The phylogeny of Opoptera butterflies, and an assessment of the systematic position of O. staudingeri (Lepidoptera, Nymphalidae)

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Abstract

This study provides a species-level phylogeny for the Neotropical brassoline genus Opoptera Aurivillius based on 37 morphological characters. A revised generic definition is given, and two species groups are supported. The syme-group includes three species from the Brazilian Atlantic forest. The aorsa-group includes O. staudingeri (Godman & Salvin) from Central America, three species from western and northern South America, and one species from the Atlantic forest. Two subspecies are elevated to species status: O. hilaris Stichel, NEW STATUS and O. bracteolata Stichel, NEW STATUS. Two new combinations are proposed: O. hilaris fuscata Stichel, NEW COMBINATION and O. hilaris colombiana Rothshild, NEW COMBINATION. Diagnoses and illustrations of habitus and genitalia are provided for the eight recognized Opoptera species. Wing color, male scent organs, and male and female genitalic morphology are described and discussed.

Key words: bracteolata, hilaris, new status, new combination, Brassolini

Introduction

The genus Opoptera Aurivillius is a small group of brassoline butterflies that ranges from Mexico to southern South America. As a group, it includes eight species (this study, Fig. 1–2) plus a species from Peru that awaits formal description (Casagrande 2004). In the introduction to the genus Opsiphanes Doubleday, Godman & Salvin (1879) noted that this genus was “divisible into several groups, and it is very probable that at some future time it will be found advisable to split up the genus into several minor ones” (p 125). Indeed, Opoptera was described initially as a subgenus of Opsiphanes by Aurivillius (1882), and later Stichel (1902) separated Opsiphanes sensu lato into four genera; i.e., Opoptera, Catoblepia Stichel, Selenophanes Staudinger and Opsiphanes sensu strictu. Although Stichel (1902) did not follow the exact sections proposed by Godman & Salvin (1879), he nonetheless considered these four genera as closely related, a view that was shared with other workers of the time. For example, Fruhstorfer (1912) kept these taxa subordinate to Opsiphanes to emphasize their relatedness, but noted that Opoptera was “nearly entitled to generic rank” (p 291). A recent cladistic analysis suggested that Opoptera may actually be more closely related to Dasyophthalma Westwood than to any of the aforementioned genera (Penz 2007). Phylogenetic relationships aside, Stichel’s choice to separate Opoptera from Opsiphanes was appropriate and has been broadly adopted (e.g., Casagrande 1982, 1995, Ackery 1988).

Stichel’s (1902) first classification of Opoptera included three species groups: the aorsa-, syme- and staudingeri-groups. In his subsequent works, these were further arranged into the sections Desmididocosmeti, which contained the groups Aorsiformes and Symiformes, and Peragnosti, including only O. staudingeri (Stichel 1904, 1909, 1925, 1932). Table 1 lists Stichel’s defining characters for his sections and groups, and
Fig. 3A shows a scheme of relationships representing his classification. A critical examination of Stichel’s defining characters indicates that there are a few inconsistencies. For example, Desmidocosmeti was defined by “an approximately round forewing apex” so to accommodate for members of the groups Symiformes and Aorsiformes which in fact differ in the shape of their forewing apex (compare *O. syme* (Hübner) and *O. aorsa* (Godart), Fig. 1A and D). Furthermore, the definition of Peragnosti includes characters that are also present in members of Desmidocosmeti (e.g., male scent organ at vein Cu2). These observations make it apparent that group-level definitions within *Opoptera* need to be re-evaluated.

Stichel’s classification of *Opoptera* remained unchanged until Casagrande (1982) separated section Peragnosti from the remaining species. Its single member *O. staudingeri* became the type species of the genus *Mimoblepia* Casagrande, named to indicate small size and color similarity with *Catoblepia*. Casagrande’s (1982) defining characters for *Mimoblepia* are listed in Table 1, including her comparison to *Opoptera*. The description of *Mimoblepia* segregated *O. staudingeri* into its own genus and emphasized characters unique to this species, but characters shared with other *Opoptera* species were not taken into account.

The cladistic analysis by Penz (2007) showed that all species of *Opoptera sensu lato* share two unique male genitalia characters. These are a sclerotization of the dorsal edge of the valva that encircles the valva tip (i.e., the ‘sclerotized carena’ of Casagrande 1982), and the presence of minute ribbed serrations on the sclerotized carena (characters 26:2 and 28:0 in Penz 2007). That study also suggested that *O. staudingeri* is nested within *Opoptera*, which argues against maintaining Casagrande’s (1982) *Mimoblepia*. Nonetheless, in that analysis the Central American *O. staudingeri* appeared as sister taxon to *O. syme* and *O. fruhstorferi* (Röber), both from southeastern Brazil. These relationships implied a disjunct distribution of the clade (*syme, fruhstorferi, staudingeri*), thus warranting further investigation.

**TABLE 1.** A, Species groups of *Opoptera* proposed by Stichel (1904, 1909; translated from Stichel 1909), with current venation terminology in square brackets. The tree in Fig. 3A follows Stichel’s classification. B, Original description of *Mimoblepia* by Casagrande (1982).

