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## Wing pattern diversity in Brassolini butterflies (Nymphalidae, Satyrinae)

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PENZ, C.M. & MOHAMMADI, N. **Wing pattern diversity in Brassolini butterflies (Nymphalidae, Satyrinae).** Biota Neotrop. 13(3): <http://www.biotaneotropica.org.br/v13n3/en/abstract?article+bn03613032013>

**Abstract:** This study describes and compares the diverse dorsal and ventral wing color patterns of Brassolini butterflies. Thirty-three species are illustrated, where pattern elements of the nymphalid ground plan are labeled in color. In general, a larger number of pattern elements can be identified on the ventral than on the dorsal surface of both wings, and the forewing has a larger number of discernible pattern elements than the hind wing. The dorsal elements are broad, diffuse, and more difficult to identify against the typically brown brassoline wing background color. Species with a light colored dorsal background served as a guide for our proposal that fewer pattern elements are present dorsally, particularly on the hind wing. Colorful bands or markings generally present on the dorsal surface seem to be associated with specific pattern elements and have correspondence to the ventral pattern. We refer to these as trailing bands, and they constitute a predominant feature of the brassoline dorsal coloration. We propose a subordinate groundplan for brassolines and interpret some of the ventral pattern variation in light of their phylogeny. Dorsal color pattern variation that leads to sexual dimorphism and mimetic resemblance are also discussed.

**Keywords:** butterfly, wing color, nymphalid ground plan, eyespots, ocelus, Caligo.

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**Resumo:** Este estudo descreve e compara os diversos padrões de coloração dorsal e ventral das borboletas da tribo Brassolini. Com o objetivo de demarcar os elementos do padrão de base dos ninfalídeos ('pattern elements of the nymphalid ground plan'), 33 espécies são ilustradas. De maneira geral, o número de elementos-padrão identificados na face ventral é maior do que o da face dorsal em ambas as asas, e a asa anterior contém um número maior de elementos visíveis do que a posterior. Os elementos da face dorsal são mais largos e difusos, e também mais difíceis de identificar devido à usual coloração de fundo marrom escuro dos brassolíneos. Espécies que apresentam coloração de fundo clara serviram como guia para a nossa interpretação de que a superfície dorsal das asas apresenta um número reduzido de elementos-padrão, especialmente a da asa posterior. Faixas ou manchas coloridas que geralmente aparecem na superfície dorsal estão aparentemente associadas com elementos-padrão específicos, e apresentam correspondência com faixas que aparecem na face ventral. Estas faixas ('trailing bands') se alastram a partir da borda de certos elementos e constituem uma característica predominante da coloração dorsal dos brassolíneos. Nós propomos um padrão de base para os brassolíneos que é subordinado ao dos ninfalídeos, e utilizamos a filogenia do grupo para interpretar alguns aspectos da variação de elementos-padrão da superfície ventral. As variações de padrão e cor que resultam em dimorfismo sexual e mimetismo são discutidas.

**Palavras-chave:** borboleta, coloração das asas, padrão de base dos ninfalídeos, manchas ocelares, ocelo, Caligo.

## Introduction

Wing colors play vital and diverse roles in Lepidoptera, spanning from physiology (e.g., thermoregulation) to inter and intraspecific interactions. Camouflage, large eyespots for startle or deflection, aposematism and mimicry are notable adaptations that reduce predation risk (e.g., Vane-Wright & Ackery 1984, Chai 1990). Although different in their evolutionary outcome, all of these phenotypic defenses involve impressive modifications of wing pattern elements (Nijhout 1991). For example, some nymphalid butterflies closely resemble dead leaves, a useful appearance at rest of when feeding on fallen rotting fruit (e.g., *Zaretis itys* (Cramer, 1777), Nymphalidae, Charaxinae; *Kallima inachus* (Boisduval, 1846), Nymphalidae, Nymphalinae; see <http://biology.duke.edu/nijhout/patterns2.html> for a demonstration; last accessed 7 March 2013). In contrast, brightly colored butterflies incur a predation risk that can only be defused if they are chemically protected, mimetic, or too difficult to catch. Among these, mimicry is a particularly complex defense because wing colors play a role in both predator-prey and model-mimic interactions while being also used to mediate male-female, intraspecific communication. In fact, mate-choice experiments suggest that assortative mating based on wing color led to genetic divergence and speciation of the sister taxa *Heliconius cydno* Doubleday, 1847 and *H. melpomene* (Linnaeus, 1748) (Nymphalidae, Heliconiinae), which belong to separate mimicry rings (Jiggins et al. 2001). Furthermore, instances of female-limited mimicry also demonstrate the importance of color for mate recognition in butterflies (e.g., Kunte 2008, 2009), implying a potential tradeoff between defensive coloration and mating success in the male sex.

The utility of color for intraspecific interactions likely depends on light levels in the environment. Not surprisingly, nocturnal moth wing colors do not play a role in mate location, recognition, or courtship; chemical communication is favored instead (e.g., Birch 1970), which also seems to be the case in day-flying moths (e.g., Eisner & Meinwald 1995). In contrast, butterfly wing colors are commonly used for male-male and male-female interactions, and the highly visible, territorial male *Morpho* butterflies (Nymphalidae, Satyrinae, Morphini) provide a fitting example of both. While dorsal blue colors have a role in male-male and perhaps male-female interactions (Fruhstorfer 1912, Penz & DeVries 2002, DeVries et al. 2010), the dark and camouflaged ventral wing coloration likely protects both sexes at rest. Thus, the *Morpho* dorso-ventral differentiation seems to fit the situation described by Oliver et al. (2009) for *Bicyclus* (Nymphalidae, Satyrinae, Satyrini), where the dorsal color pattern is shaped by sexual selection, while natural selection operates on the camouflaged ventral surface. Members of the Satyrinae tribe Brassolini, sister group to Morphini (Wahlberg et al. 2009), might be under similar selection regimes given the remarkable color pattern differences between their dorsal and ventral wing surfaces.

With few exceptions, Brassolini butterflies are crepuscular. While they may be found feeding or puddling during the day, reproductive activities (mating behavior and oviposition) typically occur at dawn or dusk. Most brassolines are relatively dull colored dorsally, and if their colors have a role in male-female interactions in this butterfly group, then they must be discernible at low light levels of crepuscular hours. Although pattern elements of the nymphalid ground plan are easily recognizable on the ventral surface across the tribe, they are subdued in some taxa and striking in others (e.g., *Penetes* vs. *Caligo*). Ventral ripple patterns, striations that resemble windblown sand, are common throughout the Satyrinae (Nijhout 1991), and excepting *Penetes* all brassolines have ripple patterns. Ventral eyespots also occur across the tribe exhibiting a wide range of sizes and complexity. With the wings folded at rest some brassolines are camouflaged (e.g., *Dynastor*

*napoleon* Doubleday, 1849 resembles a dead leaf) while others are quite visible (e.g., some *Caligo* species have conspicuous eyespots). The richness of color patterns, coupled with differing activity periods (crepuscular vs. diurnal) and flight behaviors, constitute an open field of investigation for this butterfly tribe.

This study represents the first broad survey of color pattern diversity in Brassolini. Here we provide a framework for understanding color pattern variation among genera, which constitutes a required foundation for future work on evolution, development and genetics of wing color patterns in this butterfly group. Ventral patterns are described in detail and dorsal patterns are explained here for the first time. We identify and illustrate pattern elements using the nymphalid ground plan proposed by Schwanwitsch (1924) and Süffert (1927), and modified by Nijhout (1991). We then propose a subordinate groundplan for the Brassolini that is placed in a phylogenetic context. Finally, we briefly discuss instances of sexual dimorphism and color convergence across genera.

## Material and Methods

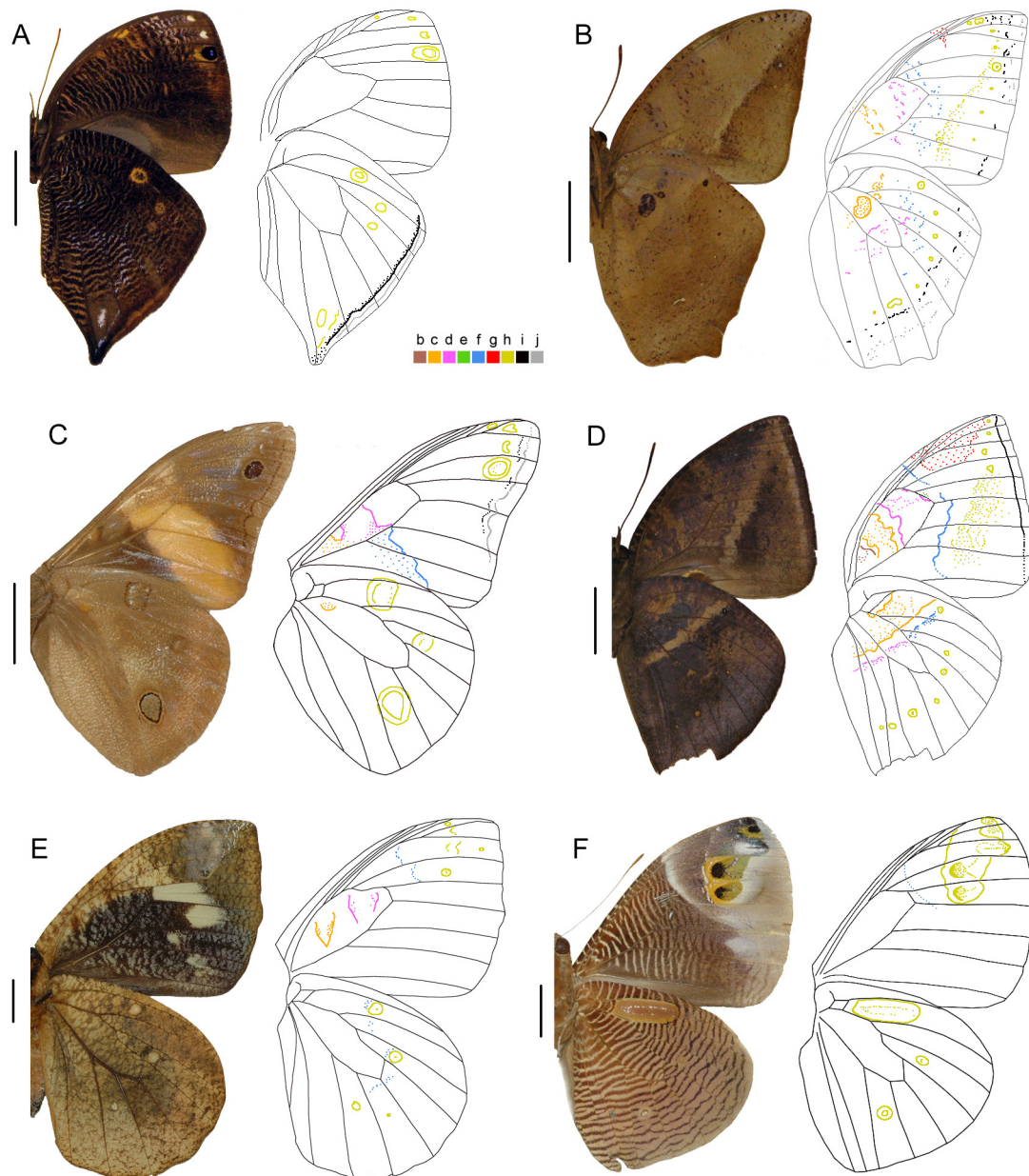
### 1. Specimens, species and illustrations

Appendix 1 lists locality data and museum deposition of 554 specimens from 75 species that were examined directly (73% of the Brassolini species diversity), plus sources of photographs of additional taxa. Thirty-three species are illustrated here (usually male). For economy of space, not all species mentioned in the text are included in the figures, but male and female photographs of most brassolines can be found at <http://fs.uno.edu/cpenz/Brassolini.html> (last accessed 12 August 2013). Photographs were taken with a Cannon G9 digital camera and processed in Adobe Photoshop (Adobe Systems Inc.). Figures with a color-coded key identifying wing pattern elements were prepared using either the type species or an alternative representative of each genus depending on availability of material and/or particular characteristics of their wing patterns. To document variation, multiple species of the same genus were sometimes illustrated. Although body size varies broadly within Brassolini, all images used to describe pattern elements were converted to a similar size to facilitate comparison (Figures 1-7). Images that illustrate sexual dimorphism and color resemblance across genera are scaled proportionately to life size (Figure 9).

### 2. Homology and the identification of pattern elements

Pattern elements of the nymphalid ground plan (NGP) are discrete components of wing color differentiation expressed on the wing surface (Nijhout 1991 and references therein). Within the comparative context of the NGP, the term 'homology' is generally used to indicate the repetition of a pattern element among cells on the same wing (serial homology), the mirror image of elements between wing surfaces (dorso-ventral homology), and the equivalence of pattern elements across species. Although the latter clearly corresponds to evolutionary homology (i.e., characters shared by common ancestry), the identification of NGP pattern elements is somewhat subjective and should therefore be considered a hypothesis of homology that might be tested through a genetic or phylogenetic framework. As such, the coding of pattern elements for species included in this study constitutes a set of working hypotheses.

Our method for the identification of NGP pattern elements followed three steps. First, we studied the pattern element variation across nymphalid subfamilies to build a framework for size and color diversity, as well as the sequential location of individual pattern elements along wing cells (topographical correspondence can be used to infer homology; e.g., DePinna 1991, Rieppel & Kearny



**Figure 1.** Male wings in ventral view plus a schematic drawing showing color-coded pattern elements. Scale bars: 1 cm. **A**, *Bia actorion*, Suriname; **B**, *Narope cyllastros*, no data; **C**, *Brassolis sophorae*, French Guiana; **D**, *Aponarope sutor*, Brazil, Rondônia; **E**, *Dynastor napoleon*, Brazil, Santa Catarina; **F**, *Dynastor macrosiris macrosiris*, French Guiana.

2002). We did this to be consistent with previous work (Nijhout 1991, 1994, 2001) that formed the basis of more recent research on evolution of development. Second, we examined and compared a large number of species, including all brassoline genera. To account for variation within species, specimens from various localities were studied whenever possible. A large sample size allowed us to use intermediate phenotypes as clues for the identification of pattern elements within and between genera (as suggested by Nijhout 1991). Finally, after pattern elements were color-coded for each species, we checked our identifications of pattern elements for consistency throughout the Brassolini.

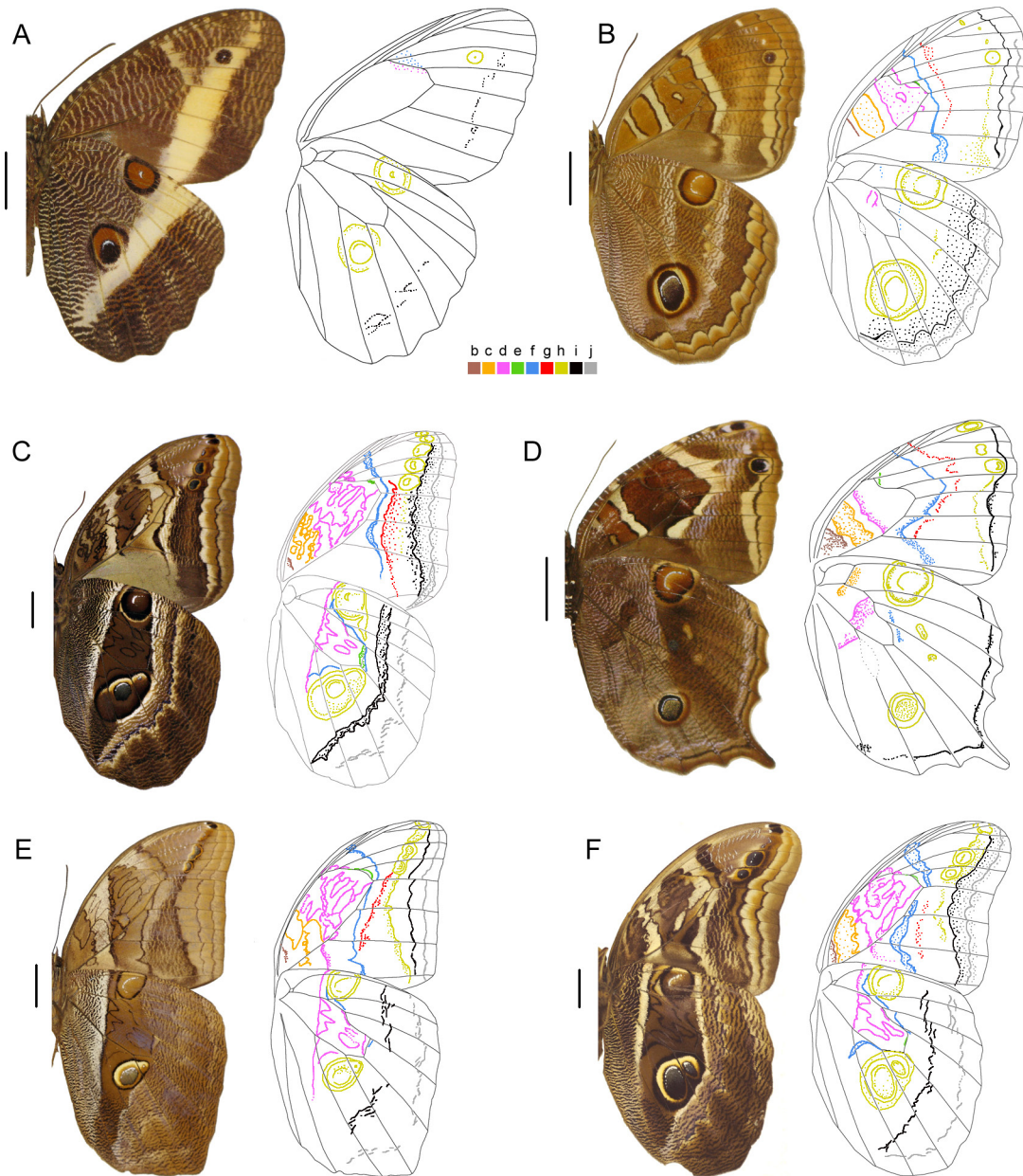
### 3. Terminology and character optimization

Terms and definitions used throughout the text are listed below, including pertinent baseline information:

- *Wing background*: The background corresponds to the canvas upon which patterns elements are expressed, and background color may or may not be homogeneous across the wing surface (Nijhout 1991);
- *Nymphalid ground plan (NGP) pattern elements*: The nine pattern elements found in Brassolini are indicated by letters *b* to *j* from the wing base to the distal edge, following Nijhout (1991, p.43);
- *Pattern element h, ocelus, and eyespot*: Pattern element *h* corresponds to a series of ocelli, and given this fact, the letter *h* is used here in reference to the whole series while the terms ocelus and ocelli are used when referring to specific units (within particular cells). The term ‘eyespot’ does not necessarily correspond to NGP pattern element *h* across butterflies (Nijhout 1991) and



## Brassolini wing color patterns



**Figure 2.** Male wings in ventral view plus a schematic drawing showing color-coded pattern elements. Scale bars: 1 cm. **A**, *Dasyophthalma rusina*, South Brazil; **B**, *Ooptera syme*, Brazil, São Paulo; **C**, *Caligopsis seleucida*, Peru, Madre de Dios; **D**, *Ooptera aorsa*, Brazil, Paraná; **E**, *Eryphanis automedon*, Ecuador, Sucumbios; **F**, *Eryphanis bubocula*, Costa Rica, Guanacaste.

