1987 and Appendix 1). Contrasting the closely related *E. automedon*, the range of *E. lycomedon* includes Central America and western South America, but is extended eastward into southern Brazil. Although I haven't seen specimens from Paraguay, it would not be surprising if this species occurred in that country.

Species status. Two issues need to be considered regarding this species: name and status. The taxon demonstrated here to be distinct from *E. automedon* corresponds to what has been previously known as *E. polyxena* Meerburgh, 1780, or *E. polyxena lycomedon* (see DeVries 1987). Nonetheless, the name '*polyxena*' is preoccupied and thus invalid (Cowan 1974, Casagrande 2004). The type locality for *E. polyxena*

is 'America', but given that Meerburgh was a Dutchmen the material he studied probably came from Surinam, which is also the type locality of *E. automedon*. Therefore, Casagrande (2004) correctly considered *E. polyxena* a synonym of *E. automedon*. Note that the replacement name *E. automedaena* (Hübner, 1819) was proposed for *E. automedon* by Hübner (1819:51) to address an issue of gender agreement with his genus *Moera* Hübner (junior synonym of *Amathusia* Fabricius, see Hemming 1967), and this name was also synonymized by Casagrande (2004).

Examination of a series of specimens of *E. lycomedon* and *E. automedon* verified that these two taxa show clear and consistent differences both in wing color and genitalic morphology (Fig. 1-2, 4-6). Males of *E. lycomedon* differ from *E. automedon* by the wing iridescence forming a diffuse sheen on the HW (compare Fig. 1A and B), and the valva being sub-terminally narrow and broadening at the very tip (compare Fig. 4A and B), which can be seen in pinned specimens without dissection. Females are distinguished from *E. automedon* by the faintness or absence of the iridescence inside the FW discal cell, the smaller iridescent patch on the HW plus the usually well developed dorsal HW pale brown outline (compare Fig. 2A and B), and the posterior edge of sterigma with delicate transverse ribs (compare Fig. 6A and B). Furthermore, these species have overlapping geographical distribution (males in Fig. 1A and B were both collected in Cali, Colombia; see also Appendix 1). In combination, color pattern, genitalia, and sympatry provide strong evidence that *E. lycomedon* and *E. automedon* constitute separate species. Finally, the *E. lycomedon* specimens studied here (Fig. 1B, Appendix 1) match the type locality and original description in Felder and Felder (1862), and also the description in Frühstorfer (1912).

Remarks. Six dissected males from five countries (Appendix 1) show consistent genitalic morphology. In a few of these specimens the HW iridescence is strong, approximating the pattern in some of the less iridescent *E. automedon* males (see above). Examination of type specimens will be necessary to verify if there are any valid, described subspecies that could be assigned to *E. lycomedon*. For example, the descriptions of *E. automedon novicia* (type locality Ecuador, Los Rios) in Stichel (1909) and Frühstorfer (1912) seem to match the general wing color of *E. lycomedon*. In females of both *E. lycomedon* and *E. automedon* the HW projection at vein Cu1 varies in size (e.g., it is short in Costa Rican specimens, see DeVries 1987; it is long in Colombian specimens, Fig. 2B). A brief life history account is given by DeVries (1987) for Costa Rican *E. lycomedon*.

***Eryphanis aesacus* (Herrich-Schäffer, 1850)**
(Fig. 1E, 2E, 4E, 5E, 6E)

Type locality. Mexico.

Diagnosis. Males similar to *E. bubocula*, but distinguished from this species by the smaller size, the reduced dorsal iridescent patch of the FW, and by the HW iridescent patch that extends toward the medial area around the anterior edge of the black androconial patch. Males have square-shaped gnathos, narrower valva in ventral view, and constricted tegumen in dorsal view. Females easily distinguished from *E. bubocula* by their smaller size, well defined dorsal purple iridescent patches on FW and HD, and sterigma with a narrower posterior ridge and smaller midline keel.

Annotated redescription. Male. FW length 47-50 mm (n=4). Dorsal FW and HW with conspicuous and localized mid-night blue to purple iridescent patches. Iridescent patch extends from medial to postmedial areas of the FW, occupying the distal one-third of the FW discal cell. HW iridescent patch extends around the anterior edge of the black androconial patch toward the medial area, and also along the wing margin. Dorsal FW submarginal line usually faint (but can be well defined in some specimens), diffuse, continuous. HW edge rounded with a vestigial marginal outline dorsally. Dorsal HW with a large broad patch of black androconial scales above tornus. Androconial patch generally occupying a smaller space inside cell M2 than *E. bubocula*. Ventral FW and HW main color light brown. Ventral HW with a well-developed white postmedial transverse band. HW ventral eyespot in cell Cu1 large, expanding to cell Cu2. Uncus elongate and slender, valva narrow, gnathos square-shaped.

Female. FW length 53-58 mm (n=5). Dorsal FW and HW with conspicuous and localized purple iridescent patches extended across discal cell of the FW and between submedial and medial areas of the

HW. Dorsal FW orange submarginal line well developed, continuous. Submarginal and postmedial branches of submarginal line start slightly above M1. Dorsal HW marginal outline diffuse. HW edge rounded and slightly undulated. Ventral FW and HW as in male. Sterigma with a narrow posterior ridge and narrow projections.

Distribution. Mexico, Guatemala, and Nicaragua (Frühstorfer 1912), extended here to El Salvador (Appendix 1). Based on collection labels, this species seem to occur from 500-1,800 m (Appendix 1).

Remarks. In male specimens from Nicaragua and El Salvador the dorsal FW submarginal line is stronger than in Mexican specimens, but can still be considered 'faded' in comparison with males in the *zolvivora*-group where this band is well defined and vividly colored. I have not seen specimens from either Honduras or Nicaragua.

***Eryphanis bubocula* (Butler, 1872), status revised**
(Fig. 1D, 2D, 4D, 5D, 6D)

Type locality. Costa Rica.

Diagnosis. Males similar to *E. aesacus*, but distinguished from this species by the larger size, the larger dorsal FW iridescent patch, and by the reduced size of the dorsal HW iridescent patch, which usually does not extend toward the medial area. Males have rounded gnathos, and wider valva in ventral view. Females distinguished from *E. aesacus* by their larger size, pale grayish blue dorsal iridescent sheen from basal to medial areas of both wings, and sterigma with a broader posterior ridge and larger midline keel.

Annotated redescription. Male. FW length 60 mm (n=1). Dorsal FW and HW with conspicuous and localized mid-night blue to purple iridescent patches extended from medial to postmedial areas of the FW, occupying half the length of the FW discal cell. Iridescent patches restricted to the postmedial area of the HW. Dorsal FW submarginal line faint, diffuse, continuous. HW edge rounded with a vestigial marginal outline dorsally. Dorsal HW with a large broad patch of black androconial scales above tornus. Androconial patch usually occupying a larger space of cell M2 than *E. aesacus*, taking up approximately one-third of the length of the cell. Ventral FW and HW main color brown. Ventral HW white postmedial transverse band well developed. HW ventral eyespot in cell Cu1 large, expanding to cell Cu2. Uncus elongate and slender, valva narrow, and gnathos rounded.