<table>
<thead>
<tr>
<th>A.</th>
<th>Stichel (1909)</th>
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<tbody>
<tr>
<td>I.</td>
<td>SECTION DESMIDOCOSMETI</td>
</tr>
<tr>
<td></td>
<td>Forewing apex approximately round. Male hindwing with a hairpencil in the cell, or a hairbrush in the submedian [Cu2].</td>
</tr>
<tr>
<td>a.</td>
<td>Group Aorsiformes</td>
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<tr>
<td>b.</td>
<td>Group Symiformes</td>
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<tr>
<td></td>
<td>Forewing with rounded apex, third and fourth subcostals [R3, R4] running into the rounded apex. Hindwing without a tail.</td>
</tr>
<tr>
<td>II.</td>
<td>SECTION PERAGNOSTI</td>
</tr>
<tr>
<td></td>
<td>Forewing with pointed apex. Hindwing without a tail. Male without hairpencil. Lower median [Cu2] rising near the wing base, and with a deep bag-like fold filled with flour-like dust.</td>
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</tbody>
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<table>
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<tr>
<th>B.</th>
<th>Casagrande (1982)</th>
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<tr>
<td>Mimoblepia</td>
<td></td>
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<tr>
<td>Males – meso- and metathoracic tibia and proximal tarsomers with short spines that are evenly distributed on all sides throughout their extension. Valva with a smooth distal margin, twisted inward anteriorly, and with a sclerotized carena. Differs from the genus <em>Opoptera</em> … by having the forewing vein m-cu longer than cu1-cu2; external margin of the forewing slightly sinuous and with a weakly projected apex; hindwing with a scent organ at the base of vein Cu2 that lacks a hairpencil.</td>
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This study expands on previous work by assessing the phylogenetic relationships among all described species of *Opoptera*. Here, an expanded set of characters allowed for a revised phylogeny and associated classification of *Opoptera* to be proposed. The analysis allowed me to evaluate whether *O. staudingeri* should be kept separate from other *Opoptera* species (as per Stichel 1904 and Casagrande 1982), or if it is closely
related to *O. syme* (as per Penz 2007). In the course of this investigation it became necessary to elevate two subspecies to species status.

**FIGURE 1.** *Opoptera* adult males, dorsal side on the left, ventral side on the right. Scale bar next to A = 1 cm. (A) *syme*, Brazil, São Paulo. (B) *sulcius*, Brazil, Santa Catarina, Taió. (C) *fruhstorferi*, Brazil, Santa Catarina, Taió. (D) *aorsa*, Brazil, Paraná, Toledo. (E) *hilaris*, Middle Ecuador. (F) *staudingeri*, Costa Rica, Heredia, Puerto Viejo. (G) *arsippe*, Peru, Chuchurras. (H) *bracteolata*, Bolivia. Schematic representation and photographic detail of the HW discal cell region showing male sent organs. Venation terminology is given in I. Dashed lines represent the scent-pocket next to vein Cu2. (I) *sulcius*, Brazil, Santa Catarina, Taió; note thin hairpencil inserted into scent-pocket. (J) *hilaris*, Bolivia; note the three hairbrushes. (K) *staudingeri*, note the broad hairbrush inside discal cell. (L) *arsippe*, Peru, Chuchurras; note the open scent organ and long HW discal cell hairbrush.

**Material and methods.**

**Species sampled.** Appendix 1 provides information on the materials used here (species, specimen locality data). Outgroups were selected based on Penz (2007). Two species of the putative sister genus *Dasyophthalma* were used; *D. creusa* (Hübnner) and *D. rusina* (Godart). The ingroup included eight taxa; the five *Opoptera* species recorded by Casagrante (2004) in the checklist for Brassolini, plus *O. staudingeri* as per Penz (2007), *O. hilaris* Stichel, **NEW STATUS** and *O. bracteolata* Stichel, **NEW STATUS.** The Species Identification section includes morphological information and a diagnosis for all taxa, thus verifying their identity for future reference. Estimated geographical distributions are based on published records and collection specimens.
Characters and terminology. Pinned adults were used to examine external morphology. Abdomens and legs were prepared using a 10% solution of KOH, and subsequently stored in a 3:1 solution of glycerol and 70% ethanol. All structures were examined using an optical stereomicroscope with light and dark field and magnification up to 130 X. Appendices 2 and 3 include a list of 37 characters and associated character matrix. New and traditional characters (Stichel 1909, Casagrande 1982, Penz 2007) were used in the analysis, including characters based on wing coloration as was done in Penz (2008). Morphological terminology follows Kristensen (2004). Abbreviations used throughout are: FW, forewing; HW, hindwing; CI, consistency index; RI, retention index.

Phylogenetic analysis. Parsimony was used to infer phylogenetic relationships among species of Opoptera. All characters had equal weight and multi-state characters were set as unordered. Heuristic searches in PAUP 4.0b10 (Swofford 2002) used stepwise addition with 500 tree-bisection-reconnection replicates starting from random trees. Estimates of branch support were calculated from 1000 jackknife replicates (50% deletion) excluding uninformative characters. MacClade 4 (Maddison & Maddison 2000) was used for tracing character changes and tree editing. Terms used to indicate character status in Fig. 3B–C follow MacClade 4.

FIGURE 2. Opoptera adult females, dorsal side on the left, ventral side on the right. Scale bar next to A = 1cm. (A) syme, South America. (B) sulcius, Brazil, Santa Catarina. (C) fruhstorferi South Brazil. (D) aorsa, Brazil, Rio de Janeiro, Nova Friburgo. (E) hilaris, Ecuador, Sucumbios. (F) staudingeri, Costa Rica, Heredia, Puerto Viejo. Venation of O. syme, drawn from the ventral side. Vein thickness is not represented. (G) male FW. (H) male HW, note the bulge on the wing surface at vein Cu2 that represents the scent-pocket.
Results

Parsimony analysis of 37 characters yielded two most parsimonious trees 50 steps long (CI excluding uninformative characters=0.8200, RI=0.8393; Fig. 3B–C). The analysis provides additional character support for the
monophyly of *Opoptera* (Fig. 3B–C) and indicates that this genus can be divided into the *syme-* and *aorsa-*
groups, where *O. staudingeri* is a member of the latter. Interestingly, the two most parsimonious trees differed
in the position of *O. staudingeri*. While in Fig. 3B this species appears as sister to *O. arsippe* (Hopffer), in
Fig. 3C it is sister to all other species of the *aorsa*-group. The hindwings of *O. staudingeri* and *O. arsippe* are
similar in the relatively smooth margin, and conspicuous, continuous marginal band (see characters 10 and 11
in Fig. 1F–G). However, the wing pattern of *O. staudingeri* might represent a case of convergent mimicry
(Casagrande 1982), and not similarity due to common ancestry. To investigate the impact of color characters
in the results, I excluded characters 3–8 and 11 (Appendix 2), and ran another parsimony analysis using struc-
tural characters only (same settings as above). One single tree was obtained, identical to that in Fig. 3C (tree
length 38; CI excluding uninformative characters=0.8684, RI=0.8936). Jackknife support values for the anal-
ysis of structural characters only were slightly higher overall than those yielded by the complete data set
(except for the grouping of *O. syme* and *O. sulcius* (Staudinger), which was mostly based on color, Fig. 3C).
This study will therefore focus on Fig. 3C as the preferred species-level hypothesis of relationships for
*Opoptera*. Below I characterize the genus *Opoptera* and its species groups based on character changes noted
in Fig. 3C, including color characters. Other observations are also reported when appropriate.