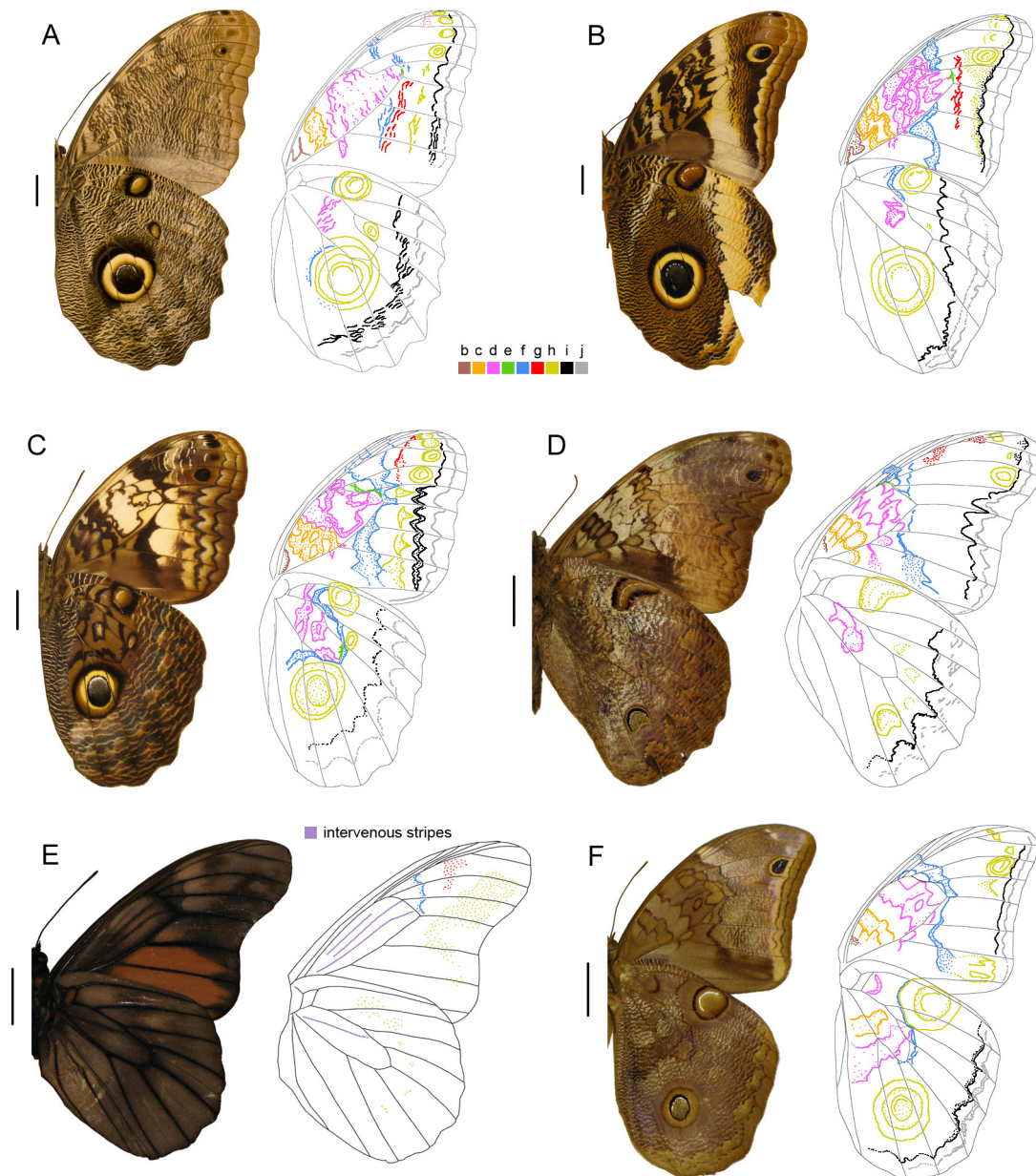
it is not used in the descriptions below. Ocelli can be simple (one solid spot) or complex (a spot encircled by rings);

- *Ripple patterns*: These correspond to striations or granular markings typically found on the ventral wing surface of satyrines. Development of ripple patterns precedes that of NGP pattern elements (Nijhout 2001), and our descriptions and discussion take this into account;
- *Trailing bands*: The space between certain pattern elements may contain a bright band (white, cream, yellow or orange) that contrasts the dorsal or ventral wing background. We coined the term ‘trailing bands’ for these because, on the ventral surface, they are usually contiguous to one pattern element and diffuse at the opposite side (see Figures 5A for identification on the ventral and dorsal surfaces, and 8A for a

schematic representation). Nonetheless, they can also fill the entire space between two flanking elements, or be diffuse in both the distal and proximal edges. It is, therefore, possible that they are developmentally associated with various pattern elements. Dorsal and ventral trailing band homologues vary in width and color, and may be expressed in the same, or slightly offset, locations. The trailing bands differ from, and should not be confused with, “patterned background colors” described by Nijhout (1991, p.38);

- *Wing venation nomenclature* follows the Comstock-Needham system (indicated in Figure 8A).

We used MacClade (Maddison & Maddison 2005) to optimize variation of selected pattern elements onto a genus-level phylogeny (annotated from Penz 2007; the slight differences in topology between



**Figure 3.** Male wings in ventral view plus a schematic drawing showing color-coded pattern elements. Scale bars: 1 cm. **A**, *Caligo eurilochus*, Ecuador, Sucumbios; **B**, *Caligo atreus*, Colombia, Antiochia; **C**, *Caligo martia*, Brazil, Santa Catarina; **D**, *Selenophanes cassiope*, Peru, Chanchamayo; **E**, *Penetes pamphanis*, Brazil, Paraná; **F**, *Catoblepia xanthus*, Brazil, Pará.

the tree used here and that in Penz et al. 2013 did not affect character optimization).

## Results

Pattern elements of the nymphalid ground plan were easily identified in most brassolines, although some species had reduced patterns. Color-coded identification diagrams in Figures 1-7 together with Tables 1 and 2 facilitate comparison across genera. Individual pattern elements are more readily recognized on the ventral surface of the wings. Therefore, we address the ventral coloration first, and use it as a guide for the identification of dorsal pattern elements and trailing bands. Based on our comparative study of 75 species, we then propose a subordinate groundplan for Brassolini and place the variation in key characteristics in a phylogenetic context (Figure 8),

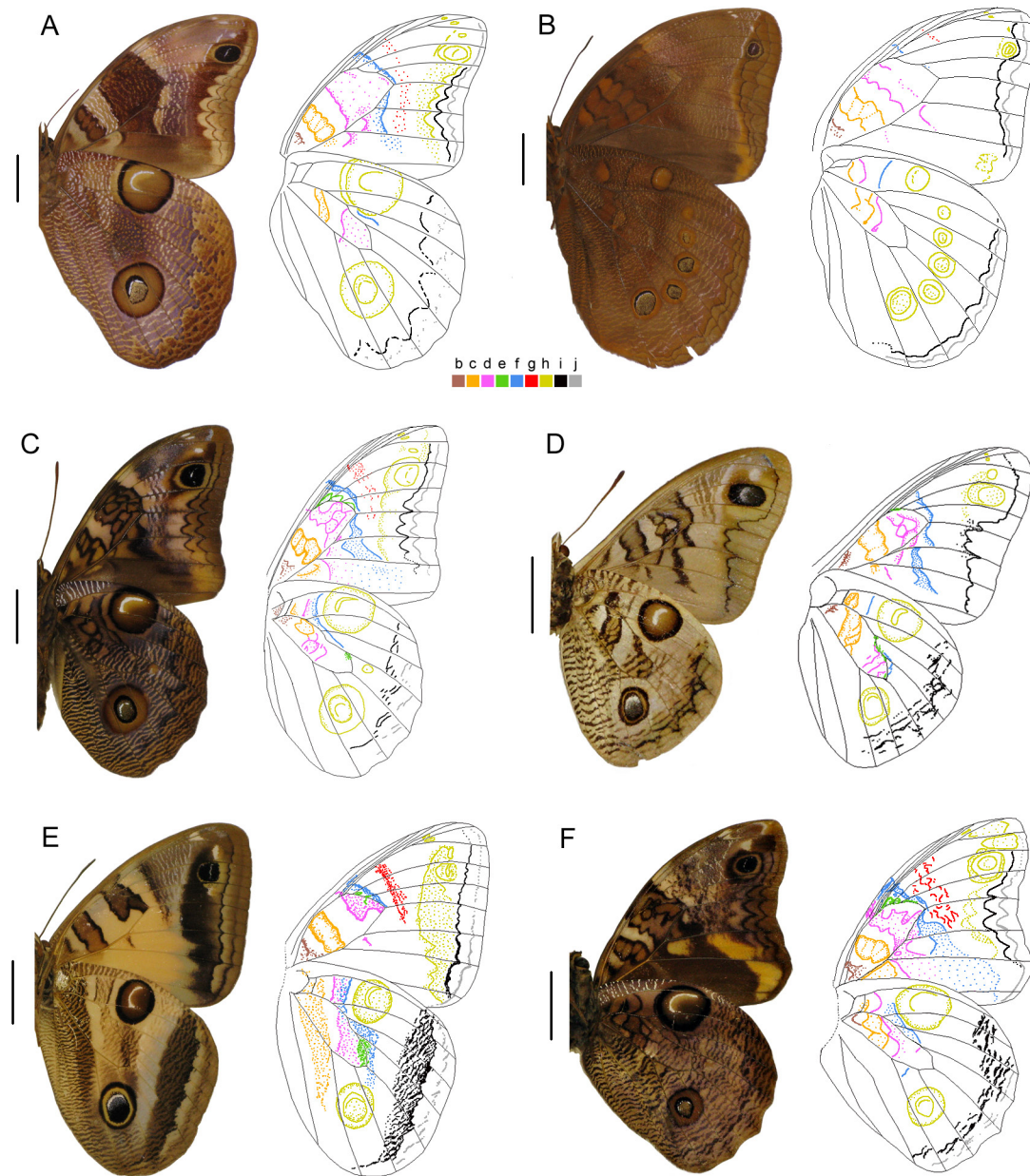
noting that some taxa depart from the groundplan. Finally, we describe instances of sexual dimorphism and color pattern convergence among genera (Figure 9).

### 1. Ventral wing surface

The diversity of ventral patterns within Brassolini is illustrated in Figures 1-4 and described in Table 1. The number of visible ventral pattern elements varies broadly between and sometimes within genera, and the ventral forewing (VFW) usually contains a larger number of visible elements than the ventral hind wing (VHW). The VFW typically includes elements *b* to *j*. Element *e* and *g* are usually obscured by ripple patterns, being vestigial or absent in several taxa as a result (see Figures 1-4). Two VFW submarginal bands (*i* and *j*) are visible in most species, but one or both can be absent (e.g.,



## Brassolini wing color patterns



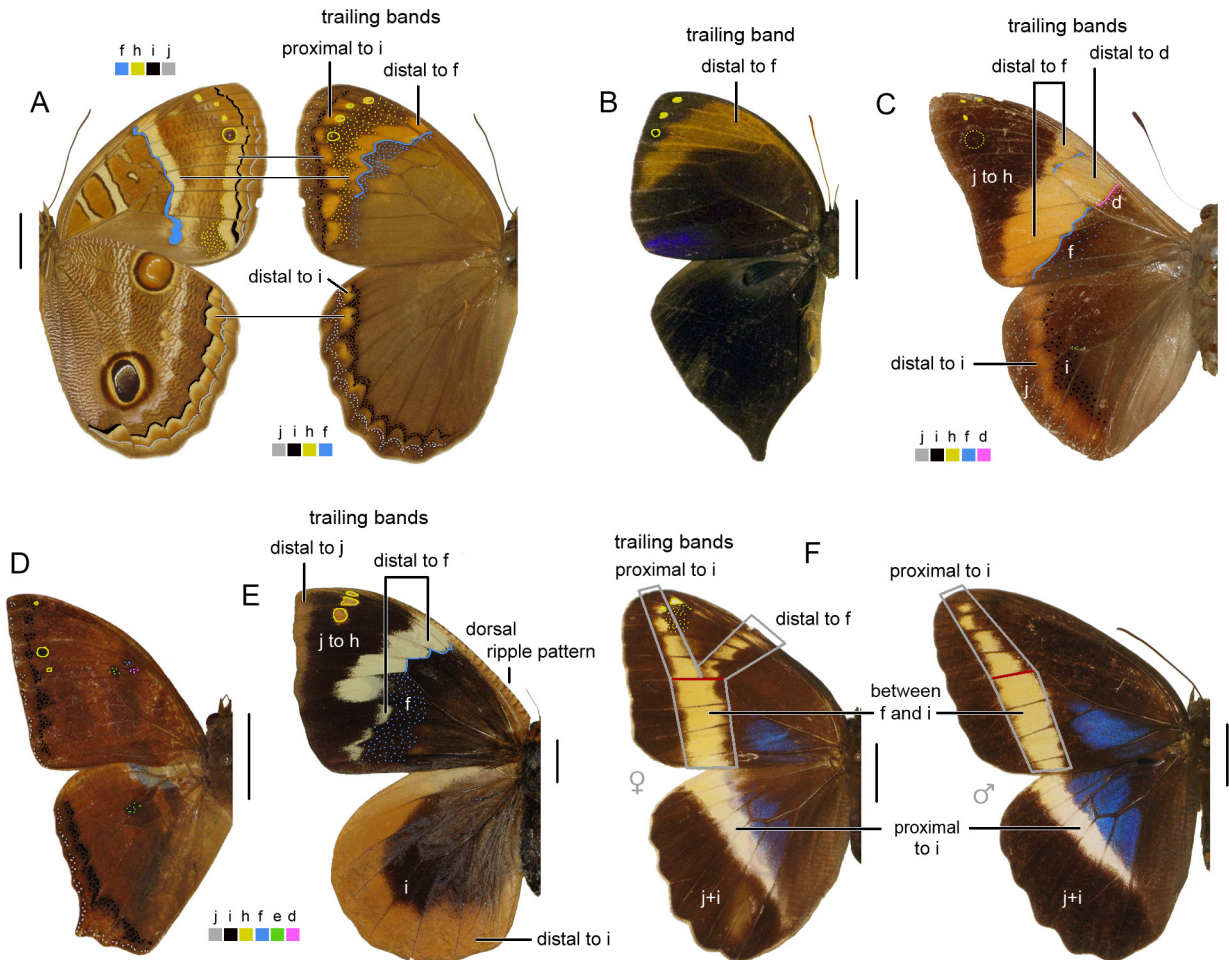
**Figure 4.** Male wings in ventral view plus a schematic drawing showing color-coded pattern elements. Scale bars: 1 cm. **A**, *Catoblepia orgetorix championi*, Panama, Chiriqui; **B**, *Catoblepia berecynthia*, Central Peru; **C**, *Mielkela singularis*, Mexico, Chiapas; **D**, *Orobrassolis ornamentalis*, Brazil, São Paulo; **E**, *Blepopenis bassus*, Brazil; **F**, *Opsiphanes sallei*, Peru, Pasco.

*Orobrassolis ornamentalis* (Stichel, 1906), Figure 4D; *Bia actorion* (Linnaeus, 1763), Figure 1A). The VHW typically includes elements *c*, *d*, *f*, *h*, *i* and *j*, and although very reduced *b* and *e* are also present in some taxa (see Figures 1-4). Element *g* is absent from the VHW of all species examined. The VHW submarginal bands (*i* and *j*) can be absent or present (e.g., absent in *Dynastor darius* (Fabricius, 1775), Figure 1E; present, sharp in *Opoptera syme* (Hübner, 1821), Figure 2B; blurred in *Caligo eurilochus* (Cramer, 1775), Figure 3A).

The position and appearance of pattern elements varies between the VFW and VHW, as it could be expected from their different shape (Figures 1-4). The elements of the central symmetry system (*d*, *e*, *f*) and border ocelli (*h*) are located more distally on the VFW than on the VHW. Element *f* is usually more visible and expressed across a larger number of wing cells on the VFW than the VHW. The serial

expression of element *h* on the VFW usually includes simple spots anterior to vein M1 and a complex ocellus in the cell below this vein, but some taxa also have an additional ocellus in the cell below M2 (*Dynastor*, Figure 1F; *Caligopsis* and *Eryphanis*, Figure 2C, E, F). From veins M2 or M3 to the posterior portion of the VFW, *h* can be absent, fragmented, continuously diffuse, or form a uniquely broad band as in *Blepopenis* (Figure 4E).

Element *h*, suitably referred to as border ocelli, constitutes a notable and easily recognizable wing color component in satyrine butterflies. Within Brassolini, the different manifestations of *h* on the VHW can be divided in three categories: (1) *Narope* and *Aponarope* have a small spot in most cells (Figure 1B, D); (2) some *Catoblepia* have a complex ocellus of similar size in most cells (Figure 4B); and (3) the majority of brassolines have two large, usually complex ocelli



**Figure 5.** Wings in dorsal view (except for A, left side) indicating color-coded pattern elements and trailing bands. Mostly males, except when indicated. Scale bars: 1 cm. **A**, *Opoptera syme*, Brazil, São Paulo, ventral view on the left; **B**, *Bia actorion*, Suriname; **C**, *Brassolis sophorae*, French Guiana; **D**, *Narope cyllastros*, no data; **E**, *Dynastor napoleon*, Brazil, Santa Catarina; **F**, *Dasyophthalma rusina*, female on the left and male on the right, both from South Brazil.