Female. FW length 67 mm (n=2). Dorsal FW and HW with pale grayish blue iridescent sheen extended from basal to postmedial areas of the FW, stronger below Cu2, and from basal to medial areas of the HW, slightly more intense than in the FW. Dorsal FW orange submarginal line well developed, continuous, fading in cell Cu2. Submarginal branch of FW submarginal line starts above M1, and postmedial branch starts at wing margin or below the R stem. Dorsal HW marginal outline absent. HW edge rounded and slightly undulated. Ventral FW and HW as in male. Sterigma with a broad posterior ridge and narrow projections.

Distribution. Costa Rica to Colombia and the Amazon basin (Godman and Salvin 1879, Frühstorfer 1912, Appendix 1). In Costa Rica it is reported from 500 to 1,800 m on both slopes (Cubero 1985, DeVries 1987).

Species status. *Eryphanis bubocula* differs from *E. aesacus* in wing pattern and genitalia. Godman and Salvin (1879) considered these taxa separate species, and pointed to diagnostic differences in wing length and color for both sexes. Their characters were confirmed here, and additional diagnostic characters are also provided for both taxa (see diagnoses). It is worth noting that *E. bubocula* females resemble *Caligo illioneus oberon* Butler, 1870 (see DeVries 1987 for illustrations) while those of *E. aesacus* assume a more ordinary *Eryphanis* female pattern (compare Fig. 2D and E). In concert, differences in both wing characters and genitalia support the reinstatement of species status of *E. bubocula*.

Remarks. It would be interesting to compare specimens from higher elevations with those from the Amazon Basin (possibly from the subspecies *juruaana* Frühstorfer, 1912), which were unavailable to me for examination. The life history of *E. bubocula* was described and illustrated by Cubero (1985) from Costa Rica, including observations on adult behavior.

***Eryphanis reevesii* (Doubleday, 1849)**
(Fig. 1C, 2C, 4C, 5C, 6C)

Type locality. [Brazil].

Diagnosis. Males small, with deep purple to reddish purple dorsal iridescent sheen on FW and HW, and lacking a dorsal FW submarginal line. Among all *Eryphanis* species, *E. reevesii* males have the smallest scent organ in cell Cu2. Females have deep purple dorsal iridescent patches on FW and HW, and the FW postmedial branch of submarginal line starts at wing margin, being clearly visible in the cell below the R veins.

Annotated redescription. Male. FW length 49-50 mm (n=2). Dorsal FW and HW with deep purple to reddish purple iridescent sheen distributed on submedial areas of both wings (slightly pinkish in some specimens). In the FW, it occupies the distal third of the discal cell, extending almost to the wing margin. Dorsal FW submarginal line absent. Dorsal HW with a vestigial marginal outline and with a projection at vein Cu1 that extends beyond anal margin. Ventral FW and HW caramel color. Ventral HW white postmedial transverse band vestigial. Ventral HW eyespot in cell Cu1 contained within cell. Uncus humped, valva narrow.

Female. FW length 53 mm (n = 2). Wing color pattern different from male. Dorsal FW and HW with deep purple iridescent patches limited to submedial areas of both wings. FW submarginal line dark to pale orange, conspicuous, continuous or interrupted, wavy, variable in thickness. Submarginal branch of FW submarginal line starts at M1 or below, decreasing in width from M3 to 2A, and postmedial branch starts at wing margin ends in the M2 cell. HW with a vestigial marginal outline. Ventral surface of wings as in male. Sterigma broad and with rounded projections.

Distribution. Central and southern Brazil to Paraguay (Frühstorfer 1912, Casagrande 2004, Appendix 1), at elevations of 200 to 1,000 m (e.g., Blumenau, and Nova Friburgo, Brazil).

Remarks. Casagrande (2004) recognized two subspecies, the nominate subspecies being from Brazil (deep purple), and *reevesii pusillus* Stichel, 1904 (reddish purple) from Paraguay. I have seen reddish specimens from Santa Catarina, Brazil (not illustrated). The larval stages were described by Müller (1886) from southeastern Brazil. A brief account of time of development and flight period are provided by Frühstorfer (1912) based on Adolfo Mabilde's rearing records for Southern Brazil [as *E. gerhardi pusillus*].

***Eryphanis gerhardi* (Weeks, 1902)**
(Fig. 1F, 2F, 4F, 5F, 6F)

Type locality. Bolivia.

Diagnosis. Males with deep purple iridescent sheen dorsally on FW and HW, plus a distinctive ventral caramel to orange coloration and white spot at crossvein m2-m3. Females with purple iridescent patched on FW and HW, and same diagnostic ventral color and white HW spot as in males.

Annotated redescription. Male: FW length 57-60 mm (n=4). Dorsal FW and HW with deep purple iridescent sheen that can be sufficiently strong to resemble iridescent patches in both wings in some specimens. Dorsal FW and HW iridescence extended from submedial to postmedial areas of both wings. Dorsal FW submarginal line usually faint (but can be well defined in some specimens), diffuse, continuous. Dorsal HW marginal outline absent. HW with a projection at vein Cu1 that extends beyond anal margin. Ventral FW and HW orange to faded caramel color. Ventral HW white postmedial transverse

band absent for the most part, leaving a residual thin line at crossvein m1-m2. Broad white spot at crossvein m2-m3. Ventral HW eyespot in cell M3 absent or reduced, detached from large eyespot in cell Cu1. Ventral HW eyespot in cell Cu1 contained within cell, and with a gray-brown posterior spot inside inner circle. Uncus humped, valva narrow and with few small spines.

Female. FW length 61 mm (n=1). Wing color pattern different from male. Dorsal FW and HW with deep purple iridescent patches limited to medial area of both wings. FW submarginal line orange, conspicuous, continuous, wavy. Submarginal branch of FW submarginal line starts at M1, decreasing in width from M3 to 2A, and postmedial branch starts at M1 and ends in the M2 cell. Ventral surface of wings as in male. Sterigma projections broad and slightly pointed.

Distribution. Ecuador to Bolivia (Frühstorfer 1912, Appendix 1), at elevations of 200 to 400 m (e.g., Jaru, Brazil and Buenavista, Ichilo, Bolivia).

Remarks. Of all *Eryphanis* species, *E. gerhardi* has the smallest male genitalia relative to its wingspan. Casagrande (2004) lists no subspecies for *E. gerhardi*.

***Eryphanis zolzivora* (Hewitson, 1877)**
(Fig. 1G, 2G, 4G, 5G, 6G)

Type locality. Bolivia.

Diagnosis. Males and females reddish-brown with conspicuous FW orange submarginal line. Distinguished from *E. opimus* and *E. greeneyi* by the dorsal FW orange submarginal line forming a thin, yet conspicuous distal orange crescent mark that is unique to this species. Here the postmedial branch of this line extends anteriorly to the wing margin, and the HW projection at Cu1 is vestigial or small, not extending beyond the anal margin.

Annotated redescription. Male. FW length 57-60 mm (n=3). Dorsal FW and HW with reddish-brown background and very faint pinkish iridescent sheen from submedial to postmedial areas of the FW, starting approximately at midlength of the discal cell, but barely visible on the HW. Dorsal FW with a well-defined orange submarginal line interrupted by small gaps below M3, and forming a V-shaped mark with the arms directed distally in cell M3. Submarginal branch of FW submarginal line starts in cell M2, and postmedial branch starts at wing margin, being clearly visible below the R veins. Wing apex with a thin, orange crescent mark. Dorsal FW and HW with well-developed orange marginal outline. HW with a small projection at vein Cu1 that does not extend beyond anal margin. Ventral FW and HW main color brown. Ventral HW white postmedial transverse band well developed, continuous. Ventral HW with brown wavy lines across discal cell. Ventral HW eyespot in cell Sc+Rs not outlined by a pale halo. Ventral HW eyespot in cell Cu1 very large, expanding to cell Cu2. Inner dark circle larger than in *E. opimus* and *E. greeneyi*. Uncus humped, valva with subterminal swelling.