**Genus Opoptera Aurivillius, 1882**

Seven unambiguous character changes support the monophyly of *Opoptera* (Fig. 3C, character illustrations in
Fig. 1–2, 4–6). As a group, *Opoptera* is not homogeneous in either wing shape or color (Fig. 1–2). The FW
apex can be rounded (*syme, sulcius, fruhstorferi*), mildly pointed (*staudingeri*) or angular (*aorsa, hilaris,
arsippe, bracteolata*; character 2). FW with three apical white spots and intersected by an incomplete ‘Y-
shaped’, usually orange, postmedial band (white in *fruhstorferi*, character 7:2), a pattern element that is shared
with most brassolines. The proximal arm of this band can be either continuous or broken (*bracteolata*, charac-
ter 6). Ventral FW with an eyespot at cell M1, discal cell intersected by two bands. Ventral HW broadly rip-
pled and with well developed eyespots in cells Sc+Rs and Cu1. The HW contour can be nearly smooth
(*staudingeri, arsippe*), but it is usually mildly scalloped with or without a tail at M3 (character 10). HW pre-
costal cell arched-out and large within the context of Brassolini (Fig. 2H, see Stichel 1909 for a comparison
with other genera). There is no sexual dimorphism in color, but females may be slightly larger and paler than
males, and may have a faint HW iridescence (Fig. 1–2).

Depending on the species, male HW androconial organs may vary. A patch of androconial scales is
located immediately adjacent to vein Cu2 (character 15), where the wing membrane is folded over to form a
‘scent-pocket’ (15:2, Fig. 1K). Within Brassolini, this scent-pocket is unique to *Opoptera*, and it is present in
all species of the genus except for *O. arsippe* in which it constitutes a shallow depression on the wing mem-
brane (15:1, Fig. 1L). Some species (*syme, sulcius, fruhstorferi, bracteolata*) possess a thin hairpencil inside
the discal cell that crosses over vein Cu1-Cu2 (character 12:1). This hairpencil is formed by thin, elongate
scales closely joined together, as can be seen by their insertion sockets, and it fits inside the scent-pocket (see
Fig. 1A and B). In species lacking this hairpencil, different hairbrushes can be found. Elongate, dense HW
discal cell ‘hairs’ form a ‘discal cell hairbrush’ present in two *Opoptera* species (*staudingeri, arsippe*; charac-
ter 13:1; Fig. 1K). Furthermore, elongate, dense HW ‘hairs’ in cells Cu1 and Cu2 form two hairbrushes that
are in close proximity to the scent-pocket (*aorsa, hilaris, Fig. 1J). Finally, HW ‘hairs’ in cell Cu2 form a long
‘Cu2 hairbrush’ (character 14:1, *aorsa, hilaris*, Fig. 1J). The hairpencil and hairbrushes are both associated
with the Cu2 androconial organ.

The male valva has two defining characters: a sclerotization of the dorsal edge that encircles the valva tip
(i.e., sclerotized carena), and bears minute ribbed serrations (characters 21:2 and 22:0; Fig. 4). The female
stergma is highly variable in shape (Fig. 6), and has a continuous anterior section (character 33:0). The cor-
pus bursa lacks signa (Fig. 6).

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FIGURE 4. Opoptera male genitalia in lateral view. Scale bar next to A = 1mm. (A) syme, Brazil, Rio de Janeiro, Nova Friburgo, 01-43 Dissected by C.M.Penz. (B) sulcius, Brazil, São Paulo, Pinhal, 06-12 Dissected by C.M.Penz. (C) fruhstorferi, South Brazil, 01-60 Dissected by C.M.Penz. (D) aorsa, Brazil, Paraná, Toledo, 08-17 Dissected by C.M.Penz. (E) hilaris Ecuador, Oriente, 08-34 Dissected by C.M.Penz. (F) staudingeri, Costa Rica, Heredia, Puerto Viejo, 01-57 Dissected by C.M.Penz. (G) arsippe, Peru, Chuchurras, 06-22 Dissected by C.M.Penz. (H) bracteolata, Bolivia, 01-59 Dissected by C.M.Penz. Detail of the valva apex in lateral view, localities same as in F, G and H. Setae omitted. Scale bar next to H = 1mm. I, staudingeri. J, arsippe. K, bracteolata.
FIGURE 5. *Opoptera* male genitalia in ventral view (setae omitted from right side of figure), with separate drawings of the juxta and dorsal view of tegumen+uncus. Scale bar next to A = 1mm. (A) *syme*, Brazil, Rio de Janeiro, Nova Friburgo, 01-43 Dissected by C.M. Penz. (B) *sulcius*, Brazil, São Paulo, Pinhal, 06-12 Dissected by C.M. Penz. (C) *fruhstorferi*, South Brazil, 01-60 Dissected by C.M. Penz. (D) *aorsa*, Brazil, Paraná, Toledo, 08-17 Dissected by C.M. Penz. (E) *hilaris*, Ecuador, Oriente, 08-34 Dissected by C.M. Penz. (F) *staudingeri*, Costa Rica, Heredia, Puerto Viejo, 01-57 Dissected by C.M. Penz. (G) *arsippe*, Peru, Chuchurras, 06-22 Dissected by C.M. Penz. (H) *bracteolata*, Bolivia, 01-59 Dissected by C.M. Penz. Detail of the gnathos in lateral view, localities same as in F and G. Gnathos of *arsippe* drawn in ventrolateral view (different angle from that in Fig. 4F). Scale bar next to H = 1mm. (I) *staudingeri*. (J) *arsippe*. 
Species groups

syme-group

The name of this group is maintained from the original classification by Stichel (1902). *Opoptera* syme (type-species of the genus), *O. sulcius* and *O. fruhstorferi* form a monophyletic group supported by the following unambiguous character changes (Fig. 3C): presence of a thin hairpencil inside HW discal cell (character 12:1, also present in *O. bracteolata*; Fig. 1I); mid- and hindlegs, color of the distal edge of each segment and subsegment similar to the color of the segments themselves (17:0, unique); setose portion of valva tip flattened, palmate (26:1, unique; Fig. 4A).