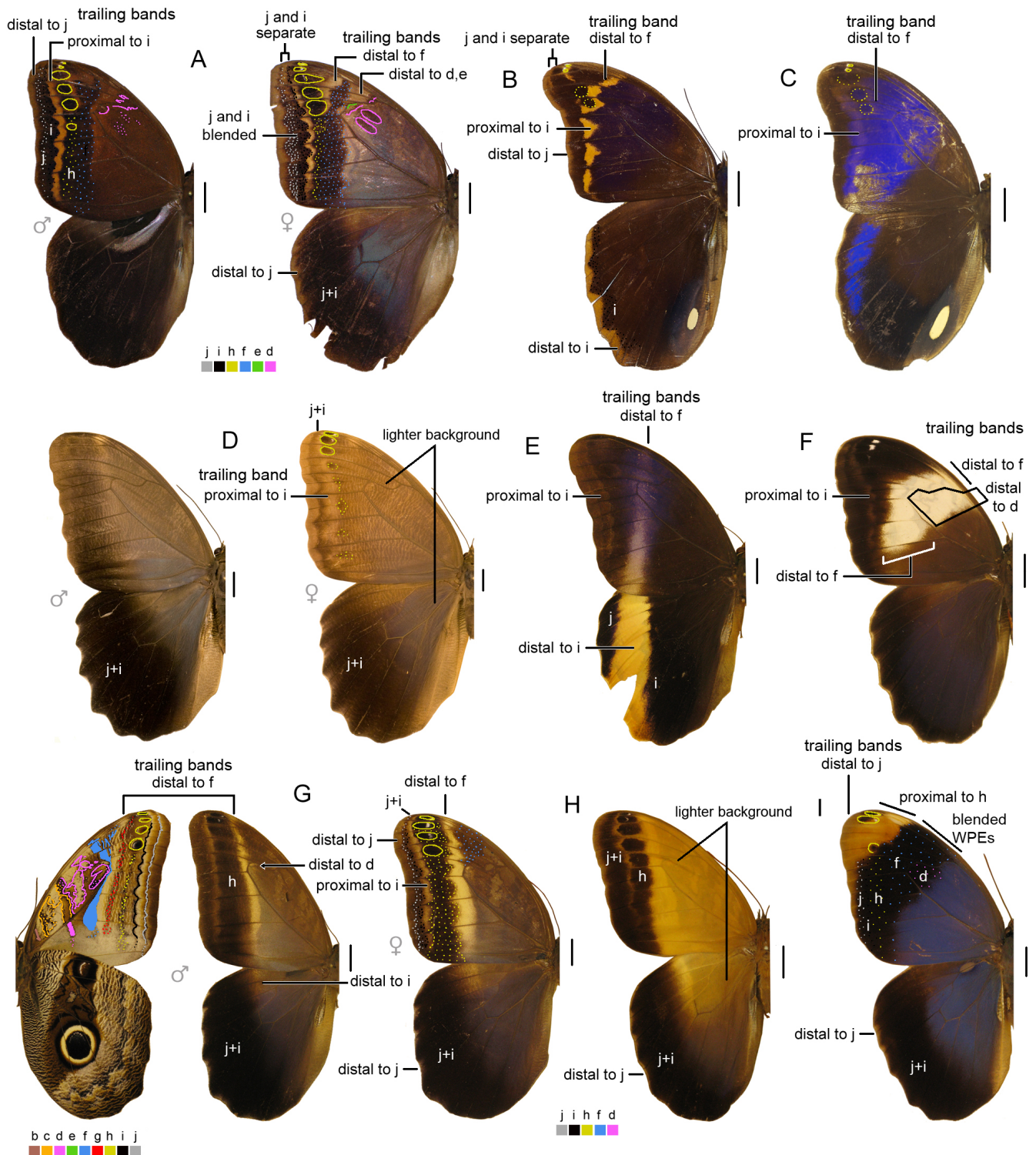
located below Sc+R1 and Cu1 (anterior and posterior ocelli), which are sometimes accompanied by one or two (infrequently three) additional markings. While these markings are usually located below M1 or M2 (Figures 1C, 2E, 3A), *Caligopsis* (Figure 2C) and *Eryphanis* (Figure 2E, F) are unique in having a well-developed ocellus below M3. Within category (3) above, the anterior ocellus of the VHW may diverge from the usual, round shape (e.g., *Selenophanes cassiope* (Cramer, 1775), Figure 3D), and the posterior ocellus may be quite large, expanding across veins Cu1 and Cu2 (e.g., *Caligo*, Figure 3A-C). The location of the posterior ocellus varies in the proximal-distal axis of the Cu1 cell: it is positioned at the base of the tail near the wing margin in *Bia* (Figure 1A), very near the discal cell in *Dasyophthalma* (Figure 2A), *Caligopsis* (Figure 2C), *Eryphanis* (Figure 2E, F) and *Caligo* (Figure 3A, B, C), and approximately at mid-length of the Cu1 cell in the remaining genera. When present, the submarginal bands (*i* and *j*) are always thin and distinctive on the VFW, but those on the VHW can be either thin (e.g., *Opoptera syme*, Figure 2B), or broad and diffuse (e.g., *Caligo eurilochus*, Figure 3A).

The presence, width, color and intensity of trailing bands vary between genera (Figures 1-4). In several species, the contrast between the dark NGP pattern elements and the white trailing bands produces a striking contrast (e.g., *Eryphanis bubocula* (Butler, 1872), Figure 2F), and in others the ventral expression of such band is faint (e.g.,

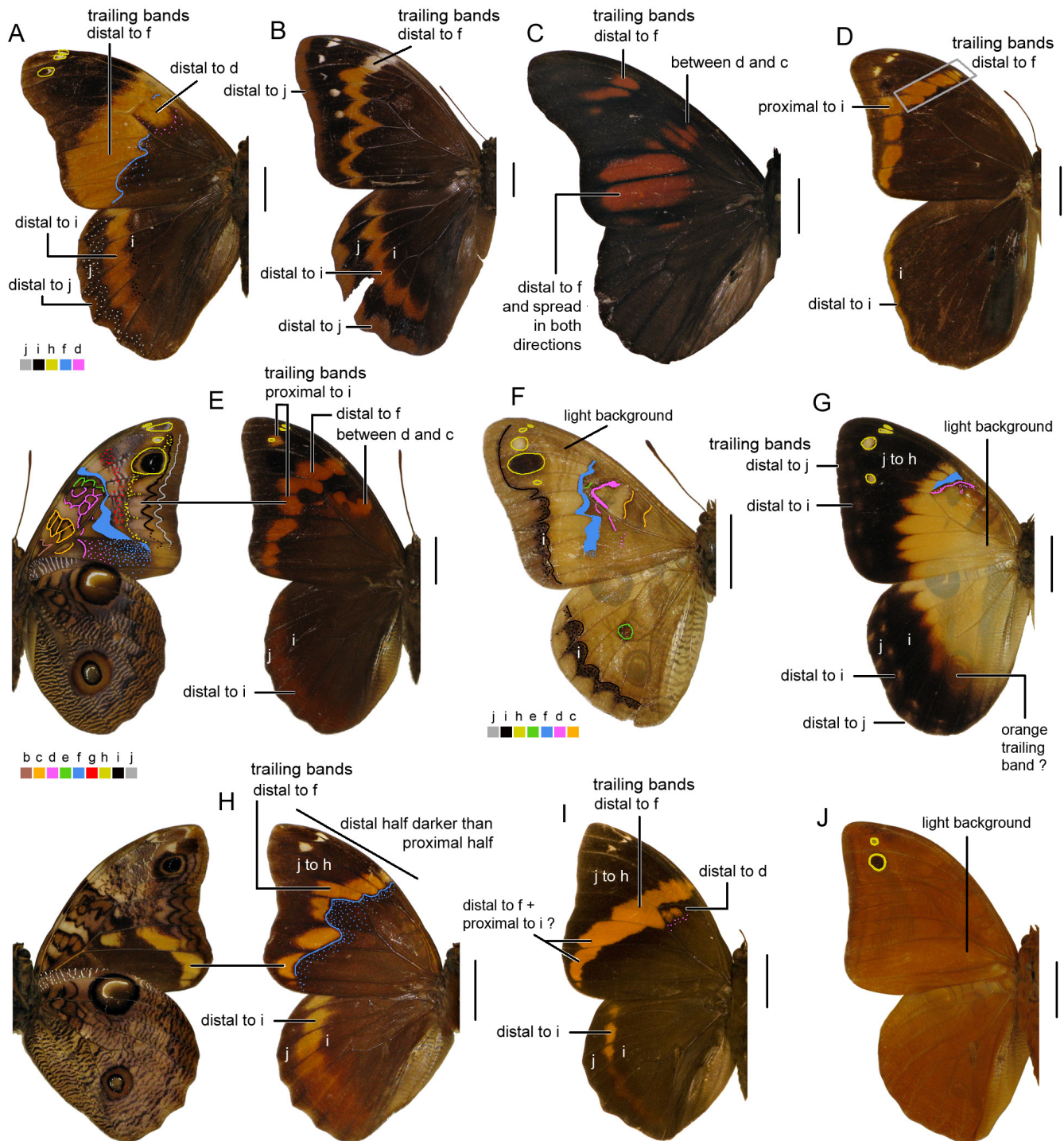
*Catoblepia xanthus* (Linnaeus, 1758), Figure 3F). A trailing band may also be located in an area of the VFW that is not visible when the butterfly is at rest (e.g., *Penetes pamphanis* Doubleday, 1849; Figure 3E). Trailing bands constitute a key feature of the dorsal color pattern and will be addressed in more detail below.

Three attributes of the ripple patterns are worth emphasizing. First, they vary from granular (*Narope*, Figure 1B; *Aponarope*, Figure 1D; *Brassolis*, Figure 1C) to striated (e.g., *Dynastor macrosiris* (Westwood, 1851), Figure 1F), and can be well-defined or blurry (*Dynastor napoleon*, Figure 1E). Second, they can either be prevalent on both wings (Figure 2A), or be expressed on the VHW but reduced to a localized portion of the VFW, usually between *f* and *h* (Figure 4E). Although most genera are uniform in this regard, species of *Caligo* and *Catoblepia* vary in the VFW expression of ripple pattern (compare *Caligo* in Figure 3A, B, C and *Catoblepia* in Figures 3F, 4A, B). Finally, the ripple pattern can be absent from a specific region of the VHW. *Caligopsis seleucida* (Hewitson, 1877), all *Eryphanis* and some *Caligo* species lack ripple pattern in the area between the anterior and posterior ocelli, which is sometimes outlined by pale-colored trailing bands (Figures 2C, E, F and 3C). The lack of ripple pattern in that area makes element *d* clearly visible, and this dark “ripple-free” area is a prominent visual component of the VHW because it highlights the anterior and posterior ocelli. In contrast,





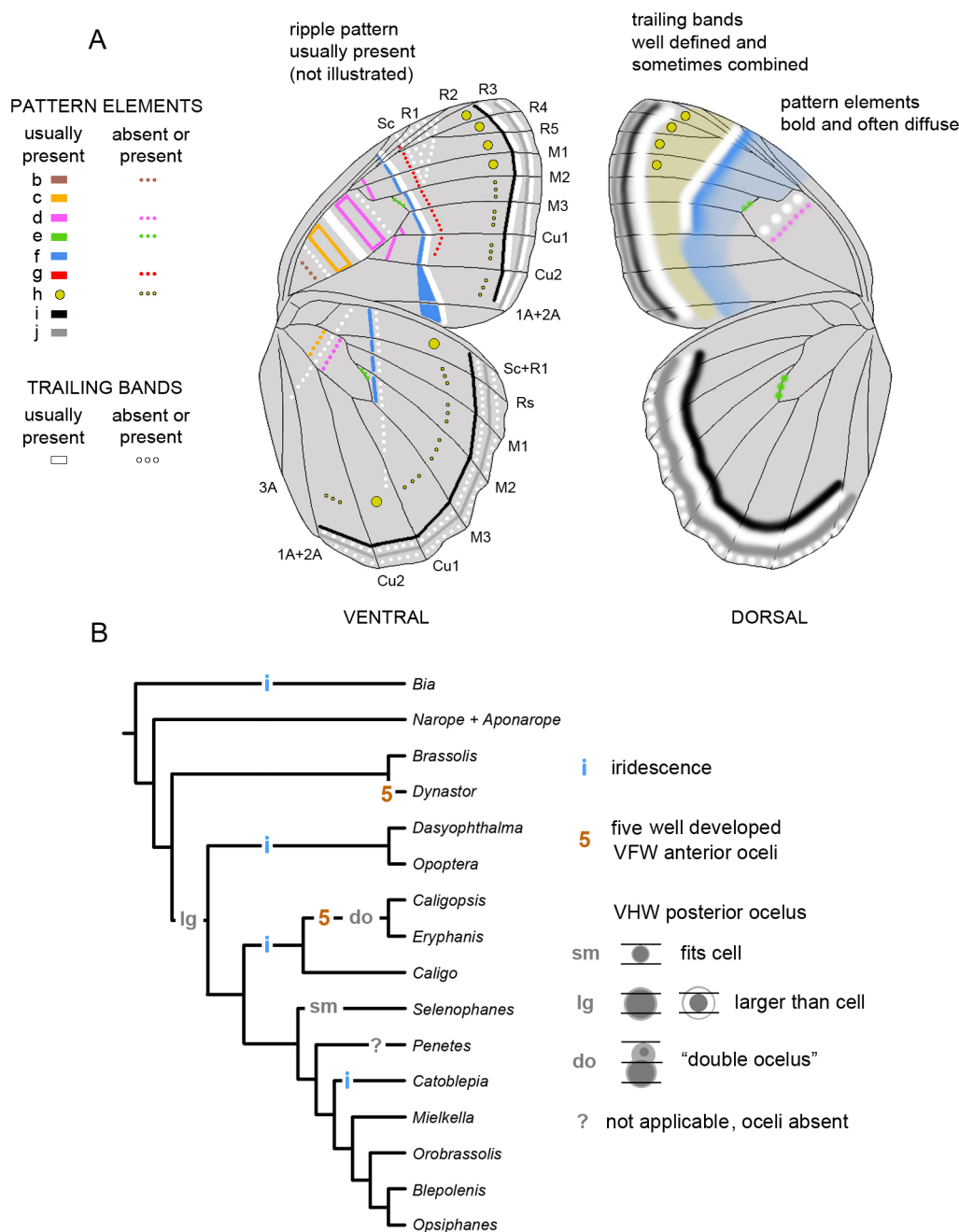
**Figure 6.** Wings in dorsal view (except for G, left side) indicating color-coded pattern elements and trailing bands. Mostly males, except when indicated. Scale bars: 1 cm. **A**, *Caligopsis seleucida*, male on the left and female on the right, both from Peru, Madre de Dios; **B**, *Eryphanis zolvizora*, Bolivia; **C**, *Eryphanis bubocula*, Costa Rica, Guanacaste; **D**, *Caligo eurilochus*, male on the left and female on the right, both from Ecuador, Sucumbios; **E**, *Caligo atreus*, Colombia, Antiochia; **F**, *Caligo martia*, Brazil, Santa Catarina; **G**, *Caligo oileus*, male on the left (in ventral and dorsal views) and female on the right, from Peru, Huanuco and Ayacucho, respectively; **H**, *Caligo arisbe*, Brazil; **I**, *Caligo beltrao*, Brazil, Santa Catarina.



**Figure 7.** Male wings in dorsal view (except for E and H, left side) indicating color-coded pattern elements and trailing bands. Scale bars: 1 cm. **A**, *Selenophanes cassiope*, Peru, Chanchamayo; **B**, *Selenophanes supremus*, Peru, Chanchamayo; **C**, *Penetes pamphanis*, Brazil, Paraná; **D**, *Catoblepia xanthus*, Brazil, Pará; **E**, *Mielkela singularis*, Mexico, Chiapas, ventral view on the left; **F**, *Orobrassolis ornamentalis*, Brazil, São Paulo; **G**, *Blepolenis bassus*, Brazil; **H**, *Opsiphanes sallei*, Peru, Pasco, ventral view on the left; **I**, *Opsiphanes cassina*, Ecuador, Sucumbios; **J**, *Opsiphanes boisduvallii*, Mexico.



## Brassolini wing color patterns



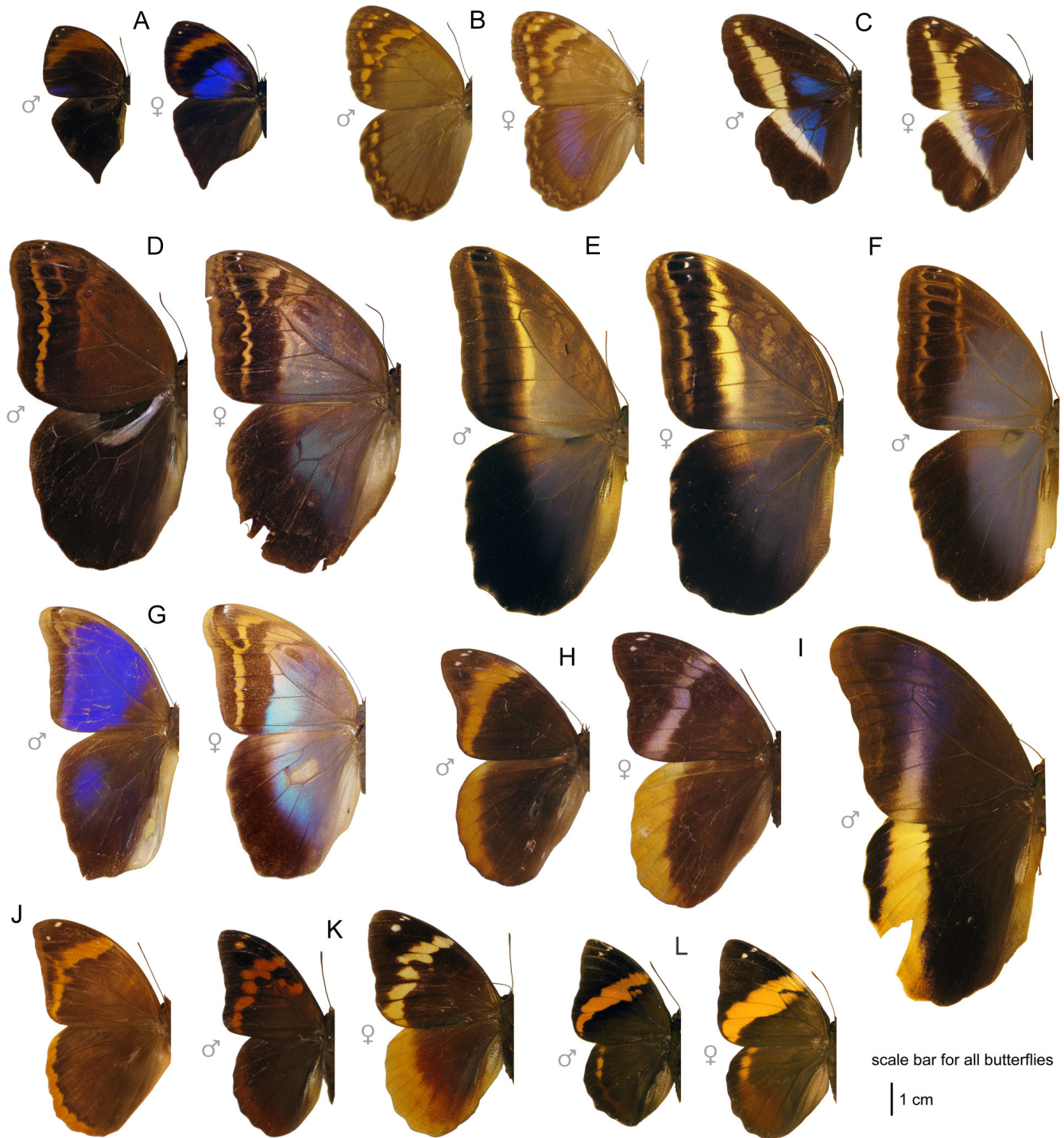
**Figure 8. A**, Subordinate groundplan for the Brassolini ventral and dorsal wing surfaces. Continuous lines (or a large circle for element *h*) indicate pattern elements or trailing bands that are usually present, and small dots or dotted lines denote those that are often absent. The wing outline corresponds to *Oopoptera syme*. **B**, Annotated Brassolini phylogeny on which selected wing color characters have been optimized.

*Mielkella singularis* (Weymer, 1907) and all *Opsiphanes* have a small and inconspicuous VHW area lacking ripple patterns close to the wing base (Figure 4C, F), which is not present in *Blepolepis* or *Orobrassolis*.

## 2. Dorsal wing surface

The dorsal color patterns are simpler than those on the ventral surface. They typically include a reduced number of pattern elements, trailing bands, and iridescent patches that are not part of the NGP (Table 2). We selected *Oopoptera syme* (Figure 5A) as a starting point for the identification of dorsal pattern elements and trailing bands

for three reasons: (1) its dorsal pale brown background allowed us to identify dark brown pattern elements, (2) its ventral color patterns are well defined and easy to recognize, and (3) dorsal pattern elements are almost perfectly aligned with their ventral homologues. The four pattern elements that can be identified on the DFW of *O. syme* are *f*, *h*, *i*, and *j* (the latter being barely visible in some specimens, absent in others), and elements *i* and *j* are visible on the DHW (Figure 5A, see also Figure 9B). Some of the ventral, pale yellow trailing bands have orange dorsal homologues. By comparing the ventral and dorsal images in Figure 5A, note that the two orange bands on the DFW correspond to VFW trailing bands distal to *f* and proximal to *i* (see



**Figure 9.** Sample of brassoline species showing sexual dimorphism and color convergence. Scale bar for all images: 1 cm. **A**, *Bia actorion* male, Suriname and female, Ecuador, Sucumbios; **B**, *Opoptera syme* male, Brazil, São Paulo and female (no data); **C**, *Dasyophthalma rusina* male on the left and female on the right, both from South Brazil; **D**, *Caligopsis seleucida* male on the left and female on the right, both from Peru, Madre de Dios; **E**, *Caligo oileus* male on the left and female on the right, from Peru, Huanuco and Ayacucho, respectively; **F**, *Caligo illioneus* male, Ecuador Sucumbios; **G**, *Eryphanis automedon* male on the left and female on the right, from Colombia, Cali and Paraguay, San Juan Caballero, respectively; **H**, *Catoblepia orgetorix championi* male, Panama, Chiriqui and *C. orgetorix magnalis* female Ecuador, Pastaza; **I**, *Caligo atreus* male, Colombia, Antiochia; **J**, *Opoptera staudingeri* male, Costa Rica, Heredia; **K**, *Mielkela singularis* male on the left and female on the right, both from Mexico, Chiapas; **L**, *Opsiphanes cassina* male on the left and female on the right, both from Ecuador, Sucumbios.