Female. FW length 66 mm (n=1). Dorsal FW and HW with reddish-brown background that is not as dense as in male, producing a semi-transparent effect. Both wings with pinkish iridescent sheen in the medial area, faint overall, but stronger in the HW. Dorsal FW with a well defined, thick orange submarginal line, barely interrupted at the wing veins below M3, and forming a V-shaped mark with the arms directed distally in cell M3. Submarginal branch of FW submarginal line starts in cell M2. Postmedial branch of submarginal line starts at wing margin, clearly visible in the cell below the R stem. Wing apex with a thin, orange crescent mark, as in male. HW projection at Cu1 can be less distinct than in male, and very small in some specimens. Ventral surface of wings as in male. Sterigma projection with an elongated arm, and multiple points anteriorly.

Distribution. Bolivia, perhaps reaching southern Peru (Frühstorfer 1912, Appendix 1). Collection labels list an elevation of 1,650 m (El Palmar, Cochabamba, Bolivia).

***Eryphanis opimus* (Staudinger, 1887), status revised**
(Fig. 1I, 4I, 5I)

Type locality. Colombia.

Diagnosis. Males and females reddish-brown with conspicuous FW orange submarginal line. Examined males are distinguished from *E. zolzivora* and *E. greeneyi* by the thinner dorsal FW orange submarginal line, and the postmedial branch of this line that does not extend to the wing margin. The HW projection at Cu1 is intermediate in size: longer than *E. zolzivora*, but smaller than *E. greeneyi*. Thin lines always present ventrally in HW discal cell.

Annotated redescription. Male. FW length 62 mm (n=1). Dorsal FW and HW with reddish-brown background and a faint pinkish iridescent sheen from submedial to postmedial areas of the FW, starting approximately at midlength of discal cell, and barely visible on HW. Dorsal FW with a well-defined, thin orange submarginal line, interrupted by small gaps below M3, and forming a V-shaped mark with the arms directed distally in cell M3. Submarginal branch of FW submarginal line starts in cell M2. Postmedial branch of submarginal line starts at cell M1. Dorsal FW and HW marginal outline well developed. HW projection at Cu1 present, extending beyond anal margin, but not as long or well defined as in *E. greeneyi*. Ventral FW and HW main color light brown. Ventral HW white postmedial transverse band well developed, continuous. Ventral HW with brown wavy lines across discal cell. Ventral HW eyespot in cell Sc+Rs outlined by a pale halo. Ventral HW eyespot in cell Cu1 large (smaller than *E. zolzivora* but larger than *E. greeneyi*) expanding to cell Cu2. Uncus humped, valva narrow, phallus prong displaced anteriorly from the distal opening.

Female. Not available for examination.

Distribution. Colombia (see comments on *E. zolzivora* in Frühstorfer 1912, Appendix 1), occurring in Cali at an elevation of ca. 1,000 m.

Species status. Morphological differences between the Colombian *E. opimus* and the Bolivian *E. zolzivora* warrant species status. Male *E. opimus* differ from *E. zolzivora* in wing color and shape (compare Fig. 1G and I, see diagnoses). Furthermore, there are significant differences in male genitalia. The male valva is narrow in *E. opimus*, but in *E. zolzivora* it bears a large and distinctive subterminal swelling (compare Fig. 4G and I). This evidence supports the revised status for *E. opimus* as a separate species from *E. zolzivora*.

***Eryphanis greeneyi* Penz and DeVries, new species
(Fig. 1H, 2H, 4H, 5H, 6H)**

Type locality. Ecuador, Napo Province, Cosanga.

Diagnosis. Males and females reddish-brown with conspicuous FW orange submarginal line. Distinguished from *E. zolzivora* and *E. opimus* by the postmedial branch of the FW orange submarginal line that does not extend to the costal wing margin, and the longer HW projection at Cu1. Ventral HW white postmedial transverse band branched into crossvein m1-m2, and brown lines in discal cell absent or vestigial. Male valva with a weak subterminal swelling more distal than in *E. zolzivora*.

Description. Body dark brown dorsally, lighter brown ventrally. Antennae brown with narrow clubs. Eyes reddish brown. Palps light brown with a dark brown lateral stripe. Legs dark brown.

Male wings. FW length 55-65 mm (n=4). Dorsal FW and HW with opaque dark brown to reddish-brown background and a very faint pinkish iridescent sheen from submedial to postmedial areas of the wings, barely visible on the HW. Dorsal FW with a well defined, thick orange submarginal line interrupted by small gaps at the wing veins below M3, and forming a V-shaped mark with the arms directed distally in cell M3. Submarginal branch of FW submarginal line starts in cell M2. Postmedial branch of submarginal line starts in cell M1. Dorsal FW and HW with well-developed orange marginal outline. HW projection at Cu1 present, extending beyond anal area. Ventral FW and HW brown to dark caramel color. Ventral FW and HW with well-developed white postmedial band that branches into crossvein m1-m2 of the HW. Ventral HW brown wavy lines across discal cell faint or absent. Ventral HW eyespot in cell

Sc+Rs outlined by a nearly complete pale halo. Ventral HW eyespot in cell M3 present, large, fused to that in cell Cu1, nearly reaching crossvein m3-cu1. Ventral HW eyespot in cell Cu1 large, yet smaller than *zolzivora* and *opimus*, barely expanding into cell Cu2.

Male genitalia. Uncus humped, valva with mild subterminal swelling, phallus prong displaced anteriorly from the distal opening.

Female wings. FW length 64 mm (n=2). Dorsal FW and HW with dark brown background that is not as dense as in the male, producing a semi-transparent effect. Both wings with pinkish iridescent sheen in the medial area, faint overall yet stronger in the HW. Dorsal FW with a well defined, thick orange submarginal line paler than in males, barely interrupted at the wing veins below M3, and forming a V-shaped mark with the arms directed distally in cell M3. HW projection at Cu1 less distinct, and dorsal HW marginal outline paler than in males. Remaining characters similar to males.

Female genitalia. Sterigma shaped as a curved plate with an indentation and a small ridge at midline. Sterigma projections with two points; anterior point short, posterior long and narrow. Corpus bursa oval with paired signa.

Etymology. This species is named for the contemporary naturalist Harold Francis Greeney III in recognition of his many contributions to our understanding of the natural history of the Ecuadorian invertebrate and vertebrate fauna.