Male genitalia are very similar within the syme-group. All species have long, narrow valvae that extend nearly to, or beyond the uncus tip in lateral view (Fig. 4A–C). *Opoptera* syme and *O. sulcius* share the presence of a spine-like expansion on the proximal region of the gnathos (30:1, Fig. 4A), and the palmate valva tip is more strongly projected ventrally in lateral view than in *O. fruhstorferi* (27:0; Fig. 4A–C). Although *O. sulcius* and *O. fruhstorferi* share a broad proximal arm of the FW postmedial band, the grouping of these two species as sister taxa increases tree length by one step.

aorsa-group

The name of this group is maintained from the original classification by Stichel (1902). *Opoptera staudingeri*, *O. aorsa*, *O. hilaris*, *O. arsippe* and *O. bracteolata* form a monophyletic group supported by three unambiguous character changes (Fig. 3C): in dorsal view, anterior edge of tegumen markedly concave (character 19:1, Fig. 5F); presence of projected ‘flaps’ on lateral edges of sterigma (35:1, Fig. 6D–F); intersegmental sac between seventh abdominal sternite and sterigma with two lateral pockets (37:1, Fig. 6F). Although I was
unable to borrow females of *O. arsippe* and *O. bracteolata* for examination, based on the above distribution of character changes I predict that characters 35:1 (or variation thereof) and 37:1 will also be found in these species.

The grouping of *O. aorsa*, *O. hilaris*, *O. arsippe* and *O. bracteolata* is supported by two unambiguous character changes (Fig. 3C): presence of a HW tail at vein M3 (character 9:1; Fig. 1E); Lateral uncus wings expanded laterally to form two dorsolateral keels (28:2, Fig. 5D, H). Furthermore, these four species have an angular FW apex due to a small depression of the wing membrane at vein M3 (character 2:2; Fig. 1D).

Two other character changes are also of interest within this group. *Opoptera bracteolata* is the only member of the *aorsa*-group in which the males possess a thin hairpencil inside the HW discal cell (12:1, a secondary gain). *Opoptera arsippe* is the only species in the genus in which the scent organ at HW vein Cu2 constitutes a shallow depression (15:1, Fig. 1L) and not a ’scent-pocket’ (15:2, Fig. 1K; see Discussion).

**Species identification**

Below I provide a diagnosis for currently recognized *Opoptera* species, plus a status change in two subspecies which can be considered an update to the Brassolini checklist by Casagrande (2004).

*Opoptera syme* (Hübner, 1821)

*(Fig. 1A, 2A, 2G–H, 4A, 5A, 6A)*

Type species of the genus by original designation.

**Type locality.** Brazil.

**Diagnosis.** Male FW length range 38.9–42.7 mm (based on specimens in Appendix 1). Wings with pale brown background from base through medial (FW) or postmedial areas (HW), turning darker brown distally. Overall background coloration slightly darker than *O. sulcius*. FW with a conspicuous, orange ‘Y-shaped’ postmedial band that has a narrow proximal arm, and a well-developed (although broken) distal arm that intersects and obscures the subapical white spots. HW with a faded submarginal band. Males have a HW discal cell hairpencil and a scent-pocket. Ventral HW with a well-defined white postmedial band distal to the eyespots. Females similar to, but paler than males dorsally, and with a pale blue iridescence across the medial area of the HW.


**Remarks.** Casagrande (2004) lists no subspecies for *O. syme*. It is unlikely that the specimen described by Rothshild (1916) as ssp. *colombicola* Rothshild was actually collected in Colombia. Although the male genitalia is nearly identical to *O. sulcius*, differences were found in the female genitalia. *Opoptera syme* and *sulcius* seem to co-occur in a few sites along their ranges, such as Campos do Jordão and Reserva Estadual do Morro Grande, Cotia (both in São Paulo state), and Nova Friburgo and Petrópolis (Rio de Janeiro; A.V.L. Freitas and K.S. Brown, pers. comm.).

*Opoptera sulcius* (Staudinger, 1887)

*(Fig. 1B, 1I, 2B, 4B, 5B, 6B)*

**Type locality.** Brazil (Santa Catarina).

**Diagnosis.** Male FW length range 41.3–43 mm (based on specimens in Appendix 1). Wings with pale brown background from base through medial (FW) or postmedial areas (HW), turning darker brown distally. Overall background color slightly lighter than *O. syme*. FW with a conspicuous, orange ‘Y-shaped’ postme-
dial band that has a broad proximal arm, a well-developed (although broken) distal arm that intersects and obscures the subapical white spots, plus a thin submarginal band. HW with a well-developed orange submarginal band, plus a thin orange marginal band. Males have a HW discal cell hairpencil and a scent-pocket. Ventral HW with a faded white postmedial band distal to the eyespots. Females similar to, but paler than males dorsally, and devoid of iridescence.


**Remarks.** Casagrande (2004) lists no subspecies for *O. sulcius*. Although the male genitalia are nearly identical to *O. syme*, differences were found in the female genitalia.

*Opoptera fruhstorferi* (Röber, 1896)
(Fig. 1C, 2C, 4C, 5C, 6C)

**Type locality.** Brazil (Santa Catarina).

**Diagnosis.** Male FW length range 37.5–38 mm (based on specimens in Appendix 1). Wings with dark brown background. FW with a conspicuous, broad, white postmedial band and three subapical white spots. HW with a faded submarginal band. Males have a HW discal cell hairpencil and a scent-pocket. Ventral HW with a faded white postmedial band distal to the eyespots. Male genitalia more delicate than those of *O. syme* and *O. sulcius*. Females similar to, but paler than males dorsally.