Table 1. General description of ventral patterns (all links last accessed 1 April 2013).

Genus	VFW pattern elements	VHW pattern elements	Trailing bands	Ripple pattern	Notes
<i>Bia</i> <a href="http://fs.uno.edu/cpenz/bia.html">http://fs.uno.edu/cpenz/bia.html</a> Figure 1A	<i>h</i> present in both sexes, usually 4 ocelli, that below M1 being the largest; females may also show <i>c</i> , <i>d</i> and <i>f</i>	<i>h</i> , <i>i</i> , <i>j</i> present in both sexes, females may also show <i>f</i> ; 3-4 ocelli, that below Cu1 elongated and near wing edge and tail	on the VFW of females between <i>i</i> and <i>j</i> ; on the VHW of both sexes between <i>i</i> and <i>j</i>	striated; widespread on both the VFW and VHW	females may have more sparse VFW ripple pattern thus showing more yellow color and visible pattern elements than males
<i>Narope</i> and <i>Aponarope</i> <a href="http://fs.uno.edu/cpenz/harope.html">http://fs.uno.edu/cpenz/harope.html</a> <a href="http://fs.uno.edu/cpenz/aponarope.html">http://fs.uno.edu/cpenz/aponarope.html</a> Figure 1B and D	<i>b</i> to <i>i</i> may be present in both sexes, depending on the species; 4-7 small ocelli; pattern elements usually highly fragmented or blurred, but better defined in <i>N. denitculatus</i> and <i>N. anartes</i> (not illustrated)	<i>c</i> to <i>i</i> may be present in both sexes; typically 7 small ocelli; pattern elements usually highly fragmented or blurred, but better defined in <i>N. denitculatus</i> and <i>N. anartes</i> (not illustrated)	visible on both wings when present; variable: delicate (Figure 1B), or well-developed (Figure 1D); considering the group as a whole, most conspicuous in <i>N. nesope</i> and <i>N. denitculatus</i> (not illustrated)	granulated, sparse; widespread on both the VFW and VHW	pattern elements simpler and less developed in females than in males
<i>Brassolis</i> <a href="http://fs.uno.edu/cpenz/brassolis.html">http://fs.uno.edu/cpenz/brassolis.html</a> Figure 1C	<i>c</i> , <i>d</i> , <i>f</i> , <i>h</i> , <i>i</i> and <i>j</i> present in both sexes; the absence of <i>i</i> and <i>j</i> is a diagnostic character for <i>B. haenschii</i> (not illustrated); 4 ocelli, that below M1 being the largest	<i>c</i> and <i>h</i> present in both sexes; 3 ocelli, anterior and posterior slightly exceeding cell width	on VFW of both sexes, distal to <i>d</i> and <i>f</i>	minute, regular dots; widespread on both the VFW and VHW	pattern similar between the sexes
<i>Dynastor</i> <a href="http://fs.uno.edu/cpenz/dynastor.html">http://fs.uno.edu/cpenz/dynastor.html</a> Figure 1E and F	<i>c</i> , <i>d</i> and <i>f</i> vestigial or absent; <i>h</i> present in both sexes; 4-5 ocelli with the three anterior near the wing margin and the posterior more proximally placed, the ocelli can be small ( <i>D. darius</i> ) or large ( <i>D. macrosiris</i> )	<i>h</i> present in both sexes; usually 3 ocelli, 5 in <i>D. macrosiris stryx</i>	on the VFW distal to <i>f</i> , and in <i>D. m. macrosiris</i> and <i>D. m. stryx</i> these are also found distal to <i>h</i>	granulated or striated; widespread on both the VFW and VHW	pattern similar between the sexes; species broadly different from each other ventrally due to the appearance of the ripple pattern and ocelli size
<i>Dasypophthalma</i> <a href="http://fs.uno.edu/cpenz/dasypophthalma.html">http://fs.uno.edu/cpenz/dasypophthalma.html</a> Figure 2A	<i>d</i> and <i>f</i> vestigial or absent; <i>h</i> visible in both sexes, 1 or 2 well developed ocelli (below R5 and below M1); <i>i</i> vestigial, blurry, more conspicuous in females ( <i>D. rusina</i> , Figure 2A, and <i>D. geraensis</i> , not illustrated) or absent ( <i>D. creusa</i> and <i>D. verbehralis</i> , not illustrated)	<i>h</i> present in both sexes as 2 or 3 well developed ocelli, that below M1 is well developed in <i>D. creusa</i> and <i>D. verbehralis</i> (not illustrated); <i>i</i> vestigial, blurry, or absent	on the VFW distal to <i>f</i> and proximal to <i>i</i> ; on the VHW proximal to <i>i</i> , but vestigial in <i>D. creusa</i> (not illustrated)	striated; widespread on both the VFW and VHW	pattern similar between the sexes
<i>Opoptera</i> <a href="http://fs.uno.edu/cpenz/opoptera.html">http://fs.uno.edu/cpenz/opoptera.html</a> Figure 2B and D	<i>b</i> to <i>i</i> present in both sexes; 4 ocelli, that below M1 being the largest; <i>j</i> present or absent	<i>c</i> , <i>d</i> , <i>f</i> , <i>h</i> , <i>i</i> and sometimes <i>j</i> present in both sexes; usually 4 ocelli, with those below M1 and M2 being rudimentary	on the VFW, present between <i>b</i> and <i>c</i> , <i>c</i> and <i>d</i> , sometimes within <i>d</i> , distal to <i>f</i> , proximal to <i>i</i> , and sometimes distal to <i>i</i> ; on the VHW, distal to <i>d</i> , proximal to <i>i</i> , distal to <i>i</i> and <i>j</i>	striated; limited between <i>f</i> and <i>h</i> on the VFW	pattern similar between the sexes; female paler than male
<i>Caligopsis</i> <a href="http://fs.uno.edu/cpenz/caligopsis.html">http://fs.uno.edu/cpenz/caligopsis.html</a> Figure 2C	<i>b</i> to <i>j</i> present in both sexes, <i>c</i> and <i>d</i> composed of multiple twisted lines inside the discal cell; 5 ocelli, those below M1 and M2 being the largest	<i>d</i> , <i>e</i> , <i>f</i> , <i>h</i> , <i>i</i> and <i>j</i> present in both sexes; <i>i</i> and <i>j</i> located far from the wing margin; 3 ocelli, with the 2 posterior ones being interconnected; <i>f</i> is adjacent to the anterior and posterior ocelli	on the VFW proximal to <i>d</i> , between <i>d</i> and <i>f</i> , distal to <i>i</i> , distal to <i>j</i> ; on the VHW proximal to <i>d</i> , between <i>h</i> and <i>i</i> , distal to <i>i</i>	striated; limited between <i>f</i> and <i>h</i> on the VFW; the region between the anterior and posterior VHW ocelli lacks ripple pattern and, as a result, <i>d</i> is visible inside the discal cell	pattern similar between the sexes; female paler than male
<i>Eryphanis</i> <a href="http://fs.uno.edu/cpenz/eryphanis.html">http://fs.uno.edu/cpenz/eryphanis.html</a> Figure 2E and F	<i>b</i> to <i>j</i> present in both sexes, <i>c</i> and <i>d</i> composed of multiple twisted lines inside the discal cell; <i>g</i> absent or present; 5 ocelli, well-developed or rudimentary	<i>d</i> , <i>e</i> , <i>f</i> , <i>h</i> , <i>i</i> and <i>j</i> present in both sexes; <i>i</i> and <i>j</i> located far from the wing margin; 3 ocelli, with the 2 posterior ones being interconnected (the small ocellus below M3 may be absent); <i>f</i> is adjacent to the anterior and posterior ocelli	on the VFW proximal to <i>d</i> , between <i>d</i> and <i>f</i> , distal to <i>i</i> and distal to <i>j</i> in some species; on the VHW proximal to <i>d</i> , between <i>h</i> and <i>i</i> , distal to <i>i</i> and <i>j</i> in some species	striated; limited between <i>f</i> and <i>h</i> on the VFW; the region between the anterior and posterior VHW ocelli lacks ripple pattern and, as a result, <i>d</i> is visible inside the discal cell	pattern similar between the sexes; females paler than males; pattern elements thinner in the <i>automedon-</i> group and wider in the <i>volvizon-</i> group

Table 1. Continued...

Genus	VFW pattern elements	VHW pattern elements	Trailing bands	Ripple pattern	Notes
<i>Caligo</i> <a href="http://fs.uno.edu/cpenz/caligo.html">http://fs.uno.edu/cpenz/caligo.html</a> Figure 3A, B and C	<i>b</i> to <i>j</i> present in both sexes; <i>c</i> and <i>d</i> usually composed of multiple twisted lines inside the discal cell, but sometimes vestigial (Figure 3A); <i>g</i> absent or vestigial; 4 ocelli, 1-3 well-developed, but element <i>h</i> may be expressed across the entire wing (e.g., Figure 3C)	<i>d</i> , <i>e</i> , <i>f</i> , <i>h</i> , <i>i</i> and <i>j</i> present in both sexes; <i>i</i> and <i>j</i> located far from the wing margin; 2-3 ocelli, small ocellus below M1 sometimes vestigial (Figure 3B) or absent; <i>f</i> may be visible adjacent to the anterior and posterior ocelli in some species	sometimes absent or faded (Figure 3A); on the VFW, may be visible distal to <i>c</i> , distal to <i>f</i> , distal to <i>i</i> ; on the VHW, proximal to <i>d</i> , distal to <i>i</i> and <i>j</i>	striated; on the VFW, variable from widespread (Figure 3A) to localized between <i>f</i> and <i>h</i> (Figure 3B) to nearly absent (Figure 3C); on the VHW, variable from tight striations that are widespread (Figure 3A, B) to loose striations absent from the submedial area (Figure 3C)	pattern similar between the sexes; females paler than males
<i>Selenophanes</i> <a href="http://fs.uno.edu/cpenz/selenophanes.html">http://fs.uno.edu/cpenz/selenophanes.html</a> Figure 3D	<i>b</i> to <i>j</i> present in both sexes; <i>c</i> and <i>d</i> composed of multiple twisted lines inside the discal cell; <i>g</i> absent or vestigial; 4-6 ocelli, that below M1 being the largest and most complex	<i>d</i> , <i>h</i> , <i>i</i> and <i>j</i> present in both sexes; anterior ocellus round ( <i>S. josephus</i> , not illustrated) or sickle-shaped (Figure 3D); 2-6 ocelli, anterior and posterior well-developed	on the VFW trailing colors interspersed with <i>c</i> and <i>d</i> , and a subtle shade distal to <i>f</i>	striated-granular, present on the distal half of the VFW and throughout the VHW	female colors similar to male but VHW <i>h</i> series may be more visible
<i>Penetes</i> <a href="http://fs.uno.edu/cpenz/penetes.html">http://fs.uno.edu/cpenz/penetes.html</a> Figure 3E	pattern elements extremely reduced in both sexes; <i>f</i> , <i>g</i> and <i>h</i> diffuse, barely noticeable	pattern elements extremely reduced in both sexes; <i>h</i> diffuse and barely visible	on the VFW, distal to <i>f</i> (weak)	absent	pattern similar between the sexes; females paler than males
<i>Catoblepia</i> <a href="http://fs.uno.edu/cpenz/opsiphanes.html">http://fs.uno.edu/cpenz/opsiphanes.html</a> Figs 3F, 4A and B	quite variable among species; <i>b</i> to <i>j</i> present in both sexes of some species, but <i>e</i> , <i>f</i> and <i>g</i> vestigial or absent in others; <i>c</i> and <i>d</i> may be simple or intricate inside the discal cell; 4 ocelli, that below M1 being the largest	in both sexes <i>c</i> , <i>d</i> , <i>f</i> , <i>h</i> , <i>i</i> , and <i>j</i> present and <i>f</i> may be vestigial (Figure 3F); 2-6 ocelli, depending on the species (compare Figure 4A and B); pattern elements quite variable among species	quite variable among species; on the VFW of <i>C. xanthus</i> (Figure 3F) trailing colors are subdued distal to <i>f</i> and proximal to <i>i</i> , and are diffuse on the VHW; in <i>C. orgetorix</i> (Figure 4A) they are prominent on the VFW between <i>b</i> and <i>c</i> , <i>c</i> and <i>d</i> , distal to <i>f</i> , and proximal to <i>i</i> and are diffuse on the VHW	striated to granular, variable in contrast from faded to bold; present on the VFW discal cell and space between <i>f</i> and <i>h</i> , and throughout the VHW	pattern similar between the sexes; females may be paler than males
<i>Mielkella</i> <a href="http://fs.uno.edu/cpenz/mielkella.html">http://fs.uno.edu/cpenz/mielkella.html</a> Figure 4C	<i>b</i> to <i>j</i> present in both sexes; 4 ocelli, that below M1 being the largest	<i>b</i> , <i>c</i> , <i>d</i> , <i>e</i> , <i>f</i> , <i>h</i> , <i>i</i> , <i>j</i> present in both sexes; <i>i</i> and <i>j</i> fragmented; 2-3 ocelli, the anterior being the largest, and that below M2 may be vestigial or absent	on the VFW, visible between <i>c</i> and <i>d</i> , distal to <i>f</i> and proximal to <i>i</i> ; poorly developed on the VHW for a localized region near the wing base	striated; limited to a narrow stripe between <i>f</i> and <i>h</i> on the VFW, present throughout the VHW except for a localized region near the wing base	pattern similar between the sexes; females paler than males
<i>Orobassolis</i> <a href="http://fs.uno.edu/cpenz/orobassolis.html">http://fs.uno.edu/cpenz/orobassolis.html</a> Figure 4D	<i>b</i> , <i>c</i> , <i>d</i> , <i>e</i> , <i>f</i> , <i>h</i> , <i>i</i> present in both sexes; 3-4 ocelli, that below M1 being the largest	<i>b</i> , <i>c</i> , <i>d</i> , <i>e</i> , <i>f</i> , <i>h</i> , <i>i</i> present in both sexes, but <i>f</i> barely noticeable and <i>i</i> fragmented; 2 ocelli, the anterior being the largest	on the VFW, visible between <i>b</i> and <i>c</i> , <i>c</i> and <i>d</i> , distal to <i>f</i> ; and distal to <i>i</i> ; on the VHW, visible between <i>b</i> and <i>c</i> , and <i>c</i> and <i>d</i>	striated; limited to a narrow stripe between <i>f</i> and <i>h</i> on the VFW, present throughout the VHW	pattern similar between the sexes; females may be slightly paler than males
<i>Blepolenis</i> <a href="http://fs.uno.edu/cpenz/blepolenis.html">http://fs.uno.edu/cpenz/blepolenis.html</a> Figure 4E	<i>b</i> to <i>j</i> present in both sexes; <i>h</i> particularly well developed across the entire wing, forming a dark band that is unique to <i>Blepolenis</i> among all brassoline genera; 4-5 ocelli, that below M1 being the largest	<i>c</i> , <i>d</i> , <i>e</i> , <i>f</i> , <i>h</i> , <i>i</i> , <i>j</i> present in both sexes; <i>j</i> fragmented; 2 ocelli of approximately the same size	on the VFW, visible between <i>b</i> and <i>c</i> , <i>c</i> and <i>d</i> , and distal to <i>f</i> ; on the VHW, visible between <i>b</i> and <i>c</i> , distal to <i>f</i> , proximal and distal to <i>i</i>	striated; limited to a triangle between <i>g</i> and <i>h</i> on the VFW, present throughout the VHW	pattern similar between the sexes; females paler than males
<i>Opsiphanes</i> <a href="http://fs.uno.edu/cpenz/opsiphanes.html">http://fs.uno.edu/cpenz/opsiphanes.html</a> Figure 4F	<i>b</i> to <i>j</i> visible in both sexes; 3-4 ocelli, that below M1 being the largest	<i>b</i> , <i>c</i> , <i>d</i> , <i>e</i> , <i>f</i> , <i>h</i> , <i>i</i> , <i>j</i> present in both sexes, but <i>f</i> and <i>e</i> vestigial or absent, and <i>i</i> and <i>j</i> fragmented; 2 ocelli, the anterior usually larger	variable among species from being nearly absent ( <i>O. cassiae</i> , not illustrated) to quite conspicuous (e.g., <i>O. cassina</i> , not illustrated); on the VFW, visible distal to <i>f</i> below M3 or Cu1, and may also be present distal to <i>d</i> (Figure 4F); usually absent or very faint on the VHW (except for <i>O. blythekizimillerae</i> , not illustrated)	striated; between <i>f</i> and <i>h</i> on the VFW, present throughout the VHW, but sometimes absent from the VHW base	pattern similar between the sexes; females paler than males