Holotype. Male, three labels, separated by //, repository and other information in parentheses when applicable: Ecuador, Napo, Yanayacu Biological Station, 5km W of Cosanga, May 2007 // reared on *Chusquea scandens*, H. F. Greeney // *Eryphanis greeneyi* Penz and DeVries HOLOTYPE // (The Natural History Museum, London, UK; habitus in Fig. 1H). **Paratypes.** Five males and four females. Male, two labels: ECUADOR: Napo Prov., Yanayacu Biological Station, S00°35.9' W77°53.4, 2163 m, Reared 3001000, 2006 [handwritten on back of label] H. Greeney // *Eryphanis greeneyi* Penz and DeVries

PARATYPE // (Museo Ecuatoriano de Ciencias Naturales, Ecuador). Male, two labels: Ecuador, Provincia Napo, YYBS, 2000 m, 5-Feb-[20]02, H. Greeney, TW 1618 // *Eryphanis greeneyi* Penz and DeVries PARATYPE // (American Museum of Natural History, USA). Male, two labels: Ecuador, Provincia Napo, 12-Apr-[20]00, H. Greeney, TW 2164 // *Eryphanis greeneyi* Penz and DeVries PARATYPE // (DeVries Collection, USA). Male, four labels: Rio Blanco, near Baños, Ecuador, 1,650 m, Abril 17/[19]56 // J. R. Neidhoffer Collection, MILWAUKEE PUBLIC MUSEUM // 07-33 dissected by C.M. Penz // *Eryphanis greeneyi* Penz and DeVries PARATYPE // (genitalia in Fig. 4H and 5H). Male, four labels: Balzapampa, Ecuador, 000 // 571 // 07-96 dissected by C.M. Penz // *Eryphanis greeneyi* Penz and DeVries PARATYPE // (Florida Museum of Natural History, USA). Female, three labels: Ecuador, Napo, Yanayacu Biological Station, 5km W of Cosanga, May 2007 // reared on *Chusquea scandens*, H. F. Greeney // *Eryphanis greeneyi* Penz and DeVries PARATYPE // (The Natural History Museum, London, UK). Female, three labels: ECUADOR: Napo Prov., Yanayacu Biological Station, S00°35.9' W77°53.4, 2163 m, REARED 1218, 2005 Jan [handwritten on back of label] H. Greeney // 07-127 dissected by C. M. Penz // *Eryphanis greeneyi* Penz and DeVries PARATYPE // (Museo Ecuatoriano de Ciencias Naturales, Ecuador; genitalia in Fig. 6H). Female, two labels: ECUADOR: Napo, Biol. Yanayacu, 2000m, Reared: # 201, Dyer/Greeney, Sept 2001 // *Eryphanis greeneyi* Penz and DeVries PARATYPE // (American Museum of Natural History, USA; habitus in Fig. 2H). Female, two labels: Ecuador, Provincia Napo, San Isidro, 2000 m, 21-Dec-[19]99, H. Greeney, TW 1952 // *Eryphanis greeneyi* Penz and DeVries PARATYPE // (DeVries Collection, USA).

Distribution. Ecuador, and perhaps northern Peru (see comments on *E. zolzivora* in Frühstorfer 1912), at an elevation ranging between 1,650 and 2,163 m (Appendix 1). Carlos Peña provided me with photographs of two males from Peru: a specimen from Amazonas department (Valle de Huamanpata, Lejia, 2,150 m) closely matches the description of *E. greeneyi*, but a specimen from Cuzco department (Llactahuaman, Quebrada Bagre, 1,700 m) does not match the phenotypes of either *E. greeneyi* or *E. zolzivora*. Therefore, it would be of interest to examine a series of specimens from Peru.

Remarks. Frühstorfer's (1912) account of *E. zolzivora* included the nominate subspecies plus *E. zolzivora opimus*, and he noted that Otto Staudinger recognized some differences between these and 'an allied race

from Ecuador and Peru'. The description above provides characters that validate Staudinger's century-old suggestion that the Ecuadorian taxon is distinct from its Bolivian and Colombian relatives. This species has been reared in Ecuador by H.F. Greeney on *Chusquea scandens* Kunth. (Poaceae), and a forthcoming larval description is in preparation.

Discussion

Parsimony analysis of 43 characters did not confirm the sub-generic groups proposed by either Stichel (1904, 1909) or Frühstorfer (1912). My results strongly suggest that *E. automedon*, *E. lycomedon*, *E. aesacus* and *E. bubocula* are closely related based on seven character changes (Fig. 3A), particularly the morphology of the uncus and gnathos. These four species appear to have lost the prong usually present on the anterior ventral region of the gnathos (Fig. 4, 7F). Furthermore, comparison of *aesacus+bubocula* to *automedon+lycomedon* suggests that in the latter two species the gnathos is further reduced dorsoventrally into a sharp point (Fig. 4A-E). To my knowledge, these gnathos and uncus characters represent unique morphological patterns within the *Caligo+Caligopsis+Eryphanis* assemblage (Fig. 4; Penz 2007 and unpublished observations). The *zolzivora*-group can be set apart from the remaining *Eryphanis* based on wing color pattern, these species being unique in having reddish-brown dorsal coloration with very weak iridescence, and a well defined orange forewing submarginal band.

Relationships among species of *Eryphanis* were generally well supported, except for the placement of *E. gerhardi* and *E. reevesii*. Analysis of all available characters placed *E. gerhardi* and *E. reevesii* in the *automedon*-group (Fig. 3A), but these species were associated with *E. zolzivora* and relatives when wing color characters were excluded (Fig. 3C). *Eryphanis gerhardi* and *E. reevesii* share characters with members of both the *automedon*- and *zolzivora*-groups, but these characters do not constitute universal synapomorphies of either group. The dorsal blue or purple iridescence, of *E. gerhardi* and *E. reevesii* fit the *automedon*-group gestalt (Fig. 1), and their ventral pattern is similar to *E. automedon* and *E. lycomedon* in the lack of a FW postmedial transverse band and smaller HW eyespots (Fig 1). *Eryphanis gerhardi* and *E. reevesii* also have slightly faded ventral HW color that resembles the faded ventral color of *E. automedon* and *E. lycomedon*. Nonetheless, male genitalic morphology of *E. gerhardi* and *E. reevesii* is similar to members of the *zolzivora*-group (Fig. 4), but these characters are plesiomorphic for *Eryphanis* and occur in *Caligopsis* and *Caligo* (Penz 2007 and this study). In sum, although the support for placing *E. gerhardi* and *E. reevesii* in the *automedon*-group is weak, it is stronger than evidence for placing them elsewhere.

The genus *Eryphanis* reaches its highest species richness in South America in association with the Andes, a geological formation that has influenced the evolution of a broad array of taxa. A recent biogeographical analysis (Kattan et al. 2004) proposed two major patterns of differentiation of the Andean fauna: elevational and horizontal. These patterns describe instances in which lowland taxa disperse into the mountains (or vice versa), or cases of population differentiation among ranges or slopes. Given the dramatic altitudinal changes in climate and the complex geographical architecture of the Andes, it is not surprising that many endemic species occur there, including butterflies (e.g., Willmott et al. 2001, Hall 2005). Within *Eryphanis*, some species seem to tolerate a wide elevational range (e.g., *E. lycomedon*, 0-1,200 m). Nonetheless, from the distribution data available in Appendix 1, it appears that both elevational (*automedon*-group) and horizontal factors (*zolzivora*-group) contributed to species-level differentiation in this butterfly genus. In addition to providing characters for phylogeny reconstruction, this study demonstrated the existence of cryptic species complexes within *Eryphanis*. Although this study represents the most comprehensive sampling ever accomplished for *Eryphanis*, their broad altitudinal and latitudinal distribution suggest that new taxa might still await discovery.

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Appendix 1. Examined material with repository collection in parentheses. Dissected specimens are marked with an asterisk. Dissection numbers are provided, and illustrations are cross-referenced. Abbreviations: M, male; F, female; AMNH, American Museum of Natural History; BMNH, The Natural History Museum, London; FMNH, McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History; INBio, Instituto Nacional de Biodiversidad, Costa Rica; MECN, Museo Ecuatoriano de Ciencias Naturales; MPM, Milwaukee Public Museum; PJD, DeVries Collection; USNM, United States National Museum, Smithsonian Institution.