*Opoptera aorsa* (Godart, 1824)
(Fig. 1D, 2D, 4D, 5D, 6D)

**Type locality.** Brazil [presumably Atlantic forest]

**Diagnosis.** Male FW length range 38.1–41.6 mm (based on specimens in Appendix 1). Although very similar to *O. hilaris*, it can be distinguished by the following characters. FW with a thin orange postmedial band that is disjointed at cell M3, and a reduced distal arm that forms a very thin line that usually reaches the white crescent spot in cell M1. Posterior portion of this band usually forming a smooth curve, in contrast to a ‘coarser’ shape in *hilaris*. A continuous transverse band is present across the center of the FW discal cell. HW submarginal band faded but noticeable. Similarly to *hilaris*, *aorsa* males lack a thin hairpencil inside HW discal cell, but have a conspicuously long, dark hairbrush adjacent to vein 1A+2A, plus a smaller hairbrush inside cell Cu2 below the scent-pocket. Females are paler than males, and have brighter and thicker orange bands. The male genitalia of *aorsa* and *hilaris* are similar, being highly divergent from other *Opoptera* (Fig. 4–5). The valvae are markedly thin, narrowed at base to produce a midline gap, and the sclerotized carena is elongated to form a solid, curved prong. In dorsal view, the uncus wings of *aorsa* are conspicuously broader than those of *hilaris* (compare Fig. 5D and E). The female sterigma of *aorsa* and *hilaris* are markedly different (compare Fig. 6D and E).

**Distribution.** Brazil, Atlantic forest (Testón & Corseuil 2002, Casagrande 2004, Appendix 1).

**Remarks.** Casagrande (2004) listed four subspecies; the nominal *aorsa* from Brazil, *colombiana* (Rothschild) from Colombia, *fuscata* Stichel from Brazil (Amazonas), and *hilaris* Stichel from Ecuador, which is treated below. I dissected males and females from Espírito Santo and Paraná, Brazil (Appendix 1), and the genitalia and wing pattern were consistent among the specimen series, but differed from specimens collected in other areas (see below).
Opoptera hilaris Stichel, 1901, NEW STATUS
(Fig. 1E, 1J, 2E, 4E, 5E, 6E)

Type locality. Ecuador.

Diagnosis. Male FW length range 38.3–42.5 mm (based on specimens in Appendix 1). Although very similar to O. aorsa, it can be distinguished by the following characters. FW with a thin orange postmedial band that is disjointed at cell M3, and a reduced distal arm that forms a very thin line that usually does not reach the white crescent spot in cell M1. Posterior portion of this band usually ‘coarse’, in contrast to a somewhat smooth curve in aorsa. The transverse band present across the center of the FW discal cell is composed of a series of contiguous small rounded segments (i.e., ‘broken’). HW submarginal band barely visible, contrasting the faded, but noticeable band seen in aorsa. Similarly to aorsa, males lack a thin hairpencil inside HW discal cell, but have a conspicuously long, dark hairbrush adjacent to vein 1A+2A, plus a smaller hairbrush inside cell Cu2 below the scent-pocket. Females are paler than males, have brighter and thicker orange bands, and faint blue iridescence. The male genitalia of hilaris and aorsa are similar, being highly divergent from other Opoptera (Fig. 4–5). The valvae are markedly thin, narrowed at base to produce a midline gap, and the sclerotized carena is elongated to form a solid, curved prong. This prong is slightly wider in hilaris than in aorsa, and the serrations are slightly larger and therefore more noticeable. In dorsal view, the uncus wings of hilaris are conspicuously narrower than those of aorsa (compare Fig. 5E and D). The female sterigma of hilaris and aorsa are markedly different (compare Fig. 6E and D).

Distribution. Venezuela, Colombia, Ecuador, Peru, Bolivia, Paraguay, western Brazil (Amazon forest to Mato Grosso) (D’Abrera 1987, Casagrande 2004, A. Neild pers. comm., Appendix 1).

Justification for new status. In his original description Stichel (1901) identified two key characters that separated Ecuadorean O. aorsa hilaris from nominal aorsa from Eastern Brazil: ventral FW discal cell with a broken transverse band, and dorsal HW solid brown (i.e., lacking the orange submarginal band present in aorsa). Neither the original nor subsequent descriptions (e.g., Stichel 1902) mentioned genitalia, and I thus assume that Stichel did not dissect hilaris. I examined and dissected males from Ecuador, Peru, Bolivia and Brazil (Amazonas; Appendix 1). Although there is slight variation among these specimens, they can be consistently recognized as hilaris by the characters given here, including genitalia (Fig. 1E, 2E, 5E, 6E). The remarkable divergence in the female sterigma (Fig. 6E) provides strong support for the separation of these two taxa. Opoptera aorsa occurs in the Brazilian Atlantic forest, while O. hilaris seems to be more widespread across the Amazonian region and western side of South America. It is unknown to me whether these species occur in sympatry.

New combinations. The descriptions of the subspecies fuscata (Stichel 1908; Brazil, Amazonas, examined here) and colombiana (Rothschild 1916; Colombia, not available for examination) are consistent with the diagnostic characters of hilaris. Therefore, two new combinations are proposed: O. hilaris fuscata, NEW COMBINATION and O. hilaris colombiana, NEW COMBINATION.

Opoptera staudingeri (Godman & Salvin, 1894)
(Fig. 1F, 2F, 4F, 5F, 5I, 6F)

Type locality. Panama.

Diagnosis. Male FW length 46 mm (based on specimen in Appendix 1). FW apex slightly pointed and HW margin smooth. Wings with orange-brown background. FW with a conspicuous orange postmedial band that has a narrow proximal arm, and a reduced distal arm that is barely visible inside cells M2 and M1. HW with a well-developed orange marginal band. HW outline slightly bulging below M3, which is particularly obvious in the female in Fig. 2F. Males lack a thin hairpencil inside HW discal cell, but have a scent-pocket.
Females similar to, but paler than males. Overall gestalt similar to species of *Catoblepia*. Unique genitalic characters include: dorsal outline of tegumen flat in lateral view; twisted valvae; and sterigma with two large, lateral, folded over projections with jagged edges and minute spines.