**Table 2.** General description of dorsal patterns (all links last accessed 1 April 2013).

Genus	DFW pattern elements	DHW pattern elements	Trailing bands	Iridescence	Sexual dimorphism
<i>Bia</i> <a href="http://fs.uno.edu/cpenz/bia.html">http://fs.uno.edu/cpenz/bia.html</a> Figure 5B	difficult to identify due to dark brown background; <i>h</i> present as three anterior ocelli near wing outer edge	difficult to identify due to dark brown background	on the DFW, one trailing band distal to <i>f</i> ; absent on the DHW	<i>Male</i> : depending on the species, a strongly iridescent patch near DFW tornus, a strongly iridescent patch occupying most of the DHW, or no visible iridescence <i>Female</i> : depending on the species, a large, diffuse iridescent patch in the posterior portion of the DFW medial area, accompanied or not by a small diffuse iridescent patch centrally on the DHW	coloration clearly dimorphic due to differences in iridescence; wing shape similar between the sexes
<i>Narape</i> and <i>Aponarape</i> <a href="http://fs.uno.edu/cpenz/narape.html">http://fs.uno.edu/cpenz/narape.html</a> <a href="http://fs.uno.edu/cpenz/aponarape.html">http://fs.uno.edu/cpenz/aponarape.html</a> Figure 5D	some species are homogeneously brown, so pattern elements could not be identified (e.g., <i>N. cyllastros</i> , not illustrated); <i>d</i> to <i>j</i> (minus <i>g</i> ) are visible in some species (e.g., <i>N. cyllastros</i> , Figure 5D); <i>N. guilhermei</i> (not illustrated) is exceptional in which all pattern elements seem to be present dorsally, especially in the female	some species are homogeneously brown, so pattern elements could not be identified; when pattern elements are visible, typically <i>e</i> , <i>i</i> and <i>j</i> only can be identified	absent from DFW and DHW; we hypothesize that the orange patches present in <i>N. guilhermei</i> (not illustrated) constitute background coloration not covered by the bold dorsal pattern elements	absent from both sexes	some species clearly dimorphic; others mildly dimorphic in color; wing shape dimorphic
<i>Brassolis</i> <a href="http://fs.uno.edu/cpenz/brassolis.html">http://fs.uno.edu/cpenz/brassolis.html</a> Figure 5C	<i>d</i> to <i>j</i> (minus <i>g</i> ) are visible	<i>i</i> and <i>j</i>	on the DFW, distal to <i>d</i> and distal to <i>f</i> , amalgamated but <i>f</i> sometimes visible at the edge of the discal cell; on the DHW, distal to <i>i</i>	absent from both sexes	mildly dimorphic in color; wing shape dimorphic
<i>Dynastor</i> <a href="http://fs.uno.edu/cpenz/dynastor.html">http://fs.uno.edu/cpenz/dynastor.html</a> Figure 5E	possibly <i>f</i> to <i>j</i> (minus <i>g</i> ) given that the distal portion of the wing is darker than the basal to medial area	<i>i</i> only, or <i>i</i> and <i>j</i> faintly visible	on the DFW, a broken band distal to <i>f</i> ; and a continuous band distal to <i>j</i> ; on the DHW, distal to <i>i</i> and distal to <i>j</i>	absent from both sexes	mildly dimorphic in color; wing shape slightly dimorphic
<i>Dasyophthalma</i> <a href="http://fs.uno.edu/cpenz/dasyophthalma.html">http://fs.uno.edu/cpenz/dasyophthalma.html</a> Figure 5F	difficult to identify from the brown background. <i>h</i> barely visible in female <i>D. rusina</i> only (Figure 5F, left image)	<i>i</i> and <i>j</i> faintly visible, slightly darker brown than the rest of the wing	on the DFW, bands distal to <i>f</i> and between <i>f</i> and <i>i</i> ; on the DHW, a band proximal to <i>i</i>	present in the post-basal and posterior DFW and medial area of the DHW of both sexes of <i>D. rusina</i> and <i>D. geraensis</i> , females having smaller patches	dimorphic in color mostly due to the anterior trailing band distal to <i>f</i> present in females, but the band between <i>f</i> and <i>i</i> is more tilted diagonally in males; wing shape slightly dimorphic
<i>Opoptera</i> <a href="http://fs.uno.edu/cpenz/opoptera.html">http://fs.uno.edu/cpenz/opoptera.html</a> Figure 5A	<i>f</i> to <i>j</i> (minus <i>g</i> ) are visible in some species (e.g., <i>O. syme</i> Figure 5A), but in others the wing background is dark and only <i>h</i> and sometimes <i>i</i> can be identified	<i>i</i> only, or <i>i</i> and <i>j</i>	on the DFW, bands distal to <i>f</i> and proximal to <i>i</i> ; on the DHW, a band distal to <i>i</i> and sometimes one distal to <i>j</i>	absent from males; a patch present on the DHW of <i>O. syme</i> females; widespread and very faint iridescence present on both wings of female <i>O. aarisa</i> and <i>O. hilaris</i>	species vary in being monomorphic (females only slightly paler in <i>O. sulcius</i> and <i>O. fruhstorferi</i> ) to mildly dimorphic; wing-shape similar between males and females
<i>Caligopsis</i> <a href="http://fs.uno.edu/cpenz/caligopsis.html">http://fs.uno.edu/cpenz/caligopsis.html</a> Figure 6A	<i>d</i> to <i>j</i> (minus <i>g</i> ; <i>e</i> absent or present); <i>h</i> present as anterior ocelli becoming a bold band posteriorly	difficult to identify from the brown background, but <i>i</i> and <i>j</i> can be seen in the female in Figure 6A	on the DFW, bands distal to <i>d</i> , distal to <i>f</i> , proximal to <i>i</i> , proximal to <i>j</i> are visible in the female, but only the latter two can be identified in the male; on the DHW, a faint band is visible distal to <i>j</i> on the female	faint iridescence on the medial to basal area of both wings in the female; males of some locations display iridescence that is stronger than in females	dimorphic in color; wing-shape similar between males and females, but male forewing posterior margin bowed
<i>Eryphanis</i> <a href="http://fs.uno.edu/cpenz/eryphanis.html">http://fs.uno.edu/cpenz/eryphanis.html</a> Figure 6B and C	difficult to identify from the brown background; <i>h</i> present as three to five anterior ocelli	difficult to identify from the brown background; <i>i</i> only, or <i>i</i> and <i>j</i> are sometimes visible	on the DFW, bands distal to <i>f</i> , proximal to <i>i</i> and distal to <i>j</i> are absent or present depending on the species; on the DHW, a band distal to <i>i</i> is absent or present depending on the species	variable between the sexes and between species; when clear blue iridescence is present in both sexes, it is stronger in the male than in the female sex; in some species the male has a sheen that gives out a faint insinuation of iridescence (Figure 6B), while the females clearly have pale blue iridescent areas on both wings	dimorphic in color; wing shape similar between males and females

Table 2. Continued...

Genus	DFW pattern elements	DHW pattern elements	Trailing bands	Iridescence	Sexual dimorphism
<i>Caligo</i> <a href="http://fs.uno.edu/cpenz/caligo.html">http://fs.uno.edu/cpenz/caligo.html</a> Figure 6D to I	<i>d</i> to <i>j</i> or <i>h</i> to <i>j</i> (minus <i>g</i> ; <i>e</i> absent or present); in some species <i>h</i> is present as anterior ocelli becoming a bold band posteriorly	difficult to identify from the brown background, but <i>i</i> and <i>j</i> can be seen in some species	on the DFW, a band distal to <i>f</i> is present in several species, proximal to <i>i</i> in some, and distal to <i>d</i> in <i>C. martia</i> (Figure 6F); two species have a band distal to <i>i</i> on the DHW ( <i>C. atreus</i> , Figure 6E; and <i>C. uranus</i> , not illustrated), and that of <i>C. oberthurii</i> (not illustrated) seems to be located proximal to <i>i</i> ; some species are hypothesized to have light or colorful background that produces a similar appearance to trailing bands	in both sexes, absent or present in one wing only or both	mildly dimorphic in color; wing shape similar between males and females
<i>Selenophanes</i> <a href="http://fs.uno.edu/cpenz/selenophanes.html">http://fs.uno.edu/cpenz/selenophanes.html</a> Figure 7A and B	difficult to identify from the brown background, presumably <i>d</i> to <i>j</i> or <i>h</i> to <i>j</i> (minus <i>g</i> ); <i>h</i> forms a long series of spots in <i>S. supremus</i> (Figure 7B)	difficult to identify from the brown background	on the DFW, a band distal to <i>f</i> only, or combined with one distal to <i>d</i> ; on the DHW, bands distal to <i>i</i> and distal to <i>j</i> present or absent	absent from both sexes	monomorphic to mildly sexually dimorphic in color; wing shape similar between males and females
<i>Penetes</i> <a href="http://fs.uno.edu/cpenz/petes.html">http://fs.uno.edu/cpenz/petes.html</a> Figure 7C	difficult to identify from the brown background	difficult to identify from the brown background	on the DFW, a discontinuous band distal to <i>f</i> and another between <i>c</i> and <i>d</i> ; on the DHW, a spot near the anterior margin that presumably corresponds to the band distal to <i>i</i>	absent from both sexes	monomorphic in color, but females slightly paler than males; wing shape similar between males and females
<i>Catoblepia</i> <a href="http://fs.uno.edu/cpenz/catoblepia.html">http://fs.uno.edu/cpenz/catoblepia.html</a> Figs 7D	difficult to identify from the brown background, presumably <i>d</i> to <i>j</i> or <i>f</i> to <i>j</i> (minus <i>g</i> ); <i>h</i> usually appears as white spots above M1 and an oculus below this vein, more spots are occasionally present below M2	difficult to identify from the brown background; <i>i</i> and <i>j</i> , or <i>i</i> only, presumably present	on the DFW, a continuous or broken band distal to <i>f</i> combined with one proximal to <i>i</i> ; on the DHW, a band distal to <i>i</i> that may or may not reach the wing margin	absent from both sexes	wing shape similar between males and females but variable between species
<i>Mielkella</i> <a href="http://fs.uno.edu/cpenz/mielkella.html">http://fs.uno.edu/cpenz/mielkella.html</a> Figure 7E	difficult to identify from the brown background, presumably <i>d</i> to <i>j</i> (minus <i>g</i> ); <i>h</i> usually appears as small spots above M1 and a faint oculus below this vein	difficult to identify from the brown background; <i>i</i> and <i>j</i> presumably present	on the DFW, a band distal to <i>f</i> combined with one proximal to <i>i</i> ; on the DHW, a band distal to <i>i</i>	absent from both sexes	sexual dimorphism in wing color and shape
<i>Orobassolis</i> <a href="http://fs.uno.edu/cpenz/orobassolis.html">http://fs.uno.edu/cpenz/orobassolis.html</a> Figure 7F	<i>c</i> to <i>i</i> (minus <i>g</i> ); <i>h</i> appears as small white spots above M1 an oculus below this vein and a white spot below M2	<i>e</i> and <i>i</i>	difficult to identify due to the light background	absent from both sexes	monomorphic, but females slightly paler; wing shape similar between males and females
<i>Blepolepis</i> <a href="http://fs.uno.edu/cpenz/blepolepis.html">http://fs.uno.edu/cpenz/blepolepis.html</a> Figure 7G	<i>d</i> to <i>j</i> (minus <i>g</i> ); <i>h</i> appears as small white spots above M1 a faint brown oculus below this vein and one or two white spots below M2	<i>i</i> and <i>j</i>	difficult to identify due to the light background; it is possible that the diffuse dark orange edges of the blended pattern elements could be a trailing band	absent from both sexes	mildly sexually dimorphic in color; wing shape similar between males and females, but female wings slightly broader
<i>Opsiphanes</i> <a href="http://fs.uno.edu/cpenz/opsiphanes.html">http://fs.uno.edu/cpenz/opsiphanes.html</a> Figure 7H to J	for most species, difficult to identify from the brown background, presumably <i>d</i> to <i>j</i> or <i>f</i> to <i>j</i> (minus <i>g</i> ); <i>h</i> usually appears as white spots above M1 and a faint oculus below this vein; <i>h</i> only in <i>O. boisduvallii</i> , <i>h</i> and <i>i</i> in <i>O. blythekitzmilleriae</i>	for most species, difficult to identify from the brown background; <i>i</i> and <i>j</i> presumably present; all pattern elements absent in <i>O. boisduvallii</i> , <i>i</i> only present in <i>O. blythekitzmilleriae</i>	on the DFW, a band distal to <i>f</i> possibly blended with one proximal to <i>i</i> ; on the DHW, a band distal to <i>i</i> is usually present; absent from <i>O. boisduvallii</i> and <i>O. blythekitzmilleriae</i>	absent from both sexes	mildly sexually dimorphic in color; wing shape dimorphic



horizontal lines connecting the images). The trailing band distal to *f* is shorter and more diffuse on the DFW than on the VFW. A diffuse and broken band is located distal to *i* on DHW, and its ventral homologue is better defined. *Ooptera syme* females show a faint iridescent patch on the DHW that is not associated with any of the NGP pattern elements (Figure 9B). The fortuitous dorsal coloration of this species allowed us to build a comparative framework used to interpret the dorsal patterns of other brassolines (Figures 5-7).

Few pattern elements can be identified on the dorsal wing surface (Table 2). Visible pattern elements are broad and diffuse, usually blending with the brown wing background (Figures 5-7). Therefore, in species with predominantly dark brown wings, identification of pattern elements was not possible (e.g., *Bia*, Figure 5B; *Penetes*; Figure 7C; Table 2). *Orobrassolis* constitutes an exception where the pale wing background allowed for the identification of six pattern elements on the DFW (*c*, *d*, *e*, *f*, *h*, and *i*; Figure 7F). Element *f* and those distal to it are generally expressed on the DFW except for *g*, and the homogeneously dark distal half of the DFW of some taxa suggests that such pattern elements blend together (e.g., *Opsiphanes*, Figure 7H, I). Nonetheless, elements *c* and *d* are visible on the DFW of some taxa (*Brassolis*, Figure 5C; *Caligopsis*, Figure 6A; *Orobrassolis*, Figure 7F; *Blepolenis*, Figure 7G). Element *h* usually appears as a series of two or three anterior, simple spots and one diffuse oculus below M1. However, additional spots are found in some species (e.g., *Selenophanes supremus* Stichel, 1901; Figure 7B), or *h* may be extended across the entire DFW in others (e.g., *Caligo eurilochus* and *C. oileus* C. Felder & R. Felder, 1861; Figure 6D, G). Most brassolines seem to lack pattern elements proximal to *i* on the DHW, but *e* is present in a few taxa (*Narope*, Figure 5D; *Orobrassolis*, Figure 7F). In contrast to other brassolines, element *e* is present on both the DFW and DHW of most species of *Narope* (Figure 5D). The dark distal portion of the DHW of some species of *Caligo* (e.g., *C. eurilochus*, Figure 6D) expands over an area that includes element *h* on the ventral surface. Although it is possible that *h* might be present on the dorsal surface of such species, we conservatively interpreted all brassolines as lacking *h* on the DHW.

Light-colored trailing bands constitute a highly visible component of the dorsal brassoline coloration because they contrast the brown wing background. As shown in Figures 5-7 (see also Table 2), these bands are found on both wings, varying in position, width, length, amalgamation, color, and intensity. Most brassolines have a band across the DFW, and the two main components of this band can be easily identified in *Ooptera syme* (Figure 5A); i.e., the trailing bands distal to *f* and proximal to *i*. Amalgamation of the same two DFW trailing bands in *Ooptera staudingeri* (Godman & Salvin, 1894) (Figure 9J) result in a single, continuous, curved band, an arrangement that is also found in *Catoblepia* (example in Figure 7D). Some taxa have a band distal to element *d* that blends with that distal to *f* (e.g., *Brassolis*, Figure 5C; *Caligo martia* (Godart, 1824), Figure 6F; *Selenophanes cassiope*, Figure 7A). A band between DFW elements *c* and *d* is present in a few species (e.g., *Mielkella singularis*, Figure 7E). Regarding the DHW, when a trailing band is present, it usually corresponds to that distal to element *i* (Figures 5A, C, E; 6B, E; 7A, D to H), and sometimes a faded band distal to *j* is also visible (Figure 7A, G). *Dasyophthalma* is unusual in having a trailing band located proximal to element *i* (Figure 5F).

Dorsal iridescence is present in species of seven genera, in both sexes or one sex only (Table 2). Among the species and specimens examined here, iridescence is found in both sexes of some species of *Bia*, *Dasyophthalma*, *Eryphanis*, *Caligo* and *Catoblepia orgetorix* (Hewitson, 1870), being more intense in males. Female-limited faint iridescence is visible on the DHW of *Ooptera syme* (Figure 9B) and both wings of *O. aorsa* (Godart, 1824) and *O. hilaris* Stichel, 1901

(not illustrated), *Caligopsis seleucida* (Figure 9D; but an iridescent male is illustrated by D'Abrera 1987), and *Catoblepia soranus* (Westwood, 1851) (not illustrated).

### 3. Subordinate groundplan for Brassolini

Figure 8A summarizes the proposed subordinate groundplan for Brassolini. Pattern elements and trailing bands represented by solid lines or large circles are typically present, and those indicated by dotted lines are often absent. Pattern elements are narrower and more clearly defined on the ventral than on the dorsal wing surfaces, where they are broad and diffuse. While the ventral wing coloration is derived mostly from pattern elements and ripple patterns, trailing bands constitute the most visible component of the dorsal surface.

The number of visible pattern elements decreases progressively from the VFW to the VHW, and DFW to the DHW. Pattern elements *c*, *d*, *f*, *h*, *i* and *j* are usually expressed on the VFW, and *e* and *g* were visible in fewer of the examined species. Elements *c* and *d* vary from straight lines to a complex web of interlocking lines, and they fill a large portion of the wing surface together with *f*. Round ocelli are typically visible above vein M2, and *h* may be irregularly shaped or absent below that vein. Elements *i* and *j* are typically thin and may fade towards the VFW tornus. Pattern element *h* is the dominant feature of the VHW. It can be expressed as a series of simple or complex round ocelli, but most species display two complex ocelli (anterior and posterior) that flank several irregular markings. Although *f*, *i* and *j* are often expressed, element *f* is usually visible on the anterior portion of the wing only, and *i* and *j* interact with the ripple pattern and appear more diffuse than their VFW counterparts. The DFW groundplan includes few pattern elements, typically *f* and those distal to it, except for *g*. We hypothesize that element *g* is absent from the DFW based on the dorsal patterns of *Ooptera syme* (Figure 5A) and other species that have a light background color (e.g., Figures 5D; 6D, G, H; 7F, G, J), and also because *g* is often missing from the VFW. Finally, most pattern elements are absent from the DHW, and most species display a combination of elements *i* and *j* plus a trailing band (*e* is found in a few taxa).

The ventral color patterns of *Narope*, *Aponarope* and *Penetes* are unusual within Brassolini, and depart from the groundplan. While well developed in other members of the tribe, the border ocelli of *Narope* and *Aponarope* appear as small spots that blend with their unique, finely granular ripple pattern, and the pattern elements are highly fragmented in these genera (Figure 1B, D). In *Penetes*, the few pattern elements present are diffuse and barely noticeable, and ripple patterns are also lacking (Figure 3E). Intervinous stripes that are not part of the NGP are visible inside *Penetes* VFW discal cell (3 stripes) and VHW discal cell (one stripe). Incidentally, the dark intervenous stripes in *Penetes* are indicative of unpigmented intervenous stripes that distort certain pattern elements in other brassolines. For example, in the VFW discal cell of *Selenophanes* (Figure 3D) element *c* appears as a series of four contiguous circles that possibly result from distortions from three intervenous stripes.

The wing background color of most brassolines is brown, but some taxa are notably different. We hypothesize that the vivid dorsal coloration of some species of *Narope* (Figure 5D), the two *Orobrassolis* (Figure 7F), *Opsiphanes blythekitzmilleriae* Austin & A. Warren, 2007 (not illustrated) and *O. boisduvallii* Doubleday, 1849 (Figure 7J) results from a change in background color, with an extreme reduction in the expression of dorsal pattern elements in the two *Opsiphanes*. The dorsal colors of some species of *Caligo* (e.g., Figure 6H) and all *Blepolenis* (Figure 7G) can also be interpreted as a change in background coloration, and the bold dorsal pattern elements *f* to *j* (minus *g*) are particularly well developed and bold in *Blepolenis*. This fortuitous variation in background color further

supports our hypothesis that many pattern elements are absent from the dorsal wing surface of brassolines, especially the DHW.

#### 4. Dorsal sexual dimorphism and color pattern convergence

In most brassoline species, males and females are only mildly dimorphic in their dorsal colors, and have similar wing shape (Table 2). Mild color dimorphism results from females having more clearly defined dorsal pattern elements and / or trailing bands than males. For example, in some *Caligo* (e.g., *C. oileus*; Figures 6G, 9E) both the dorsal pattern elements and trailing bands are more visible in females. The slight iridescence of some female *Opoptera* (Figure 9B) and *Catoblepia* (not illustrated), or slightly wider and paler trailing bands of *Opsiphanes* (Figure 9L) can also be considered mild color dimorphism.