Eryphanis automedon

- 1 M Venezuela, Waterworks, Puerto Cabello, Carabobo, 22 Jul 1979 (FMNH)
- 1 M Trinidad, BWI, mar 1937 (FMNH); 2 M Trinidad [18]98 (FMNH); 1 M Trinidad, Arima Valley, SIMLA Research Station, 27 Jun-3 Jul 1978 (FMNH)
- 1 M British Guyana, Kamarung, 10-14 Oct 1977 (FMNH)
- 1 M Surinam, Jan 2001 (PJD)
- 2 M French Guiana, R. Orapu (FMNH)
- 1 M* Colombia, Cali 19 Dec 1966, 07-28 dissected by C.M. Penz (MPM), habitus in Fig. 1A, genitalia in Fig. 4A and 5A; 1 M Colombia, Vaupes, San Jose del Guaviare, Dec [19]91 (FMNH); 1 M Colombia, Villavicencio, Ocoa, 27 oct 1943 (FMNH)
- 2 M Ecuador, Sucumbios, Garza Cocha, La Selva Biological Station, 17 Jan 1995 and 9 Jan 1998 (PJD); 1 M Ecuador, Napo, Limoncocha, 10 Oct 1971 (FMNH); 1 M Ecuador, Napo, Misahualli, 28 Apr 1971 (FMNH); 1 M Ecuador, Balzapampa, no date (FMNH)
- 1 M* Peru, Puerto Maldonado, Los Amigos Biological Station, 13 May 2004, 06-03 dissected by I. Garzón (PJD); 1 M Peru, Puerto Maldonado, Los Amigos Biological Station, 15 Oct 2004 (PJD); 1 M Peru, Huanuco, Tingo Maria, Rio Huallaga, 15-22 Aug 1981 (FMNH); 1 M Peru, Mogotta, 14 May 1955 (FMNH); 1 M Peru, Tingo Maria, 30 Jul 1980 (FMNH)
- 1 M* Brazil, Para, Obidos Mar 1976, 07-26 dissected by C.M. Penz (MPM); 1 M Brazil, Rondonia, Jaru, 9 Aug 1976 (FMNH); 1 M Brazil, Rondonia, Caucalandia 13 nov 1990 (FMNH); 1 M Brazil, Rondonia, Fazenda Rancho Grande 9 Nov 1990 (FMNH); 3 M Brazil, Minas Gerais, Uberaba, no date (FMNH); 1 M Brazil, Guanabara [=Rio de Janeiro], Gávea, 6 Feb 1973 (FMNH); 1 M Brazil, Santa Catarina, Blumenau, no date, coll LeMoult (FMNH)
- 1 M* Bolivia, Santa Cruz 29 Apr 1959, 07-27 dissected by C.M. Penz (MPM); 1 M Bolivia, Santa Cruz, Buenavista, Ichilo, 400 m, Feb 1946 (FMNH); 1 M Bolivia, no date (FMNH)

- 2 M* Paraguay, Amambay, Pedro Juan Caballero 4 Feb 1969, 06-23 and 07-31 dissected by C.M. Penz (MPM)
 1 F Trinidad, Maquerippe Bay, 22 Aug 1974 (FMNH); 1 F Trinidad, St. Amis, 23 Nov 1920 (FMNH)
 1 F* Surinam, Lelydorp, no date, 07-161 dissected by C.M. Penz (PJD)
 1 F French Guiana, R. Orapu (FMNH)
 2 F Ecuador, Napo, Misahualli, Elev. 1700' 3 Sep 2000 (FMNH)
 1 F* Peru, Puerto Maldonado, Los Amigos Biological Station, 14 Jul 2004, 07-124 dissected by C.M. Penz (PJD), genitalia in Fig. 6A; 1 F Peru, Tingo Maria, 30 Jul 1980 (FMNH)
 1 F Brazil, Rondonia, Fazenda Rancho Grande, 22 mar 1991 (FMNH); 1 F Brazil, Minas Gerais, Uberaba, no date (FMNH)
 1 F Paraguay, Pedro Juan Caballero 4 Feb 1969 (MPM), habitus in Fig. 2A

Eryphanis lycomedon

- 1 M Guatemala, no date (FMNH)
 1 M* Costa Rica, Puntarenas, Pto. Cortez 23 Nov 2003, 07-131 dissected by C.M. Penz (INBio); 1 M Costa Rica, Heredia, 3.8 km N of Santa Clara, 5 Sep 1987 (FMNH); 1 M Costa Rica, Alajuela, Rio Virilla, 5.5 km SW Guacima, 2 Oct 1967 (FMNH)
 1 M [Panama] Canal zone, Madden Forest, 21 Aug 1969 (FMNH); 1 M Panama, Las Cumbres, Oct 1960 (FMNH)
 1 M* Colombia, Cali 19 Dec 1966, 01-45 dissected by C.M. Penz (MPM), habitus in Fig. 1B; 1 M* Colombia, Cali 20 Oct 1965, 07-25 dissected by C.M. Penz (MPM), genitalia in Fig. 4B and 5B; 1 M Colombia, Cauca, Pescador, 1450 m, 29 Jan 1974 (FMNH); 11 M Colombia, Boyaca, Muzo, no date (FMNH); 2 M Colombia, Valle de Cauca, Cali (Cañas Gordas) 1000 m, 1 Oct 1973 and 21 Feb 1974 (FMNH); 1 M Colombia, Rio Guatiquia, Apr 1917 (FMNH); 2 M Colombia, Yacopi, 1936 and 12 Apr 1938 (FMNH)
 1 M* Ecuador, Pichincha, Santo Domingo de los Colorados 8 May 1988, 07-94 dissected by C.M. Penz (FMNH); 1 M Ecuador, Tonchigue Apr 1964 (MPM); 1 M Ecuador, Los Rios, Rio Palenque, no date (FMNH); 1 M Ecuador, Pichincha, Hotel Tinalandia, Santo Domingo de los Colorados, 750-850 m, 10 May 1988 (FMNH)
 1 M* Bolivia, no date, 08-03 dissected by C.M. Penz (FMNH); 1 M Bolivia, no date (FMNH)
 7 M Brazil, Santa Catarina, Blumenau, coll. LeMoult (FMNH)
 1 F* Costa Rica, Puntarenas, Corcovado National Park Apr 1989, 07-132 dissected by C.M. Penz (INBio); 1 F Costa Rica, Heredia, Pueblo Nuevo Sarapiquí 24 Jul- 22 Aug 1992 (INBio); 1 F Costa Rica, Cartago, Turrialba, 13 Jul 1965 (FMNH); 1 F Costa Rica, Alajuela, 6.2 km W Atenas, 16 Dec 1984 (FMNH)
 1 F Panama, Canal zone, Madden Forest, 2 Dec 1969 (FMNH); 1 F Panama, Las Cumbres, 25 Jan 1964 (FMNH)
 1 F* Colombia, Cali 27 May 1966, 01-46 dissected by C.M. Penz (MPM), genitalia in Fig. 6B; 1 F Colombia, Cali 2 Nov 1966 (MPM), habitus in Fig. 2B; 2 F Colombia, Valle de Cauca, Cali (Cañas Gordas) 1000 m, 13 Jan 1974 (FMNH); 2 F Colombia, Cali, Pance, 3000' Valle, 22 and 25 Jan 1987 (FMNH); 1 F Colombia, Cali, Valle, 9 Aug 1979 (FMNH)
 1 F Ecuador, Tonchigue Apr 1964 (MPM); 1 F Ecuador, Pichincha, Alluriquin 16 Aug 1972 (FMNH); 1 F Ecuador, Pichincha, Hotel Tinalandia, Santo Domingo de los Colorados, 750-850 m, 8 May 1988 (FMNH); 1 F Ecuador, Pichincha, Tinalandia, Santo Domingo, 2800', 5 May 1992 (FMNH)
 1 F* Brazil, Santa Catarina, Blumenau, coll. LeMoult, 08-02 dissected by C.M. Penz (FMNH)