**Distribution.** Panama, Costa Rica to Mexico (Fruhstorfer 1912, Maza & Maza 1989, Casagrande 2004).

**Remarks.** Casagrande (2004) lists two subspecies; the nominal *staudingeri* from Panama, plus *mexicana* Maza & Maza from Mexico (not available for examination). *Opoptera staudingeri* is the only species of the genus for which a description of early stages has been published (DeVries 1987).

*Opoptera arsippe* (Hopffer, 1874)
(Fig. 1G, 1K, 2G, 4G, 5G, 5J)

**Type locality.** Peru.

**Diagnosis.** Male FW length range 41.7–43.7 mm (based on specimens in Appendix 1). Wings with orange-brown background. FW with a thin orange postmedial band that can be disjointed at cell M3, and a reduced distal arm that does not reach the apical white spots. HW margins with very shallow depressions, as compared to other species of *Opoptera*. HW with a conspicuous orange marginal band, including the tail. Males lack a thin hairpencil inside HW discal cell, but instead have a conspicuously long, broad and dark hairbrush in the cell that extends over the open scent organ next to vein Cu2. The scent organ next to Cu2 consists of a shallow concavity on the wing surface.

**Distribution.** Peru, Bolivia? (Casagrande 2004).

**Remarks.** I was unable to obtain females of this species for examination. Casagrande (2004) lists two subspecies; the nominal *arsippe* from Peru, and *bracteolata* Stichel from Bolivia, elevated here to full species (see below).

*Opoptera bracteolata* Stichel, 1901, NEW STATUS
(Fig. 1H, 4H, 5H)

**Type locality.** Bolivia.

**Diagnosis.** Male FW length range 39.8–41.3 mm (based on specimens in Appendix 1). Wings with orange-brown background. FW orange postmedial band markedly reduced, broken into a series of independent spots that do not reach the anterior FW margin. HW with a thin orange marginal band. Males have a thin hairpencil inside HW discal cell, contrasting other species in the *aorsa*-group.

**Distribution.** Bolivia (Casagrande 2004).

**Justification for new status.** *Opoptera bracteolata* shows important differences from *O. arsippe* that justify full species status. These two taxa have distinctive, easily diagnosable wing color patterns, and males have different wing scent organs (compare Fig. 1H and G). *Opoptera bracteolata* and *O. arsippe* also have rather different male genitalia (Fig. 4H and G, 5H and G), and such structural differences further support the notion that they are separate species. It is unknown to me whether these two taxa overlap geographically. Note that the specimen listed by Penz (2007) as *O. arsippe* actually corresponds to *O. bracteolata*.

**Remarks.** I was unable to obtain females of this species for examination.

**Morphology of male genitalia**

Within *Opoptera*, conspicuous morphological changes have occurred on the tegumen, uncus, gnathos and valva. Some of these differences can be traced to species groups, while others are unique. By virtue of being
the ‘roof’ of the genitalic capsule, the tegumen is usually dome-shaped, being slightly raised in lateral view. Three morphological patterns are present within Opoptera (Fig. 4): a flattened (18:0), slightly raised (18:1), or markedly raised tegumen (18:2). The transformations traced in the tree topology (Fig. 3C) imply a change from character state ‘1 to 0’ in O. staudingeri, and ‘1 to 2’ at the ancestor of other species in the aorsa-group; that is, opposite modifications from the same ancestral state. Variation in tegumen length is approximately continuous, with O. fruhstorferi and O. aorsa having the shortest tegumen of all Opoptera species (Fig. 5).

Members of the syme- and aorsa-groups show conspicuous differences in the uncus. In species of the syme-group and O. staudingeri, the lateral uncus wings are small and gradually fade posteriorly such that the lateral outline of the uncus in dorsal view is concave (28:0, Fig. 5A–C). In contrast, except for O. staudingeri (Fig. 5F), species of the aorsa-group have well-developed lateral uncus wings, so that the outline of the uncus appears convex in dorsal view (28:2, Fig. 5D–E, G–H). Opoptera aorsa is the only species in the genus that has a sharply pointed uncus (posterior view).

Gnathos morphology varied both within and between species groups. The gnathos consists of an arched, narrow-pointed structure in most Opoptera species. Within the syme-group, it may have an anterior prong, and in Fig. 3C the presence of this prong appeared as a shared, derived character unique to O. syme and O. sulcius (30:1, Fig. 4A–B). Three species of the aorsa-group show an independent modification of the gnathos that is absent in the syme-group. In O. arsippe and O. bracteolata the gnathos has an enlarged extra keel with jagged edges (29:1 and 31:1, Fig. 4G–H). In O. staudingeri this extra keel is small and smooth and can easily go unnoticed, but its recognition provided support to the placement of this species within the aorsa-group (Fig. 5I). If the topology in Fig. 3C is correct, the morphological transformation implies an increase in gnathos complexity in O. arsippe and O. bracteolata as compared to O. staudingeri. In O. aorsa and O. hilaris, the gnathos is devoid of a keel or ornamentation, but it is positioned further towards the midline of the genitalic capsule, the proximal portion forming a broad plate.

The valva has undergone interesting modifications within Opoptera. The main body of the valva (excluding the sclerotized carena) is long and narrow in the syme-group, and the palmate valva tip is a shared, derived character of this group (26:1, Fig. 4A–C), a narrow valva tip being the most common condition within brassolines (Penz 2007 and unpublished). Within the aorsa-group, the body of the valva (excluding the carena) tends to be shorter, and uniquely tall in lateral view in O. bracteolata (Fig. 4H). The twisting of the sclerotized carena offered support for the aorsa-group (25:1, Fig. 4I–K). The entire valva of O. staudingeri is twisted unlike any other species of Opoptera.

Opoptera aorsa and O. hilaris have highly modified genitalia. Here the sclerotized carena is distinctly elongate and prong-shaped, and the valvae are narrowed at the base to produce a gap at midline (Fig. 4D–E, 5D–E). This latter modification of the valva may have led to associated morphological changes in the shape of the juxta (anterior outline concave) and saccus (broad weakly sclerotized region anterior to the base of valvae), and possibly the orientation of the gnathos (see above, Fig. 5D–E).