There are instances in which dorsal colors and wing shape are clearly different between the sexes (Table 2). The genus *Bia* is an interesting case in which obvious sexual differences can occur on both the dorsal and ventral wing surfaces. The DFW orange trailing band and iridescent patch are positioned more distally in the males, and females have a less intense, but larger iridescent patch extending through the discal cell in the medial area of the wing (Figure 9A; male iridescence may be absent in some forms). In some locations, the female VFW has reduced ripple patterns distal to element *f* such that the distal portion of the hind wing has a predominantly yellow appearance (not illustrated). Within *Narope*, *N. guilhermei* Casagrande, 1989 (not illustrated) is the most notable for color differences between the sexes, but males and females differ in wing shape in all species. Sexual dimorphism in *Dasyophthalma* results from differences in the DFW trailing band distal to *f* that is present in females only, and also the larger, more intense iridescent patches in males of two species (Figures 5F, 9C). In some *Eryphanis*, males are much more intensely iridescent than females (Figure 9G). Differences in wing shape plus the colors and width of trailing bands produces strong sexual dimorphism in *Mielkella singularis* (Figure 9K).

In a few cases, strong sexual dimorphism is intertwined with dorsal color convergence across genera. Female *Catoblepia orgetorix* orgetorix, *C. orgetorix magnalis* Stichel, 1902 and *C. orgetorix championi* Bristow, 1981 (Figure 9H), and both sexes of *C. orgetorix rothschildi* Casagrande & Lamas, 2004, resemble *Caligo atreus* (Kollar, 1850) and depart strongly from the typical *Catoblepia* phenotype (Figure 9I). This resemblance to *C. atreus* can be achieved with few phenotypic modifications: (1) all dorsal female trailing bands become lighter in color, (2) the DFW trailing bands are amalgamated and positioned closer to the medial area of the wing, (3) a patch of iridescent scales is superimposed onto the DFW trailing band, and (4) the DHW trailing band becomes wider, reaching the wing edge. The monomorphic *Opoptera staudingeri* differs from close relatives in the *aorsa*-group by lacking hind wing tails and in the continuous, relatively wide DFW and DHW trailing bands. Such modifications yield a resemblance to species of *Catoblepia* (compare Figure 9J and H). Finally, due to their dorsal iridescence, *Caligopsis seleucida* females (Figure 9D) more closely resemble some *Caligo* (Figure 9F) than the conspecific male.

## Discussion

This study represents the first comprehensive examination of color pattern diversity in the tribe Brassolini. Here we describe the expression of pattern elements across all genera, and propose a subordinate groundplan for the tribe (Figure 8A). Much variation was found on the ventral forewing surface, with the number of visible pattern elements ranging from one to nine. Except for *Penetes*, ripple

patterns were prevalent on the ventral hind wing and expressed to a lesser extent on the ventral forewing, varying from sharply striated, to blurry, or granular. On the dorsal wing surface pattern elements are broader and more diffuse than on the ventral surface (bold, *sensu* Nijhout & Wray 1986), and are often amalgamated. Furthermore, fewer pattern elements are identifiable on the dorsal than on the ventral surface (Figure 8A). The dorsal forewing typically includes *f*, *h*, *i* and *j*, but *e* and *d* are sometimes visible. The dorsal hind wing lacks most pattern elements, usually displaying only *i* and *j*. We hypothesize that the dorsal white, yellow or orange trailing bands might be associated with particular pattern elements, and they constitute an important feature of the brassoline groundplan. Finally, iridescent bands do not correspond to NGP elements, but may be superimposed onto them. The presence and intensity of iridescence is quite variable, appearing in different areas of the wing, and evolving independently in four separate Brassolini lineages (*sensu* Penz 2007) when optimized onto the tree using parsimony (*Bia*-clade, *Opoptera*-clade, *Caligo*-clade and *Opsiphanes*-clade; Figure 8B).

The dorsal and ventral wing surfaces of brassolines differ in the number of identifiable pattern elements, and occasionally in their background color. Similar to what Nijhout & Wray (1986) described for *Charaxes* (Charaxinae, sister to Satyrinae which includes Brassolini; Wahlberg et al. 2009), brassoline ventral pattern elements are narrower, better defined and easier to identify than the dorsal ones, which are broad and sometimes diffuse. While dorsal and ventral surfaces contain the same set of pattern elements in *Charaxes* (Nijhout & Wray 1986, p.400), we hypothesize that in most brassolines fewer elements are present dorsally, particularly on the hind wing (Figure 8A). This hypothesis is based on an inter-related series of comparative observations. First, the yellow or orange dorsal wing background color of some species markedly differs from the typical brown. This greatly facilitated the identification of pattern elements that were present, and also revealed that some were absent (e.g., *Narope cyllastros* Doubleday, 1849, Figure 5D; *Opsiphanes boisduvallii*, Figure 7J). Second, only distal pattern elements could be identified in several species that have pale brown dorsal background (e.g., *Opoptera syme*, Figure 5A; *Caligopsis seleucida*, Figure 6A; *Caligo oileus*, Figure 6G). Third, in some species the distal half of the wings is darker than the proximal half, suggesting that distal pattern elements are bold/amalgamated as in *Charaxes* (Nijhout & Wray 1986), while proximal ones are not expressed (e.g., *Brassolis*, Figure 5C; *Opsiphanes sallei* Doubleday, 1849; Figure 7H). As an alternative hypothesis, it may be that the dorsal background color changes as a gradient across the wing as in *C. eurilochus* (Figure 6D). However, the dorsal pattern of *C. eurilochus* seems to constitute a dull version of *C. arisbe* Hübner, 1822 (Figure 6H), where the yellow background highlights the same dorsal elements also present in *C. eurilochus*, especially the female.

Many nymphalid species have different dorsal and ventral background colors, and this is also the case in some brassolines. *Opsiphanes blythekeitzmilleriae* and *O. boisduvallii* constitute an interesting example because their orange-yellow dorsal background color is strikingly different from other species in the genus. Furthermore, while the ventral background color of *O. blythekeitzmilleriae* conforms to that of other *Opsiphanes*, *O. boisduvallii* has an orange-yellow ventral background similar to its dorsal color. Rountree & Nijhout (1995) described the genetic control of ventral hind wing background color in *Junonia coenia* Hübner, 1822 (= *Precis coenia*; Nymphalinae). This species exhibits seasonal polyphenism (light vs. dark ventral hind wing color), but a recessive allele at a single locus restricts the phenotype to a dark ventral hind wing background color. This suggests the change in

ventral background color in *O. boisduvallii* may have a simple genetic control.

Within Brassolini, the expression of border ocelli (*h*) varies between the forewing and hind wing, and between the antero-posterior axis and dorso-ventral surfaces of each wing. The ventral forewing element *h* typically appears as a series of distinctive light colored spots and / or complex ocelli anterior to vein M2, and is either absent or composed of brown spots, blotches, diamonds or lines posterior to that vein. As an exception, a complex ocellus posterior to M2 is only found on the ventral surface of *Dynastor* and *Caligopsis* + *Eryphanis*, representing a developmental parallel given that these genera belong to two separate clades (Penz 2007; Figure 8B). The antero-posterior modifications of *h* support the proposal that reduced covariance and genetic correlations between wing cells allow differential expression of serial homologues (Paulsen 1994; Nijhout 1994, 2001; but see also Monteiro et al. 1997, Monteiro 2008). Although diffuse and subdued, the ventral forewing expression of element *h* is mirrored on the dorsal forewing. In contrast, the prominent ventral hind wing ocelli lack dorsal homologues, thus demonstrating dorso-ventral independence of pattern formation.

We observed considerable variation in the number and size of the ventral hind wing ocelli and their putative interaction with adjacent pattern elements or other color components. In the majority of brassolines, the ventral hind wing ocelli located below veins Sc+R1 and Cu1 (anterior and posterior ocelli) are the largest and most complex, while those in other cells are smaller, simpler, vestigial, or absent. The absence of ocelli below veins M3 and Cu2 seems to have preceded and facilitated the increase in size of the posterior ocellus in several taxa, *Caligo* being the most obvious example (Figure 3A, B, C). Furthermore, differences in the organization of the posterior ocellus suggest independent evolution of increased size. For instance, in some species the dark ocellar center crosses veins M3 and Cu2 (e.g., *Caligo atreus*, Figure 3B), while in others the outermost ring only expands cell boundaries (e.g., *Catoblepia orgetorix*, Figure 4A). The unique fusion of posterior ocelli in the sister genera *Caligopsis* and *Eryphanis* is also noteworthy because it shows that serial homologues can interact to form novel designs (see Nijhout 2001 for several examples of such interaction). Finally, the posterior ocellus is contained inside cell cu1 in *Bia*, *Narope*, *Brassolis* and *Dynastor*, early lineages in the Brassolini phylogeny (Penz 2007; Figure 8B). Although a larger posterior ocellus seems to have evolved at the ancestor of the *Opoptera* + *Caligo* + *Opsiphanes*-clades (Figure 8B), this character is not homogeneous between or within the 12 genera in these lineages (compare Figure 2E and F plus Figure 4A and B) and variation in size is continuous.

The ventral hind wing of several species in the *Caligo*-clade combines a ripple-free, dark medial area with a large posterior ocellus; intriguing from both developmental and ecological perspectives. If the ripple pattern is determined before the NGP pattern elements (Nijhout 1991, 2001), a ripple-free “window” can only be produced if ripple pattern expression is blocked at that specific site early in pattern development (see Figures 2C, E, F; 3C). The large ventral hind wing ocelli of *Caligo* are quite obvious when these butterflies feed on the ground or rest on vertical tree trunks (pers. obs.), and the ripple-free medial area enhances visibility of the ocelli. There are two main hypotheses for the evolution of conspicuous ocelli in Lepidoptera (reviewed in Stevens 2005): they can be used as a deflection point (target) that directs predator attacks to non-essential body parts, or function as a startling display. In support of the deflection hypothesis, it has been demonstrated that the posterior hind wing tornus is more noticeable yet structurally weaker than the surrounding areas in a sample of African species (DeVries 2002, 2003) and South American *Pierella astyoche* (Erichson, 1849) (Nymphalidae, Satyrinae; Hill

& Vaca 2004). Although untested, Stradling (1976) hypothesized that in some *Eryphanis* and *Caligo* the posterior ocellus plus a dark band across the wing look like a reptile in profile to function as a startle display.

Field experiments and observations demonstrated that ventral ocelli play a role in mate selection. Choice trials showed that male *Lycaeides idas* (Linnaeus, 1761) (Lycaenidae) selected females based on the size of their ventral hind wing aurorae and spots (Fordyce et al. 2002), and male and female *Bicyclus anynana* show a seasonal preference for ocellus size (Prudic et al. 2011). During courtship, male *Pierella astyoche* hover by decoupling forewing from hind wing movement, and clearly display the large hind wing white spots to the potential mate (CMP pers. obs.), an additional function to anti-predator defense (see above). Male *Caligo* form mating leks at forest edges (Freitas et al. 1997, Srygley & Penz 1999). Upon arrival at the lek site, female *C. illioneus* (Cramer, 1775) appear to detect perched males visually (CMP pers. obs.). When approached, males take off and initiate aerial courtship behavior. It therefore seems possible that the ventral hind wing ocelli of *Caligo* play a role in mate location, and also function as a startle display in both sexes. Given the diversity in size, color and number of ocelli in brassolines, we might expect that ocelli may serve multiple purposes.

Brassolines defy classical definitions of Batesian and Müllerian mimicry. There are examples of color resemblance among genera, but there is no evidence of chemical protection (see Chai 1990). The most notable case involves the convergence of *Catoblepia orgetorix* onto *Caligo atreus* with which it overlaps geographically (Figure 9H, I). Four lines of evidence support this assertion: (1) the dorsal phenotype of *orgetorix* departs from the typical *Catoblepia*; (2) ventral hind wing ocelli are the largest in the genus, and resemble *Caligo*; (3) convergence is limited to females in the subspecies *orgetorix*, *championi* and *magnalis*, fitting the expectations of sex-limited mimicry (Turner 1984, Silberglied 1984) and appearing to be the ancestral condition; and (4) both sexes of *C. orgetorix rothschildi* (endemic to the Magdalena Valley, Colombia) have the mimetic phenotype, suggesting that evolution of male color convergence followed that of the female. If *Caligo* and *Catoblepia* lack chemical defenses, then the resemblance could potentially be explained by an “arithmetic” effect (safety in numbers; Vane-Wright 1976, after Van Someren & Jackson 1959). Whether the similarity among these species confers a fitness-related advantage is unknown, and fieldwork is needed to assess if predators recognize and avoid them. The resemblance between *Opoptera staudingeri* and *Catoblepia orgetorix* (Figure 9J and H), and some geographical races of *Brassolis sophorae* (Linnaeus, 1758) and *Selenophanes cassiope* (Figures 5C and 6G) also catch the eye, but remain inexplicable. These examples demonstrate that remarkable similarity can be accomplished with relatively few modifications of the trailing bands (color, width, position) and the addition of iridescence (see Results).

Some instances of color resemblance in brassolines might be due to phylogenetic relatedness or male color divergence. Bristow (1981, 1991) noted that geographical races of *Catoblepia* and *Opsiphanes* converge locally in color pattern. Although we have not examined sufficient specimens to verify this suggestion, these genera belong to the same clade (Penz 2007) and their archetypal dorsal colors closely fit the groundplan in Figure 8. Similarity due to common ancestry is therefore a valid alternative explanation for their color resemblance. Members of the *Caligo*-clade (sensu Penz 2007) also share dorsal color patterns through common ancestry. The similarity among females of *Caligopsis seleucida* (Figure 9D), *Eryphanis automedon* (Cramer, 1775) (Figure 9G, plus others not illustrated), and some species of *Caligo* (e.g., *C. illioneus*, Figure 9F) might be due to the maintenance of ancestral patterns, while the male sex diverged



though sexual selection. This suggestion is, nonetheless, tentative and requires further examination.

Much research has been done on the development, genetics, and evolution of nymphalid wing pattern elements, particularly the border ocelli. Nonetheless, the most in-depth studies have focused on *Bicyclus anynana*, *Junonia coenia*, and some *Heliconius* (for reviews, see Monteiro et al. 1997, Beldade & Brakefield 2002, Monteiro 2008, Beldade et al. 2008), and the general relevance of such work relies on the evolutionary homology of wing pattern elements across taxa. Although the long early stage development time of brassolines is a limitation for laboratory research (e.g., 70 days for *Caligo illioneus*; Penz et al. 1999), some of these butterflies are locally abundant (DeVries et al. 2011) and easily maintained in enclosures (CMP pers. obs.). The objective of this investigation was to provide a comparative framework of wing color pattern variation that can be useful for research on genetics and development of brassolines, but mostly as an impetus for fieldwork that focuses on the function of wing color patterns in the context of intra and interspecific ecological interactions. The diversity of brassoline color patterns, time of activity and mating behaviors, plus recent phylogenetic analyses, constitute the perfect ingredients for research on a key question that relates to all Lepidoptera: what are forces that drive the evolution of color pattern diversity?

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**Appendix 1** – Examined specimens and useful links (last accessed 1 April 2013). All photographs in D’Abrera (1987) and Casagrande (2002) were also examined. Abbreviations: M, male; F, female; AMNH, American Museum of Natural History, US; BMNH, The Natural History Museum, UK; CMNH, Carnegie Museum of Natural History, US; InBio, Instituto Nacional de Biodiversidad, Costa Rica; LACM, Natural History Museum of Los Angeles County, US; MAPA, Museu Anchieta (Porto Alegre), Brazil; MECN, Museo Ecuatoriano de Ciencias Naturales, Ecuador; MPM, Milwaukee Public Museum, US; NMNL, National Museum of Natural History Naturalis, The Netherlands; MZSP, Museu de Zoologia, Universidade de São Paulo, Brazil; PJD, Phil DeVries, private collection; UFL, University of Florida, US; UFSC, Universidade Federal de Santa Catarina, Brazil; USNM, United States National Museum, Smithsonian Institution, US.

### ***Bia* Hübner, 1819**

**Two species examined directly; see also <http://fs.uno.edu/cpenz/bia.html>**

#### *Bia actorion*-complex (Linnaeus, 1763)

1 M, Peru, Loreto, Iquitos (MPM); 5 M, Ecuador, Sucumbios, Garza Cocha, 7 Mar 1994, 6 Apr 1994, 17 Jan 1995, 9 Jul 1995, 10 Dec 1995 (PJD); 1 M, Venezuela, Alto Orinoco, 19 Nov 1951 (USNM); 1 M, British Guiana, Kangaruma, Potaro, 2 Nov 1908 (CMNH); 1 M, Suriname, 25 Oct 1969 (NMNL); 3 M, Brazil, Amazonas, Manaus, 6 Dec 1993, 10 Dec 1993, 15 Jul 1985 (USNM); 1 F, Peru Satipo (MPM); 4 F, Ecuador, Sucumbios, La Selva Biological Station, 6 Jan 1993, 5 Aug 1994, 7 Jul 1995, and 4 Feb 1994 (PJD); 1 F, Brazil, Amazonas, Manaus, Dec 1993 (USNM); 1F, Brazil, no date (USNM); 3 F, Peru, Madre de Dios, Manu, 15 Nov 1990, 2 May 1991, and 14 May 1991 (USNM); 2 F, Venezuela, Suapure, no date and 22 Dec 1899 (CMNH); 2 F, Brazil, Nova Olinda, Rio Purus, Jun 1922 and Mar 1922 (CMNH); 1 F, Brazil, Arima, Rio Purus, Mar 1922 (CMNH); 3 F, Bolivia, Yapacani River Feb 1915, Marc 1915, Sep 1914 (CMNH)

#### *Bia actorion decaerulea* Weymer, 1911

7 M, French Guiana, Mana River, June 1917 (CMNH); 1 M, Brazil, Amazonas, Tonantins, Aug 1923 (CMNH); 4 M, Brazil, Amazonas, Manacapuru Apr 1925 (CMNH); 1 F, French Guyana, Pied Saut, Oyapok River, Jan 1918 (CMNH); 3 F, French Guyana, Mana River, Jun 1917 (CMNH); 3 F, Brazil, Manacapuru, Mar 1925, Apr 1925, and Sep 1923

#### *Bia peruana* Röber, 1904

1 M, Peru, Chuchurras, no date (BMNH); 1 M, Peru, Pasco Pan de Azucar 25 Jul 1961 (LACM); 1 M, Peru, Huanuco, Rio Pichis, no date (UFL); 1 F, Peru, Pachitea, 7 Feb (BMNH)

### ***Narope* Doubleday, 1849**

**Six species examined directly, 11 through photographs in Casagrande (2002); see also <http://fs.uno.edu/cpenz/narope.html>**

#### *Narope cyllabarus* Westwood, 1851

1 M, Bolivia, no date (MPM)

#### *Narope cyllarus* Westwood, 1851

1 M, Brazil, Paraná, Sep 1952 (MPM)

#### *Narope cyllastros* Doubleday, 1849

1 M, no data (MPM); 1 M, Brazil, Paraná, Rio das Cobras, Feb 1942 (MPM); 1 F, Brazil, Santa Catarina, Nova Teutônia 14 Feb 1961 (MPM); 1 F, Paraguay, no date (MPM); 1 F, Brazil, Minas Gerais, no date (AMNH)

#### *Narope nesope* Hewitson, 1869

1 M, Bolivia, no date (MPM)

#### *Narope panniculus* Stichel, 1904

2 M, Ecuador, no date (AMNH); 1 M, Bolivia, Santa Cruz, Buenavista Ichilo, Mar 1954 (MPM); 1 M, Bolivia, Santa Cruz, Ichilo, Mar 1955 (UFL); 1 F, Brazil, Minas Gerais (AMNH)

#### *Narope anartes* Hewitson, 1874

1 M, Colombia, Cali 12 May 1963 (MPM)

### ***Aponarope* Casagrande, 1982**

**One species examined directly, nested within *Narope* (Penz 2007); see also <http://fs.uno.edu/cpenz/aponarope.html>**

#### *Aponarope sutor* (Stichel, 1916)

1 M, Brazil, Rondônia, Fazenda Rancho Grande, 17 Apr 1992 (UFL)

***Brassolis* Fabricius, 1807**

Six species examined directly, see also <http://fs.uno.edu/cpenz/brassolis.html>

*Brassolis sophorae* (Linnaeus, 1758)

1 M, Guiana Française (UFL); 1 M, British Guiana, Georgetown, 1959 (MPM); 1 M, Trinidad (UFL); 1 M, Ecuador, Napo Prov., Jatun Sacha Biol. Sta., 1988 (UFL); 1 M, Peru, Loreto, 1961, Pucallpa (UFL); 1 M, Bolivia, Santa Cruz (UFL); 1 M, Bolivia, Santa Cruz, 1972 (UFL); 1 M, Paraguay, Villarica, 1951 (MPM); 1 M, Brazil, Sta. Catarina, Nova Teutônia, 1960 (MPM); 1 F, Guiana Française (UFL); 1 F, Trinidad, Moruga (UFL); 1 F, Ecuador, Apuya, Napo Province, 1993; 1 F, Ecuador, Puyo, Oriente, 1950 (MPM); 1 F, Peru, Loreto, 1981 (UFL); 1 F, Bolivia, Beni Riveralta, 1986 (UFL); 1 F, Bolivia, Sta. Cruz Mineros, 1956 (MPM); 1 F, Paraguay, Villarica, 1949 (MPM); 1 F, Brazil, Nova Friburgo, Rio de Janeiro (MPM); 1 F, Brazil, São Paulo, São Carlos, 1979 (UFL).