Eryphanis aesacus

- 1 M* Mexico, San Luis Potosi 23 Jul 1937, 06-13 dissected by C.M. Penz (MPM), genitalia in Fig. 4E and 5E; 1 M [Mexico], Catemaco Nov 1965 (MPM), habitus in Fig. 1E; 2 M Mexico, Oaxaca, Monteflor Jun 1978 (FMNH); 1 M Mexico, Oaxaca, Chiltepec, 3 Sep 1976 (FMNH); 1 M Mexico, South of Tampico, 1 Nov 1975 (FMNH); 1 M Mexico, Escarcega, Campeche 2 and 5 May 1969 (FMNH); 1 M Mexico, Taumalipas, Taumazunchale, no date (FMNH); 1 M Mexico, El Pujal, San Luis Potosi, 18 Jun 1939 (FMNH)
 1 M* Guatemala, Chacoj, Pelochic, no date, #802303, 07-152 dissected by C.M. Penz (BMNH); 1 M Guatemala, Alta Verapaz, Baleu Mpio., San Cristobal, Verapaz, 1450 m, 24 Sep 1966 (FMNH)

- 1 M El Salvador, Ahuachapan, El Refugio Sep 2003 (PJD); 1 M El Salvador, Ahuachapan, La Fincona El Imposible, 850 m, 13 Sep 1984 (FMNH)
1 M Belize, Cayo Distr., Green Hills 29 Jul 2007 (PJD)
1 F* Mexico, no date, 06-14 dissected by C.M. Penz (MPM), genitalia in Fig. 6E; 1 F Mexico, Oaxaca, Tuxtepec 4 Sep 1976 (FMNH), habitus in Fig. 2E; 2 F Mexico, Presidio, Jun 1951 (FMNH); 2 F Mexico, Catemaco, Sep 1956 (FMNH)
1f Guatemala, Central Valleys, no date, #802305, (BMNH); 1 F Guatemala, Petén, Parque Nacional Tikal, 20 Sep 1993 (FMNH)
1 F El Salvador, Ahuachapan, El Refugio Sep 2003 (PJD); 1 F El Salvador V.C. Santa Ana, D.C. Santa Ana Nov 1997 (PJD); 1 F El Salvador, San Salvador, 13 nov 1984 (FMNH)

Eryphanis bubocula

- 1 M* Costa Rica, Guanacaste, Rio San Lorenzo, Tierras Morenas Aug 1992, 07-129 dissected by C.M. Penz (INBio), habitus in Fig. 1D, genitalia in Fig. 4D and 5D
1 F* Costa Rica, Cartago, Tapanti 9 Apr 1983, 07-130 dissected by C.M. Penz (INBio), habitus in Fig. 2D, genitalia in Fig. 6D
1 F Colombia, Val. Del Cauca, Calima Valley, 1200 m, 14 Feb 1989 (FMNH)

Eryphanis gerhardi

- 1 M Ecuador, Balzapampa, no date (FMNH)
1 M* Bolivia, no date, 07-45 dissected by C.M. Penz (MPM), habitus in Fig. 1F; 1 M* Bolivia, Cochabamba Mar 1955, 07-29 dissected by C.M. Penz (MPM); 1 M Bolivia, Chapare, Alto Palmar Sep 1954 (MPM); 1 M Bolivia, Cochabamba, El Palmar Chapare, Apr 1947 (FMNH); 1 M Bolivia, Cochabamba, Alto Palmar Chapare, Oct 1958 (FMNH); 1 M Bolivia, Santa Cruz, Buenavista, Ichilo, 400 m, 21 Feb 1994 (FMNH)
1 M* Brazil, Rondonia, Jaru 9 Aug 1976, 06-32 dissected by C.M. Penz (FMNH), genitalia in Fig. 4F and 5F
1 F* Brazil, Rondonia, Jaru 6 Aug 1976, 06-33 dissected by C.M. Penz (FMNH), habitus in Fig. 2F, genitalia in Fig. 6F

Eryphanis reevesii

- 1 M* Brazil, São Paulo, Pinhal Apr 1955, 01-47 dissected by C.M. Penz (MPM), habitus in Fig. 1C, genitalia in Fig. 4C and 5C; 1 M Brazil, São Paulo, Itaici 3 Sep 1961 (MPM); 1 M Brazil, Meatana [maybe Mendanha, Minas Gerais] 20 Jul 1968 (FMNH); 1 M Brazil, [São Paulo], Pinhal, Mar 1952 (FMNH); 1 M Brazil, Santa Catarina, Blumenau, no date (FMNH); 4 M Brazil, Santa Catarina, São Bento do Sul, 10 Mar 1984 (FMNH); 1 M Brazil, Santa Catarina, Trombudo Alto, 28 Mar 1957 (FMNH)
2 M Argentina, Parque Nacional Iguazu, Misiones, 18 Jun 1973; 1 M Argentina, Misiones, Rio Uruguay 19 Jun 1973 (FMNH)
1 F Brazil, Rio de Janeiro, Nova Friburgo Oct 1958 (MPM), habitus in Fig. 2C; 1 F* Brazil, São Paulo, Pinhal Apr 1955, 01-48 dissected by C.M. Penz (MPM), genitalia in Fig. 6C; 2 F Brazil, Minas Gerais, Uberaba, no date (FMNH); 1 F Brazil, Santa Catarina, Trombudo Alto, 26 Mar 1956 (FMNH)

Eryphanis zolzivora

- 1 M* Bolivia, Cochabamba Mar 1955, 07-30 dissected by C.M. Penz (MPM), genitalia in Fig. 4G and 5G; 1 M* Bolivia, no date, 07-34 dissected by C.M. Penz (MPM), habitus in Fig. 1G; 1 M* Bolivia, Cochabamba, El Palmar Apr 1947, 07-95 dissected by C.M. Penz (FMNH); 1 M Bolivia, Cochabamba, El Palmar Chapare, 1650 m, Apr 1947; 1 M Bolivia, Las Yungas, Nov 1990 (FMNH)
1 F* Bolivia, Cochabamba, Alto Palmas Sep 1958, 06-31 dissected by C.M. Penz (FMNH), habitus in Fig. 2G, genitalia in Fig. 6G

Eryphanis opimus

- 1 M* Colombia, Cali 29 Sep 1964, 07-32 dissected by C.M. Penz (MPM), habitus in Fig. 1I, genitalia in Fig. 4I and 5I