Morphology of female genitalia

While the corpus bursae in Opoptera are somewhat homogeneous in shape and devoid of signa (Fig. 6), the sterigma morphology varies quite strongly among species. The sterigma of Opoptera is a broad plate extended laterally to form two thin ‘arms’. The plate itself can be smooth or adorned with minute spines (not illustrated). The ostium bursa is located at the anterior edge of the sterigma, which is projected and usually folded over. A raised, midline ‘bump’ is located posteriorly to the ostium bursa, a feature that is widespread in basal satyrines (including brassolines and amathusines sensu Peña et al. 2006; pers. obs.).

Within the syme-group, the sterigma morphology is unadorned. The presence of a ‘midline bump’ is similar across species, being largest in O. sulcius and tilted in O. fruhstorferi (Fig. 6A–C). The small fold at the anterior edge is parted in O. syme (Fig. 6A).
In contrast, strong modifications are evident within the aorsa-group. In *O. staudingeri* the midline bump is markedly tall and expanded into transverse, lateral ridges (Fig. 6F). A very small transverse ridge is noticeable in *O. aorsa* (Fig. 6D) but not in *O. hilaris* (Fig. 6E). Here I propose that the lateral ‘flaps’ present in *O. staudingeri* (large, placed anteriorly), *O. hilaris* (large, placed posteriorly) and *O. aorsa* (small, placed posteriorly) are homologous (character 35, Fig. 6D–F).

**Discussion**

The relationships proposed here organize *Opoptera* into two species groups. The syme-group is homogeneous regarding wing shape, color, and genitalia, and this is in full agreement with Stichel’s classification (Stichel 1902, 1904). The close relationships among *O. syme*, *O. sulcius* and *O. fruhstorferi* suggest that their divergence has occurred along a north-south axis in the Brazilian Atlantic forest. This corresponds to what has been noted for other groups, for example *Actinoe* Hübner (e.g., Francini & Penz 2006, Silva-Brandão et al. 2008). Unlike the syme-group, the aorsa-group is more widespread. *Opoptera arsippe*, *O. bracteolata* and *O. hilaris* inhabit western South America, suggesting that this is an ancestral distribution for that group, and that the current distributions of *O. staudingeri* (Central America northward to Mexico) and *O. aorsa* (Atlantic forest) represent dispersal events.

The enigmatic *O. staudingeri* posed a challenge to previous research. In the original description, Godman & Salvin (1894) stated that this species “…has no near allies that we know of. As will be seen by comparison with what we have written on the arrangement of the tufts of hair on the secondaries of the males in this genus [*Opsiphanes*] … *O. Staudingeri* [sic] does not fall into any of our sections, but must stand by itself” (p 96). Stichel (1902, 1904) followed Godman & Salvin’s view by separating *O. staudingeri* into its own species group and section (Fig. 3A, Table 1), and Casagrande (1982) created a genus for this species alone (Table 1). Nonetheless, this study did not support the separation of *O. staudingeri* from other *Opoptera* species (as per Penz 2007). The conflicting placement of this species in the equally parsimonious trees in Fig. 3B and C can be attributed to its similarity in HW margin and male scent organ with *O. arsippe* (Fig. 1F–G; see tracing of characters 10, 11 and 13 in Fig. 3B). This was further strengthened by the fact that a single topology was obtained when color characters were excluded from the analysis, and that this tree had slightly higher overall estimates of support per branch (i.e., it was internally more consistent). Indeed, the exclusion of character 10 alone yielded a single tree as in Fig. 3C. It is also important to note that placing *O. staudingeri* as sister species to ((aorsa,hilaris),(arsippe,bracteolata)) implies no homoplasy regarding the shape of FW apex, or the presence of HW tails – characters that have been traditionally used to group species of *Opoptera* (e.g., Stichel 1902).

Interestingly, the HW outline of *O. staudingeri* slightly bulges below M3 (Fig. 1F, 2F), which is more similar to tail-bearing members of the aorsa-group than to the more evenly rounded wings present in species of the syme-group.

The tree proposed here can be used to examine the modifications of male scent organs within *Opoptera*. Considering the entire Brassolini, the thin HW hairpencil present in species of *Opoptera* also occurs in *Catoblepia*, *Opsiphanes* and *Blepolenis* Röber, which is likely the reason why species in these genera were grouped together in the past (e.g., Fruhstorfer 1912). In members of the latter three genera, the tip of this hairpencil usually rests over a small concavity filled by scent scales that is immediately anterior to vein Cu2 (e.g., Stichel 1909, Penz pers. obs.). *Opoptera* is the only brassoline genus in which the HW wing membrane forms a fold that encloses the scent scales adjacent to vein Cu2, for which I use the term ‘scent-pocket’. However, not all species of *Opoptera* possess a hairpencil, or a scent-pocket.

The topology in Fig. 3C suggests that the scent-pocket (character 15) arose in the ancestor of *Opoptera*, and was modified to an open concavity in *O. arsippe* (a reversal). It also implies that the thin HW hairpencil
(character 12) was independently gained twice. Males in the syme-group are uniform in having a scent-pocket plus a hairpencil, but those in the aorsa-group vary in their scent organs. Opoptera bracteolata shows the same configuration as the syme-group, and a secondary gain of a hairpencil occurs in this species. Opoptera staudingeri, O. arsippe, O. aorsa and O. hilaris possess structures collectively referred to as ‘hairbrushes’ by Stichel (e.g., 1904, 1909), but these are located in different wing cells depending on the species. In O. arsippe and O. staudingeri, hairs at the center of the HW discal cell are longer and denser than in species that possess a hairpencil, forming a broad ‘discal cell hairbrush’ (character 13). This hairbrush projects posteriorly over the edge of the discal cell towards the scent pocket in a similar way to the hairpencil. In contrast, O. aorsa and O. hilaris have two hairbrushes inside cell Cu2 that are posterior to the scent pocket, and that immediate adjacent to vein 1A+2A is markedly long (character 14). Given that the function of hairpencils is to aid in pheromone release (e.g., Vane-Wright & Boppré 2004), and the perfect fit between the scent-pocket and the thin hairpencil, it is surprising to find three distinct configurations within the aorsa-group that presumably perform the same function. Nonetheless, considering that scent organs adjacent to vein Cu2 occur in several brassoline genera, and so do the HW discal cell hairpencils, male scent organs seem to be highly homoplasious within Brassolini.