*Brassolis dinizi* d'Almeida, 1956

3 M, Brazil, Ceará, Fortaleza 1956, 1958 and 1959 (MPM); 1 M, North Brazil, 1973 (MPM); 1 M, Paraíba, Brazil, (MPM); 1 F, Brasil, Paraisa [sic] (MPM); 2 F, Brazil, Ceará Fortaleza, 1959 (MPM)

*Brassolis haenschii* Stichel, 1902

1 M, Ecuador, Balzapamba (UFL); 1 M, Ecuador, Balzapamba (BMNH); 1 F, Ecuador, Los Rios Province, Rio Palenque (UFL); 1 F, Ecuador, Los Rios Province, Rio Palenque (UFL)

*Brassolis isthmia* Bates, 1864

1 M, Costa Rica, Limon province, Puerto Viejo, 1989 (UFL); 1 M, Panama, Canal Zone, 1973 (MPM); 1 M, Panama, Balboa, 1966 (UFL); 1 F, Panama, Tocumen, 1976 (UFL)

*Brassolis granadensis* Stichel, 1902

1 M, Colombia Cali, 1956 (MPM); 1 M, no data (UFL); 1 F, Colombia, Tolima, Payande, Mina Vieja area, 1974 (UFL).

*Brassolis astyra* Godart, 1824

1 M, Brazil, 1939 (MPM); 1 M, Brazil, Pará, Obidos, 1952 (MPM); 1 M, Brazil, Rio de Janeiro, Gávea, 1960 (MPM); 1 M, Brazil, Corcovado, Rio [de Janeiro], 1910 (UFL); 1 M, Brazil, [Santa Catarina], Corupa (MPM); 1 M, Brazil, Santa Catarina (MPM); 1 M, Brazil, Gravataí, 1966 (MAPA); 1 M, Brazil, Gravataí, 1966 (MAPA); 1 F, Brazil, 1932 (MPM); 1 F, [Brazil], Rio [de] Janeiro (UFL); 1 F, Brazil, Rio de Janeiro, 1960 (MPM); 1 F, Brazil, Corcovado, Rio [de Janeiro], 1910 (UFL); 1 F, Brazil, Itaci, São Paulo, 1960 (MPM); 1 F, Brazil, Santa Catherina, Rio Tirubo, 1937 (MPM); 1 F, Brazil, Gravataí, 1966 (MAPA); 1 F, Brazil, Gravataí, 1966 (MAPA).

***Dynastor* Doubleday, 1849**

Three species examined directly, see also <http://fs.uno.edu/cpenz/dynastor.html>

*Dynastor darius* (Fabricius, 1775)

1 M, Paraguay, 1973 (MPM); 1 M, Nicaragua, Managua dept., Managua, 1858 (MPM); 1 F, Brazil, Paraná, Ponta Grossa, XI 1947 (MPM); 1 F, Brazil, Santa Catarina, "Mansa Humbolt" [sic] (MPM).

*Dynastor napoleon* Doubleday, 1849

1 M, Brazil, Santa Catarina, XI 1954 (MPM); 1 M, Brazil, Santa Catarina, IX 1964 (MPM); 1 M, Brazil, Santa Catarina, 1956 (UFL); 1 F, Brazil, Rio de Janeiro, 1920 (MPM); 1 F, no data (UFL)

*Dynastor macrosiris* (Westwood, 1851)

1 M, Guiana Française (UFL); 1 M, El Salvador, Finca El Refugio, Ahuachapan, Sep 2006 (PJD); 1 F, Mexico, Chiapas, 1973 (UFL); 1 F, El Salvador, Finca El Refugio, Ahuachapan, Sep 2006 (PJD).

***Opoptera* Aurivillius, 1882**

Eight species examined directly, see also <http://fs.uno.edu/cpenz/opoptera.html>

*Opoptera syme* (Hübner, 1821)

1 M, Brazil, R.J., Nova Friburgo, 22 Feb 1961; 1 M, Brésil, Etat de Sao Paolo, no date (UFL); 1 M, Sumaní, Guanabara [RJ], Parque da Tijuca, Brazil, Aug 14 1972 (UFL); 1 F, South America, no date (UFL); 1 F, Petropolis [RJ], Brazil, no date (USNM); 1 F, Brazil, Rio de Janeiro St., no date (USNM)

*Opoptera sulcius* (Staudinger, 1887)

1 M, Brazil, Pinhal [São Paulo], Feb 1950 (MPM); 1 M, Brazil, Santa Catarina, Taió, Feb 1959 (MPM); 1 M, Brazil, Santa Catarina, São Bento do Sul, Mar 10 1984 (UFL); 1 M, Brazil, Santa Catarina, Gaio (sic) [likely Taió], Feb 1986 (UFL); 1 F, Brazil, Santa Catarina, Feb 1964 (MPM); 1 F, South Brazil, no date (MPM); 1 F, Brazil, Joinville, 14 Mar 1964 (UFL); 1 F, Brazil, São Luis do Puruná, Paraná, 16 Mar 1984 (UFL)

*Opoptera fruhstorferi* (Röber, 1896)

1 M, Brazil, St. Catherines, no date (AMNH); 1 M, South Brazil, no date (MPM); 1 M, Brazil, Taió, St. Cath., Feb 1956 (MPM); 2 F, Itaporanga [São Paulo, Brazil], Feb 1948 and Mar 1948 (AMNH); 1 F, Brazil, Santa Catarina, 6 Feb 1963 (MPM); 1 F, South Brazil, no date (MPM)

*Opoptera aorsa* (Godart, 1824)

1 M, Brazil, Toledo, Paraná, Nov 1969 (MPM); 1 M, Espírito Santo, Brazil, no date (AMNH); 5 M Brazil, Espírito Santo, no date (AMNH); 1 M, Brazil, North Paraná, no date (AMNH); 1 M, Brazil, Paraná, no date (AMNH); 1 F, Brazil, Nova Friburgo, R.J., 3 Mar 1961 (MPM); 1 F, Brazil, North Paraná, no date (AMNH); 1 F Espírito Santo, Brazil, no date (AMNH)

*Opoptera hilaris* Stichel, 1901

1 M, Ecuador, Río Huagra-yacu, Oriente, 3 Apr 1941 (AMNH); 2 M, Ecuador, Río Huagra-yacu, Oriente, 12 and 14 Apr 1941 (AMNH); 2 M, Ecuador, no date (AMNH); 1 M, Middle Ecuador, no date (AMNH); 2 M, Oriente Ecuador, no date (AMNH); 1 M, Ecuador, Sucumbios, La Selva Biological Station, 2 Aug 1993 (PJD); 1 M, Peru, Puerto Maldonado, Los Amigos Biological Station, 13 Feb 2004 (PJD); 1 M, Peru, Chanchamayo, no date (AMNH); 1 M, Peru, Jepelacio, North no date (AMNH); 1 M, Bolivia, no date; 1 M, Brazil, Puraquequara, Amazonas, 10 Apr-10 May 1945 (AMNH); 1 F, Ecuador, Sucumbios, La Selva Biological Station, 10 Dec 1997 (PJD)

*Opoptera staudingeri* (Godman & Salvin, 1894)

1 M, Costa Rica, Heredia, Puerto Viejo, Feb 1970 (MPM); 1 F, Costa Rica, Heredia, Puerto Viejo, Feb 1970 (MPM)

*Opoptera arsippe* (Hopffer, 1874)

3 M, Peru, Pasco, Chuchurras, no date (UFL); 2 M, Peru, Huanuco, ca. 15 kms. N of Tingo Maria on Rio Huallaga, 15-22 Aug 1981 and Aug 1981 (UFL); 1 M, Peru, Tingo Maria, 19-24 Jul 1978 (LACM); 2 M, Peru, Huánuco, Tingo Maria, Dec 1984 (LACM); 2 M, Bolivia, no date (LACM); 2 M no data (LACM); 1 M, Peru, Juanjui, Iquitos, 7-19 May 1961 (UFL); 4 M, Chanchamayo, Peru, no date (AMNH)

*Opoptera bracteolata* Stichel, 1901

1 M, Bolivia, no date (MPM); 1 M, Bolivia, Cochabamba, Chapare, Alto Palmar, Dec 1956 (UFL)

***Dasyophthalma* Westwood, 1851**

**Four species examined directly, see also <http://fs.uno.edu/cpenz/dasyophthalma.html>**

*Dasyophthalma rusina* (Godart, 1824)

1 M, Brazil, Santa Catarina 26 Dec 1957 (MPM); 1 M, South Brazil, no date (MPM); 1 M, Brazil, Espírito Santo, Santa Teresa, 4-7 March 1973 (UFL); 1 M, Brazil, Rio de Janeiro, Petrópolis, Independência, 16 Jan 1972 (UFL); 1 M, Brazil, Rio de Janeiro, Petrópolis, 9-12 Jan 1971 (UFL); 1 M, Brazil, Minas Gerais, Parque Rio Doce, 26 Mar 1972 (UFL); 2 M, Brazil, Santa Catarina, São Bento do Sul, 10 Mar 1984 (UFL); 1 M, Brazil, Santa Catarina, 1 Jan 1968 (UFL); 1 M [Brazil] Sta. Catharina, no date (AMNH); 1 F, Brazil, Santa Catarina, São Bento do Sul, 25 Jan 1966 (MPM); 1 F, South Brazil, no date (MPM)

*Dasyophthalma geraensis* Rebel, 1922

1 M, Brazil, Minas Geraes, no date (MZSP); 1 M, [Brazil] Minas Geraes, no date (AMNH); 1 M Brazil, Espírito Santo, Castello, 21 Feb 1922 (UFL); 1 M, Brazil, Rio de Janeiro, Parque Nacional do Itatiaia, 13-14 Jan 1973, (UFL); 1 M, Brazil, Rio de Janeiro, Itatiaia, 21 Mar 1972 (UFL)

*Dasyophthalma creusa* (Hübner, 1821)

1 M, South Brazil, no date, (MPM); 1 M, Brazil, Santa Catarina, São Bento do Sul, 13 Feb 1966 (MPM); 1 M, Brazil, Santa Catarina, São Bento do Sul, 10 Feb (UFL); 1 M, Brazil, Santa Catarina, São Bento do Sul, 10 Feb 1984 (UFL); 1 M, Brazil, Rio de Janeiro, Dec 1943 (UFL); 1 M, Brazil, Guanabara [Rio de Janeiro], Jacarepaguá, 20 Feb 1971 (UFL); 1 F, South Brazil, no date, (MPM); 1 F, Brazil, Santa Catarina, São Bento do Sul, 13 Feb 1966 (MPM)

*Dasyophthalma vertebralis* Butler, 1869

1 M, Brazil, Espírito Santo (MZUSP); 1 F, [Brazil] East Amazonas, no date (MZUSP)

***Caligopsis* Seydel, 1924**

**One species examined directly, see also <http://fs.uno.edu/cpenz/caligopsis.html>**

*Caligopsis seleucida* (Hewitson, 1877)

2 M, Peru, Puerto Maldonado, Los Amigos Biological Station, 10 Sep 2004 and 12 Oct 2004 (PJD); 1 M, Bolivia, Cochabamba, San Francisco, Apr 1976 (MPM); 2 F, Peru, Puerto Maldonado, Los Amigos Biological Station, 9 Apr 2004 and 14 Oct 2004 (PJD); 1 F, Brazil, Amazonas, Madeira River, no date (USNM)



***Eryphanis* Boisduval, 1870**

Nine species examined directly, see also <http://fs.uno.edu/cpenz/eryphanis.html>

*Eryphanis automedon* (Cramer, 1775)

1 M, Venezuela, Waterworks, Puerto Cabello, Carabobo, 22 Jul 1979 (UFL); 1 M, Trinidad, BWI, Mar 1937 (UFL); 2 M, Trinidad [18]98 (UFL); 1 M, Trinidad, Arima Valley, SIMLA Research Station, 27 Jun-3 Jul 1978 (UFL); 1 M, British Guyana, Kamarung, 10-14 Oct 1977 (UFL); 1 M, Surinam, Jan 2001 (PJD); 2 M, French Guiana, R. Orapu (UFL); 1 M, Colombia, Cali 19 Dec 1966 (MPM); 1 M, Colombia, Vaupes, San Jose del Guaviare, Dec [19]91 (UFL); 1 M, Colombia, Villavicencio, Ocoa, 27 Oct 1943 (UFL); 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 (UFL); 1 M, Ecuador, Napo, Misahualli, 28 Apr 1971 (UFL); 1 M, Ecuador, Balzapampa, no date (UFL); 2 M, Peru, Puerto Maldonado, Los Amigos Biological Station, 13 May 2004 and 15 Oct 2004 (PJD); 1 M, Peru, Huanuco, Tingo Maria, Rio Huallaga, 15-22 Aug 1981 (UFL); 1 M, Peru, Mogotta (sic), 14 May 1955 (UFL); 1 M, Peru, Tingo Maria, 30 Jul 1980 (UFL); 1 M, Brazil, Para, Obidos, Mar 1976 (MPM); 1 M, Brazil, Rondonia, Jaru, 9 Aug 1976 (UFL); 1 M, Brazil, Rondonia, Caucalandia 13 nov 1990 (UFL); 1 M, Brazil, Rondonia, Fazenda Rancho Grande 9 Nov 1990 (UFL); 3 M, Brazil, Minas Gerais, Uberaba, no date (UFL); 1 M, Brazil, Guanabara [=Rio de Janeiro], Gávea, 6 Feb 1973 (UFL); 1 M, Brazil, Santa Catarina, Blumenau, no date (UFL); 1 M, Bolivia, Santa Cruz, 29 Apr 1959 (MPM); 1 M, Bolivia, Santa Cruz, Buenavista, Ichilo, Feb 1946 (UFL); 1 M, Bolivia, no date (UFL); 2 M, Paraguay, Amambay, Pedro Juan Caballero, 4 Feb 1969 (MPM); 1 F, Trinidad, Maquerippe Bay, 22 Aug 1974 (UFL); 1 F Trinidad, St. Amis, 23 Nov 1920 (UFL); 1 F, Surinam, Lelydorp, no date (PJD); 1 F, French Guiana, R. Orapu (UFL); 2 F, Ecuador, Napo, Misahualli, 3 Sep 2000 (UFL); 1 F, Peru, Puerto Maldonado, Los Amigos Biological Station, 14 Jul 2004 (PJD); 1 F Peru, Tingo Maria, 30 Jul 1980 (UFL); 1 F, Brazil, Rondonia, Fazenda Rancho Grande, 22 Mar 1991 (UFL); 1 F, Brazil, Minas Gerais, Uberaba, no date (UFL); 1 F, Paraguay, Pedro Juan Caballero, 4 Feb 1969 (MPM)

*Eryphanis lycomedon* (Meerburgh, 1780)

1 M, Guatemala, no date (UFL); 1 M, Costa Rica, Puntarenas, Pto. Cortez 23 Nov 2003 (INBio); 1 M, Costa Rica, Heredia, Santa Clara, 5 Sep 1987 (UFL); 1 M, Costa Rica, Alajuela, Rio Virilla, 5.5 km SW Guacima, 2 Oct 1967 (UFL); 1 M, Panama, Canal zone, Madden Forest, 21 Aug 1969 (UFL); 1 M, Panama, Las Cumbres, Oct 1960 (UFL); 1 M, Colombia, Cali, 19 Dec 1966 (MPM); 1 M, Colombia, Cali, 20 Oct 1965 (MPM); 1 M, Colombia, Cauca, Pescador, 29 Jan 1974 (UFL); 11 M, Colombia, Boyaca, Muzo, no date (UFL); 2 M, Colombia, Valle de Cauca, Cali (Cañas Gordas), 1 Oct 1973 and 21 Feb 1974 (UFL); 1 M, Colombia, Rio Guatiquia, Apr 1917 (UFL); 2 M, Colombia, Yacopi, 1936 and 12 Apr 1938 (UFL); 1 M, Ecuador, Pichincha, Santo Domingo de los Colorados, 8 May 1988 (UFL); 1 M, Ecuador, Tonchigue, Apr 1964 (MPM); 1 M, Ecuador, Los Rios, Rio Palenque, no date (UFL); 1 M, Ecuador, Pichincha, Hotel Tinalandia, Santo Domingo de los Colorados, 10 May 1988 (UFL); 1 M, Bolivia, no date (UFL); 1 M, Bolivia, no date (UFL); 7 M, Brazil, Santa Catarina, Blumenau (UFL); 1 F, Costa Rica, Puntarenas, Corcovado National Park, Apr 1989 (INBio); 1 F, Costa Rica, Heredia, Pueblo Nuevo Sarapiquí 24 Jul- 22 Aug 1992 (INBio); 1 F, Costa Rica, Cartago, Turrialba, 13 Jul 1965 (UFL); 1 F, Costa Rica, Alajuela, Atenas, 16 Dec 1984 (UFL); 1 F, Panama, Canal Zone, Madden Forest, 2 Dec 1969 (UFL); 1 F, Panama, Las Cumbres, 25 Jan 1964 (UFL); 1 F, Colombia, Cali, 27 May 1966 (MPM); 1 F, Colombia, Cali, 2 Nov 1966 (MPM); 2 F, Colombia, Valle de Cauca, Cali (Cañas Gordas), 13 Jan 1974 (UFL); 2 F, Colombia, Cali, Pance, Valle, 22 and 25 Jan 1987 (UFL); 1 F, Colombia, Cali, Valle, 9 Aug 1979 (UFL); 1 F, Ecuador, Tonchigue, Apr 1964 (MPM); 1 F, Ecuador, Pichincha, Alluriquin, 16 Aug 1972 (UFL); 1 F, Ecuador, Pichincha, Hotel Tinalandia, Santo Domingo de los Colorados, 8 May 1988 (UFL); 1 F, Ecuador, Pichincha, Tinalandia, Santo Domingo, 5 May 1992 (UFL); 1 F, Brazil, Santa Catarina, Blumenau, no date (UFL)