Eryphanis greeneyi

- 1 M Ecuador, Napo, Yanayacu Biological Station, 5km W of Cosanga, May 2007, HOLOTYPE (BMNH); 1 M Ecuador, Napo Prov., Yanayacu Biological Station, S00°35.9' W77°53.4, 2163 m, PARATYPE (MECN); 1 M Ecuador, Provincia Napo, YYBS, 2000 m, 5-Feb-[20]02 PARATYPE (AMNH); 1 M Ecuador, Provincia Napo, 12-Apr-[20]00 PARATYPE (PJD); 1 M* Ecuador, Rio Blanco, near Baños, 1,650 m, Abril 17/[19]56, 07-33 dissected by C.M.Penz, PARATYPE (MPM), habitus in Fig. 1H, genitalia in Fig. 4H and 5H; 1 M* Ecuador, Balzapampa, 07-96 dissected by C.M. Penz, PARATYPE (FMNH); 1 M* Ecuador, Zamora-Chinch. Province, Zumba-Loja 21-23 Sep 1993, 07-126 dissected by C.M. Penz (FMNH)
- 1 F Ecuador, Napo, Yanayacu Biological Station, 5km W of Cosanga, May 2007 PARATYPE (BMNH); 1 F* Ecuador: Napo Prov., Yanayacu Biological Station, S00°35.9' W77°53.4, 2163 m, 07-127 dissected by C. M. Penz, PARATYPE (MECN), genitalia in Fig. 6H; 1 F Ecuador, Napo, Biol. Yanayacu, 2000m, PARATYPE (AMNH), habitus in Fig. 2H; 1 F Ecuador, Provincia Napo, San Isidro, 2000 m, 21-Dec-[19]99, PARATYPE (PJD).

Caligopsis seleucida

- 1 M* Peru, Puerto Maldonado, Los Amigos Biological Station, 10 Sep 2004, 06-02 dissected by I. Garzón (PJD); 1 M Peru, Puerto Maldonado, Los Amigos Biological Station, 12 Oct 2004 (PJD)
- 1 M* Bolivia, Cochabamba San Francisco Apr 1976, 01-49 dissected by C.M. Penz (MPM)
- 1 F* Peru, Puerto Maldonado, Los Amigos Biological Station, 9 Apr 2004, 06-01 dissected by I. Garzón (PJD); 1 F Peru, Puerto Maldonado, Los Amigos Biological Station, 14 Oct 2004 (PJD)
- 1 F* Brazil, Amazonas, Madeira River, 01-54 dissected by C.M. Penz (USNM)

Caligo illioneus

- 1 M* Costa Rica, Heredia, Finca La Tirimbina 17 Feb 1978, 06-17 dissected by C.M. Penz (MPM)
- 1 F* Costa Rica, Heredia, Finca La Selva Feb 1969, 06-18 dissected by C.M. Penz (MPM)

Caligo idomeneus

- 1 M* East Peru, no date, 06-19 dissected by C.M. Penz (MPM)
- 1 F* East Peru, no date, 06-20 dissected by C.M. Penz (MPM)

Appendix 2. Illustrated character list, including the rescaled consistency index (RC) for each character. Note that wing color characters used in this study pertain exclusively to the specimens listed in Appendix 1, and that even though the geographical representation was thorough for some species, character scores may not represent the full range of variation for all species.

Wings

1. Male, dorsal wing iridescence: absent (0), present (1). RC= 1
2. Male, dorsal wing iridescence: reaching basal area of wings (0), not reaching basal area of wings (1). RC=1
3. Male, dorsal FW submarginal band: absent (0); present, faded (1); present, well defined (2). RC=0.25 Fig. 7A. Note: this band bifurcates near the wing apex to produce a proximal branch (toward wing base) and a distal branch (toward wing apex).
4. Male, proximal branch of dorsal FW submarginal band: expanded anteriorly to radius stem (0), not expanded to radius stem (1). RC=0 Fig. 7A. Note: *E. gerhardi* and *C. illioneus* were scored “?” because in these species the submarginal band is faded or absent.
5. Male, distal branch of dorsal FW submarginal band: forming a complete line across cells m2 and m3 (0), not forming a complete line across cells m2 and m3 (1). RC=1 Fig. 7A. Note: *E. gerhardi* was scored “?” because its submarginal band is faded anteriorly.
6. Male, ventral FW postmedial white band: absent (0), present (1). RC=0.0625 Fig. 7A. Note: This band has an equivalent in the HW.
7. Male, HW margin: clearly scalloped (0), smooth or slightly undulated (1). RC=1 Fig. 7A.