*Eryphanis aesacus* (Herrich-Schäffer, 1850)

1 M, Mexico, San Luis Potosi 23 Jul 1937 (MPM); 1 M, Mexico, Catemaco, Nov 1965 (MPM); 2 M, Mexico, Oaxaca, Monteflor Jun 1978 (UFL); 1 M, Mexico, Oaxaca, Chiltepec, 3 Sep 1976 (UFL); 1 M, Mexico, South of Tampico, 1 Nov 1975 (UFL); 1 M, Mexico, Escarcega, Campeche 2 and 5 May 1969 (UFL); 1 M, Mexico, Taulmalipas, Taumazunchale, no date (UFL); 1 M, Mexico, El Pujal, San Luis Potosi, 18 Jun 1939 (UFL); 1 M, Guatemala, Chacoj, Pelochic, no date (BMNH); 1 M, Guatemala, Alta Verapaz, Baleu Mpio., San Cristobal, Verapaz, 24 Sep 1966 (UFL); 1 M, El Salvador, Ahuachapan, El Refugio Sep 2003 (PJD); 1 M, El Salvador, Ahuachapan, La Fincon El Imposible, 13 Sep 1984 (UFL); 1 M, Belize, Cayo Distr., Green Hills 29 Jul 2007 (PJD); 1 F, Mexico, no date (MPM); 1 F Mexico, Oaxaca, Tuxtepec, 4 Sep 1976 (UFL); 2 F, Mexico, Presidio, Jun 1951 (UFL); 2 F Mexico, Catemaco, Sep 1956 (UFL); 1 F, Guatemala, Central Valleys, no date, #802305, (BMNH); 1 F, Guatemala, Petén, Parque Nacional Tikal, 20 Sep 1993 (UFL); 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 (UFL)

*Eryphanis bubocula* (Butler, 1872)

1 M, Costa Rica, Guanacaste, Rio San Lorenzo, Tierras Morenas Aug 1992 (INBio); 1 F, Costa Rica, Cartago, Tapanti 9 Apr 1983 (INBio); 1 F, Colombia, Val. Del Cauca, Calima Valley, 14 Feb 1989 (UFL)

*Eryphanis gerhardi* (Weeks, 1902)

1 M, Ecuador, Balzapampa, no date (UFL); 1 M, Bolivia, no date (MPM); 1 M, Bolivia, Cochabamba Mar 1955 (MPM); 1 M, Bolivia, Chapare, Alto Palmar, Sep 1954 (MPM); 1 M, Bolivia, Cochabamba, El Palmar Chapare, Apr 1947 (UFL); 1 M, Bolivia, Cochabamba, Alto Palmar Chapare, Oct 1958 (UFL); 1 M, Bolivia, Santa Cruz, Buenavista, Ichilo, 21 Feb 1994 (UFL); 1 M, Brazil, Rondonia, Jaru 9 Aug 1976 (UFL); 1 F, Brazil, Rondonia, Jaru, 6 Aug 1976 (UFL)

*Eryphanis reevesii* (Doubleday, 1849)

1 M, Brazil, São Paulo, Pinhal Apr 1955 (MPM); 1 M Brazil, São Paulo, Itaici 3 Sep 1961 (MPM); 1 M, Brazil, Meatana [maybe Mendanha, Minas Gerais] 20 Jul 1968 (UFL); 1 M, Brazil, [São Paulo], Pinhal, Mar 1952 (UFL); 1 M, Brazil, Santa Catarina, Blumenau, no date (UFL); 4 M, Brazil, Santa Catarina, São Bento do Sul, 10 Mar 1984 (UFL); 1 M, Brazil, Santa Catarina, Trombudo Alto, 28 Mar 1957 (UFL); 2 M, Argentina, Parque Nacional Iguazu, Misiones, 18 Jun 1973; 1 M, Argentina, Misiones, Rio Uruguay 19 Jun 1973 (UFL); 1 F, Brazil, Rio de Janeiro, Nova Friburgo Oct 1958 (MPM); 1 F, Brazil, São Paulo, Pinhal Apr 1955 (MPM); 2 F, Brazil, Minas Gerais, Uberaba, no date (UFL); 1 F Brazil, Santa Catarina, Trombudo Alto, 26 Mar 1956 (UFL)

*Eryphanis zolvizora* (Hewitson, 1877)

1 M, Bolivia, Cochabamba Mar 1955 (MPM); 1 M, Bolivia, no date (MPM); 1 M, Bolivia, Cochabamba, El Palmar Apr 1947 (UFL); 1 M, Bolivia, Cochabamba, El Palmar Chapare, Apr 1947; 1 M, Bolivia, Las Yungas, Nov 1990 (UFL); 1 F, Bolivia, Cochabamba, Alto Palmas Sep 1958 (UFL)

*Eryphanis opimus* (Staudinger, 1887)

1 M, Colombia, Cali 29 Sep 1964 (MPM)

*Eryphanis greeneyi* Penz & DeVries, 2008

1 M, Ecuador, Napo, Yanayacu Biological Station, 5km W of Cosanga, May 2007, HOLOTYPE (BMNH); 1 M, Ecuador, Napo Prov., Yanayacu Biological Station (MECN); 1 M, Ecuador, Provincia Napo, YYBS, 5-Feb-[20]02 (AMNH); 1 M, Ecuador, Provincia Napo, 12-Apr-[20]00 (PJD); 1 M, Ecuador, Rio Blanco, near Baños, Abril 17/[19]56 (MPM); 1 M, Ecuador, Balzapampa, (UFL); 1 M, Ecuador, Zamora-Chinch. Province, Zumba-Loja 21-23 Sep 1993 (UFL); 1 F, Ecuador, Napo, Yanayacu Biological Station, May 2007 (BMNH); 1 F, Ecuador: Napo Prov., Yanayacu Biological Station (MECN); 1 F, Ecuador, Napo, Biol. Yanayacu, no date (AMNH); 1 F, Ecuador, Provincia Napo, San Isidro, 21-Dec-[19]99 (PJD).

**Caligo Hübner, 1819**

**Thirteen species examined directly, see also <http://fs.uno.edu/cpenz/caligo.html>**

*Caligo arisbe* Hübner, 1822

2 M, Brazil, Paraná, São Luis do Puruna, 16 Mar 1984 (UFL); 1 M, Brazil, no date (UFL)

*Caligo atreus* (Kollar, 1850)

1 M, Colombia, Antioquia, Zaragosa (MPM); 1 M, Costa Rica, Heredia, Puerto Viejo, Finca La Selva, 1968-1970 (MPM); 1 M, Costa Rica, Heredia, Puerto Viejo, Finca La Selva, 1968-1970 (MPM); 1 F, no data (MPM)

*Caligo beltrao* (Illiger, 1801)

1 M, Brazil, Stuporanza, Dec 1950 (MPM); 1 M, Brazil, Santa Catarina, Joinville Mar 1972 (MPM); 1 F, Brazil, Stuporanza, Jan 1951 (MPM); 1 F, Brazil, Santa Catarina, Joinville, Feb 1969 (MPM)

*Caligo eurilochus* (Cramer, 1775)

1 M, Costa Rica, Heredia, Puerto Viejo, Finca La Selva, 17 Feb 1978 (MPM); 1 F, Costa Rica, Heredia, Puerto Viejo, Finca La Selva, Feb 1969 (MPM)

*Caligo idomeneus* (Linnaeus, 1758)

1 M, East Peru, no date (MPM); 1 M, Colombia, no date (MPM); 1 F, East Peru, no date (MPM), 1 F, Peru, Satipo, Nov 1952 (MPM)

*Caligo illioneus* (Cramer, 1775)

1 M, Costa Rica, Heredia, Finca La Tirimbina 17 Feb 1978 (MPM); 1 F, Costa Rica, Heredia, Finca La Selva Feb 1969 (MPM)

*Caligo martia* (Godart, 1824)

1 M, Brazil, Pinhal, no date (MPM); 1 M, Brazil, São Bento, SC, Jan 1969 (MPM); 1 F, Brazil (MPM), 1 F, Brazil, Santa Catarina, 2 Jan 1963 (MPM)

*Caligo oberthuri* (Deyrolle, 1872)

1 M, Ecuador, Riobamba, no date (UFL); 1 F, Ecuador, Riobamba, no date (UFL)

*Caligo oileus* C. Felder & R. Felder, 1861

1 M, Peru, Huanuco, Tingo Maria, Mar 1981 (UFL); 1 F, Peru, Ayacucho May 1936 (UFL)

*Caligo telamoni* (C. Felder & R. Felder, 1862)

1 M, Colombia, Cauca, May 1917 (UFL); 1 F, Colombia, Cauca Valley, no date (UFL)

*Caligo teucer* (Linnaeus, 1758)

1 M, Peru, Tingo Maria, Jul 1980 (UFL); 1 F, Peru, Tingo Maria, 25 May 1972 (UFL)

*Caligo Uranus* Herrich-Schäffer, 1850

1 M, Mexico, Chiapas, Bonampak, Jul-Aug 1976 (UFL); 1 F, Mexico, Santa Rosa Comitán, Apr 1962 (UFL)

*Caligo zeuxippus* H. Druce, 1902

1 M, Ecuador, Pichincha, Santo Domingo de los Colorados, 10 May 1988 (UFL); 1 F, Ecuador, Pichincha, Santo Domingo de los Colorados, 9 May 1988 (UFL)

*Selenophanes* Staudinger, 1887

Three species examined directly, see also <http://fs.uno.edu/cpenz/selenophanes.html>

*Selenophanes cassiope* (Cramer, 1775)

1 M, Brazil, Paraná, Rolândia, Dec 1942 (AMNH); 1 M, Peru, Chanchamayo, no date (AMNH); 2 M, Peru, Puerto Maldonado, Los Amigos Biological Station, 15 Jun 2004 and 12 Sep 2004 (PJD); 1 F, Peru, Rio Huallaga (AMNH); 2 F, Peru, Puerto Maldonado, Los Amigos Biological Station, 11 Oct 2004 and 15 Oct 2004 (PJD); 1 F, no località, 20 Sep 1922 (USNM)

*Selenophanes josephus* (Godman & Salvin, 1881)

1 M, Panama, Canal Zone, Madden Forest, 20 Jul 1970 (USNM); 1 F, Panama, Darién, Caña, 5 Jul 1981 (USNM)

*Selenophanes supremus* Stichel, 1901

2 M, Peru, Chanchamayo, no date (UFL)

*Penetes* Doubleday, 1849

One species examined directly, see also <http://fs.uno.edu/cpenz/penetes.html>

*Penetes pamphanis* Doubleday, 1849

1 M, Brazil, Paraná, Curitiba (MPM); 1 M, Paraguay, Villarica, Nov. 1948 (MPM); 1 F, Brazil, no date (MPM); 1 F, Brazil, Rio Grande do Sul, no date (USNM)

*Catoblepia* Stichel, 1901

Seven species examined directly, see also <http://fs.uno.edu/cpenz/catoblepia.html>

*Catoblepia amphirhoe* (Hübner, 1825)

1 M, Brazil, Santa Catarina, São Bento do Sul, 10 Mar 1984 (UFL); 1 M, Brazil, Santa Catarina, São Bento do Sul, 10 Feb (UFL); 1 M, Brazil, São Paulo, Araçatuba (UFL); 1 F, Brazil, São Paulo, Mendes, no date (UFL)

*Catoblepia berecynthia* (Cramer, 1777)

1 M, Central Peru, no date (MPM); 2 M, Peru, Puerto Maldonado, Los Amigos Biological Station, 10 Oct 2004 and 14 Oct 2004 (PJD); 1 F, Paraguay, no date (MPM),

*Catoblepia orgetorix* (Hewitson, 1870)

1 M, Colombia, Antioquia, Zaragosa, 18 Feb 1977 (MPM); 1 M, Ecuador, Oriente (AMNH); 1 M, Panama, Chiriqui, no date (UFL); 1 F, Colombia, Antioquia, Zaragosa, 18 Feb 1977 (MPM); 1 F, Ecuador, Pichincha, Santo Domingo de los Colorados (AMNH); 1 F, Ecuador, Canelos, no date (UFL)

*Catoblepia soranus* (Westwood, 1851)

1 M, Colombia, Amazonas, Rio Tacana, 1-13 Nov 1946 (AMNH); 1 M, Ecuador, Sucumbios, Garza Cocha, La Selva Biological Station, 26 Apr 1995 (PJD); 1 M, Peru, Rio Huallaga, no date (AMNH); 1 M, Brazil, Rondônia, Fazenda Rancho Grande, 29 Nov 1991 (UFL); 1 F, Peru, no date (USNM); 1 F, Colombia, Amazonas, Rio Tacana, 26-31 Oct 1946 (AMNH); 1 F, Peru, Iquitos, no date (AMNH); 1 F, Brazil, Rondônia, Fazenda Rancho Grande, 1 Sep 1991 (UFL)

*Catoblepia versitincta* Stichel, 1901

1 M, French Guiana, St. Jean Maroni, no date (UFL); 1 F, French Guiana, Gourdonville, no date (UFL)

*Catoblepia xanthus* (Linnaeus, 1758)

1 M, Brazil, Pará, Obidos, Nov 1965 (MPM); 2 M, Ecuador, Sucumbios, Garza Cocha, La Selva Biological Station, 10 Jul 1999 and 9 Nov 1993 (PJD); 1 F, British Guiana, Georgetown, Jan 1960 (MPM); 1 F, Ecuador, Sucumbios, Garza Cocha, La Selva Biological Station, 10 Dec 1996 (PJD)

*Catoblepia xanthicles* (Godman & Salvin, 1881)

1 M, Ecuador, Sucumbios, Garza Cocha, La Selva Biological Station, 5 May 1996 (PJD)



**Mielkella Casagrande, 1982**

**One species examined directly, see also <http://fs.uno.edu/cpenz/mielkella.html>**

*Mielkella singularis* (Weymer, 1907)

1 M, Mexico, Chiapas, no date (AMNH); 1 M, Mexico, Chiapas June 1977 (AMNH); 1 F, [Mexico] Santa Rosa Comitán 19 Jun 37 (AMNH); 1 F, Mexico, Chiapas, no date (AMNH); 1 F, Mexico, Chiapas, no date (USNM); 1 F, Mexico, Chiapas, Santa Rosa Comitán, Mar 1966 (MPM)

**Orobrassolis Casagrande, 1982**

**One species examined directly, see also <http://fs.uno.edu/cpenz/orobrassolis.html>**

*Orobrassolis ornamentalis* (Stichel, 1906)

1 M and 1 F, Brazil, São Paulo, Umuarama (MPM)

**Blepolenis Röber, 1906**

**Three species examined directly, see also <http://fs.uno.edu/cpenz/blepolenis.html>**

*Blepolenis bassus* (C. Felder & R. Felder, 1867)

2 M, Brazil (MPM); 1 M, Brazil, S. Paulo, no date (MZSP 13713); 2 M, Brazil, E. Paraná, Murtinho, Jan 1916 and 29 Jan 1916 (MZSP 13712 and 13711); 1 F, Brazil, Campos do Jordão-Lagoinha (MZSP 13714); 1 F, Brazil, C. Jordão-Lagoinha, Jan 28 1967 (MZSP 13715); 1 F, Brazil, São Bento [do Sul], [Rio Grande do Sul], Jan 1955 (MPM).

*Blepolenis batea* (Hübner, 1821)

1 M, Brazil, Serra do Caraça, Minas Gerais, 24 Mar 1972 (MZSP 13717); 1 M, Brazil, Itatiaia, E. Rio [de Janeiro], (MZSP 13604); 1 M, Brazil, Nova Friburgo, Rio de Janeiro, Nov 1957 (MPM); 1 M, Brazil, C. Jordão-Lagoinha, 28 Jan 1967 (MZSP 13721); 1 M, Brazil, Est. Biol. Boracéia, Salesópolis, São Paulo, 8 Mar 1968 (MZSP 13720); 1 M, Brazil, São Paulo, Salesópolis, Boracéia, Jan 1952 (MZSP 13723); 1 M, Brazil, Itatiba, São Paulo, Dec 1935 (MZSP 13719); 1 M, Brazil, S. Paulo, no date (MZSP 13718); 1 M, Brazil, S. Paulo, no date (MZSP 13716); 1 M, Brazil, S. Paulo, Botânica, 12 Mar 1952 (MZSP 13605); 1 M, Brazil, Santa Catarina, Nova Teutônia, 19 Jan 1961 (MPM); 1 M, Brazil, Santa Catarina, no date (AMNH); 1 M, Brazil, Santa Catarina, no date B.M. 1937-285 (BMNH); 1 M, Brazil, Porto Alegre, no date (MZSP 13709); 1 M, Brazil, Pelotas, Rio Grande do Sul, 20 Jan 1967 (AMNH); 1 F, Brazil, no date (MPM); 1 F, Brazil, Est. Biol. Boracéia, Salesópolis, São Paulo, 14 Feb 1968 (MZSP 13607); 1 F, Brazil, Est. Biol. Boracéia, Salesópolis, São Paulo, 2 Mar 1968 (MZSP 13606); 1 F, Brazil, Ypiranga, São Paulo, Jan 1929 (MZSP 13722); 1 F, Brazil, S. Paulo, 5 Feb 1939 (MZSP 13724); 2 F, Brazil, Santa Catarina, no date (AMNH)

*Blepolenis catharinae* (Stichel, 1902)

1 M, no locality, no date, B.M. 1937-285, (BMNH); 1 M, no locality, no date (MZSP 13 710); 3 M, Brazil, Lagoa do Peri, Florianópolis-SC, Jan 2008 (UFSC); 2 F, Brazil, Lagoa do Peri, Florianópolis-SC, Jan 2008 and Feb 2008 (UFSC)

**Opsiphanes Doubleday, 1849 [13]**

**Six species examined directly, see also <http://fs.uno.edu/cpenz/opsiphanes.html>**

*Opsiphanes boisduvallii* Doubleday, 1849

1 M, no data (MPM); 1 M, Mexico, no date (MPM); 1 F, Mexico (MPM); 1 F, Mexico, San Luis Potosi, 29-31 Jul 1941 (MPM)

*Opsiphanes invirae* (Hübner, 1808)

1 M, Paraguay, San Salvador (MPM); 1 M, Brazil, no date (MPM); 1 F, Brazil, Espírito Santo, Linhares (MPM); 1 F, Brazil Feb 1950 (MPM)

*Opsiphanes quiteria* (Stoll, 1780)

2 M, Peru, Puerto Maldonado, Los Amigos Biological Station, 11 May 2004 and 12 Oct 2004 (PJD); 1 F, Peru, Puerto Maldonado, Los Amigos Biological Station, 12 Nov 2004 (PJD)

*Opsiphanes tamarindi* C. Felder & R. Felder, 1861

1 M, Colombia, Cali, 15 Feb 1965 (MPM); 1 F, Colombia, Cali, 15 Feb 1965 (MPM); 1 F, Nicaragua, Managua, Managua 24 Feb 1958 (MPM)

*Opsiphanes sallei* Doubleday, 1849

1 M, Peru, Paaco, Oxapampa, no date (UFL); 1 M, Huanoabamba, Peru, no date (AMNH); 1 F, Colombia, Rio Negro, no date (USNM); 1 F, Colombia, Bogota, no date (UFL)

*Opsiphanes cassia* (Linnaeus, 1758)

1 M, Catemaco, Sep 1962 (MPM)