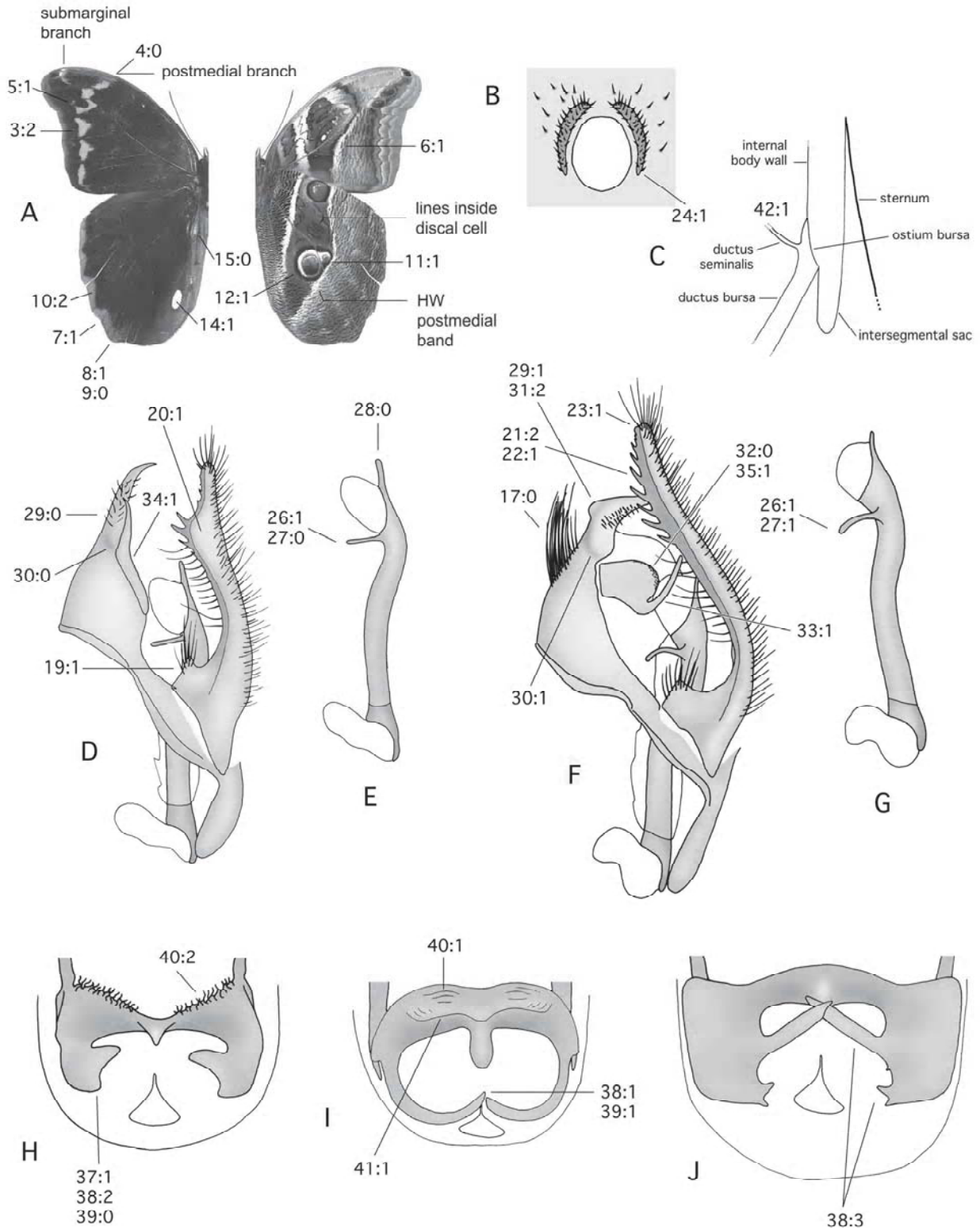


Figure 7. Illustration of characters used in the analysis. **A)** *E. zolzivora* male wings, dorsal and ventral views. **B)** schematic representation of the male diaphragm, phallus removed. **C)** schematic representation of the female ductus bursa and ductus seminalis in lateral view. **D)** and **E)** *E. automedon* male genitalia and phallus in lateral view. **F)** and **G)** *E. opimus* male genitalia and phallus in lateral view. **H)** *E. automedon* female sterigma. **I)** *E. bubocula* female sterigma. **J)** *E. zolzivora* female sterigma.

8. Male, HW projection at Cu1: more developed than other undulations (0), not more developed than other undulations (1). RC=0.375 Fig. 7A.
9. Male, HW point at Cu1: small, not surpassing anal angle (0), large, surpassing anal angle (1). RC=1 Fig. 7A. Note: species that do not have a well-developed projection (8:1) were scored “?” for this character.
10. Male, dorsal HW orange marginal edge: absent (0), vestigial (1), well developed (2). RC=1 Fig. 7A.
11. Male, ventral HW eyespot in cell M3: absent (0), present (1). RC=1 Fig. 7A.
12. Male, ventral HW eyespot in cell Cu1, outermost ring: contained inside cell (0), expanding to cell Cu2 (1). RC=0.1111 Fig. 7A.
13. Male, dorsal HW broad patch of black androconial scales extended over several wing cells above tornus: absent (0), present (1). RC=1 Fig. 1D, E.
14. Male, dorsal HW scent organ in cell Cu2: absent (0), present (1). RC= 1 Fig. 7A.
15. Male, dorsal HW hairpencil in cell 1A: absent (0), present (1). RC=1 Fig. 7A.

Male abdomen and genitalia

16. Abdominal sent organ location: A4 (0), A4-5 (1), A4-6 (2). RC=0.5
17. Hairpencil on posterior portion of tegumen: absent (0), present (1). RC= 0.4 Fig. 7F.
18. Hairpencil on medial portion of tegumen: absent (0), present (1). RC=1
19. Thin, setae-bearing flange associated with the dorsal, basal region of valva: membranous (0); sclerotized (1). RC=1 Fig. 7D.
20. Subterminal swelling of the valva: absent (0), present (1). RC=0 Fig. 7D.
21. General size of spines along dorsal edge of valva: small (0), medium (1), large (2). RC=1 Fig. 7F.
22. Spines along dorsal edge of valva: forming multiple rows (0), mostly in one row (1). RC=1 Fig. 7F.
23. Apex of valva: setose portion projected beyond sclerotized portion (0); setose portion not projected, similar to sclerotized portion (1); setose portion less projected than sclerotized portion (2). RC=0.1 Fig. 7F.
24. Diaphragma, setae-bearing region adjacent to phallus: membranous (0), partly sclerotized (1). RC=1 Fig. 7B.
25. Phallus length: short, total length 4x or less the length of the distal opening (0); long, total length 5x or more the length of the distal opening (1). RC=0
26. Phallus prong: absent (0), present (1). RC=1 Fig. 7E, G.
27. Phallus prong: adjacent to distal opening of phallus (0), anterior to distal opening of phallus (1). RC=0.375 Fig. 7E, G.
28. Distal end of phallus: projected as a hollow prong beyond opening (0), not projected as a hollow prong beyond opening (1). RC=1 Fig. 7E.
29. In lateral view, uncus: straight (0), curved (1). RC=1 Fig. 7D, F.
30. In dorsal view, proximal portion of uncus wings: not forming conspicuous lateral wings (0), forming well developed lateral wings (1). RC= 1 Fig. 7D shows the location of the uncus wings.
31. In lateral view, distal portion of uncus wings, as they project into posterior process: reduced (0); well developed, evenly arched (1), projected as a hump near proximal portion (2), projected in an arch near distal portion (3). RC=1 Fig. 7F.
32. Gnathos, posterior ventral region: conspicuously projected (0), not conspicuously projected (1). RC= 1 Fig. 7F.
33. Gnathos prong: absent (0), present (1). RC=1 Fig. 7F.
34. Gnathos, anterior ventral region: well developed (0), reduced (1). RC=1 Fig. 7D.
35. Gnathos, small spines of posterior ventral region: absent (0), present (1). RC=0.0625 Fig. 7F.

Female abdomen and genitalia

36. Anterior portion of sterigma: continuous (0), interrupted by a gap at midpoint (1). RC=1
37. Inward projections of sterigma: absent (0), present (1). RC=1 Fig. 7H.
38. Distal portion of the inward projection of sterigma: smoothly rounded (0), with one single point (1), with two blunt points (2), with one elongated projection and smaller points (3). RC=0.36 Fig. 7H, I, J.
39. Inward projections of sterigma: broad (0), thin (1). RC=1 Fig. 7H, I.

- 40. Posterior edge of sterigma: with delicate transverse ribs that do not encroach the sterigma (0), with large transverse ribs that encroach the sterigma (1), with large oblique ribs that encroach the sterigma (2). RC= 1 Fig. 7H, I.
- 41. Ridge at posterior portion of sterigma: absent (0), present (1). RC=1 Fig. 7I.
- 42. Association between ductus bursa and ductus seminalis: ductus seminalis joining ductus bursa at the antrum region (0), ductus seminalis joining a channel in the body wall that is dorsal to antrum (1). RC=1 Fig. 7C.
- 43. Signa: absent (0), present (1). RC=0.25

Appendix 3. Character matrix.

	1	2	3	4	4					
	0	0	0	0	3					
<i>C. illioneus</i>	101?0001?	0	0	100120100	101010?111	3	010	1	11100	001
<i>C. idomeneus</i>	100??101?	0	0	100120101	100000?111	3	010	0	11200	001
<i>C. seleucida</i>	0?200111?	0	1	100121001	0021010111	1	110	0	01000	010
<i>E. automedon</i>	111000101	0	1	001010011	2101110000	0	?01(0,1)		11202	011
<i>E. lycomedon</i>	111000101(0,1)	1	1	001010010	2101110000	0	?01	1	11200	011
<i>E. aesacus</i>	11100111?	1	1	111000010	2101110000	0	000	1	11111	110
<i>E. bubocula</i>	11110111?	1	1	111000010	2111110000	0	000	1	11111	110
<i>E. gerhardi</i>	111??0101	0	(0,1)	001001010	2101011011	2	010	0	11000	011
<i>E. reevesii</i>	110??0101	0	1	001011010	2111111011	2	010	0	11000	011
<i>E. zolzivora</i>	112111100	2	1	101011011	2111111011	(1,2)	010	0	11300	011
<i>E. greeneyi</i>	112111101	2	1	101011011	2111111011	2	010	1	11300	011
<i>E. opimus</i>	112111101	2	1	101011010	2111111011	2	010	1	?????	???