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Literature cited


Stichel, H. (1901) [A note with no title]. *Insekten-Börse*, 18(52), 413.


Appendix 1. Examined material with repository collection in parentheses. Dissected specimens are marked with an asterisk. Dissection numbers are provided, and illustrations are cross-referenced. Abbreviations: M, male; F, female; AMNH, American Museum of Natural History; MGCL, Florida Museum of Natural History, McGuire Center for Lepidoptera and Biodiversity; LACM, Natural History Museum of Los Angeles County; MPM, Milwaukee Public Museum; PJD, DeVries Collection; USNM, United States National Museum, Smithsonian Institution.

Opoptera syme
1M*, Brazil, R.J., Nova Friburgo, 22 February 1961, 01-43 Dissected by C.M.Penz, Fig. 4A, 5A; 1M*, Brésil, Etat de Sao Paolo, no date, 08-19 Dissected by C.M.Penz, Fig. 1A (MGCL); 1M, Sumaní, Guanabara [RJ], Parque da Tijuca, Brazil, August 14 1972 (MGCL)
1F, South America, no date, Fig. 2A (MGCL); 1F* Petropolis [RJ], Brazil, no date, 06-28 Dissected by C.M.Penz, Fig. 6A (USNM); 1F, [Brazil] Rio de Janeiro St., no date (USNM)

Opoptera sulcius
1M*, Pinhal [São Paulo], Brazil February 1950, 06-12 Dissected by C.M.Penz, Fig. 4B, 5B (MPM); 1M Brazil, Santa Catarina, Taió, February 1959, Fig. 1B (MPM); 1M*, Brazil, Santa Catarina, São Bento do Sul, March 10 1984 08-18 Dissected by C.M.Penz (MGCL); 1M, Brazil, Santa Catarina, Gaio (sic) [likely Taió], February 1986 (MGCL)
1F*, Santa Catarina, Brazil, February 1964, 01-44 Dissected by C.M.Penz, Fig. 2B, 6B (MPM); 1F, South Brazil, no date (MPM), 1F, Joinville [Santa Catarina], Brazil, 14 March 1964 (MGCL); 1F, São Luis do Puruná, Paraná, Brazil, 16 March 1984 (MGCL)

Opoptera fruhstorferi
1M, St. Catherines, Brazil, no date (AMNH); 1M*, South Brazil, no date, 01-60 Dissected by C.M.Penz, Fig. 4C, 5C (MPM); 1M, Taió, St. Cath., Brazil, February 1956, Fig. 1C (MPM)
1F*, Itaporanga [São Paulo, Brazil], February 1948, 06-07 Dissected by C.M.Penz, Fig. 6C (AMNH); 1F, Itaporanga [São Paulo, Brazil], March 1948 (AMNH); 1F, Santa Catarina, Brazil, 6 February 1963 (MPM); 1F, South Brazil, no date, Fig. 2C (MPM)

Opoptera aorsa
1M*, Toledo, Paraná [Brazil], November 1969, 08-17 Dissected by C.M.Penz, Fig. 1D, 4D, 5D (MPM); 1M* Espírito Santo, Brazil, no date, 08-31 Dissected by C.M.Penz (AMNH); 5M Espírito Santo, Brazil, no date, (AMNH); 1M North Paraná [Brazil], no date (AMNH); 1M Paraná, Brazil, no date (AMNH)
1F*, Nova Friburgo, R.J., Brazil, 3 March 1961, 01-42 Dissected by C.M.Penz, Fig. 2D, 6D (MPM); 1F* North Paraná [Brazil], no date, 08-30 Dissected by C.M.Penz (AMNH); 1F Espírito Santo, Brazil, no date, (AMNH)

Opoptera hilaris
1M* Río Huagra-yacu, Oriente, Ecuador 900m, 3 April 1941, 08-34 Dissected by C.M.Penz, Fig. 4E, 5E (AMNH); 1M Río Huagra-yacu, Oriente, Ecuador 900m, 12 April 1941 (AMNH); 1M Río Huagra-yacu [Ecuador] 900m, 14 April 1941; 2M Ecuador, no date (AMNH); 1M Middle Ecuador, no date Fig. 1E (AMNH); 2M Oriente Ecuador, no date (AMNH); 1M, Ecuador, Sucumbios, La Selva Biological Station, 2 August 1993 (PJD); 1M*, Peru, Puerto Maldonado, Los Amigos Biological Station, 13 February 2004, 08-20 Dissected by C.M.Penz (PJD); 1M, Chanchamayo, Peru, no date (AMNH); 1M Jepelacio, North Peru, no date (AMNH); 1M*, Bolivia, no date 01-41 Dissected by C.M.Penz; 1M*, Puraquequara, Amazonas, Brazil, 10 April-10 May 1945, 08-32 Dissected by C.M.Penz (AMNH)
1F* Ecuador, Sucumbios, La Selva Biological Station, 10 December 1997, 08-37 Dissected by C.M.Penz, Fig. 2E, 6E (PJD)

Image links for Opoptera hilaris:
http://neotropicalbutterflies.com/Site%20Revision/Pages/Nymphalidae_Pages/Brassolinae/Owl_Pages/
   Opoptera_aorsa.html (accessed October 6, 2008)

Opoptera staudeingeri
1M*, Costa Rica, Heredia, Puerto Viejo, February 1970, 01-57 Dissected by C.M.Penz, Fig. 1F, 4F, 5F (MPM)
1F*, Costa Rica, Heredia, Puerto Viejo, February 1970, 01-58 Dissected by C.M.Penz, Fig. 2F, 6F (MPM)
**Opoptera arsippe**

1M*, Peru, Pasco, Chuchurras, no date, 06-22 Dissected by C.M. Penz, Fig. 4G, 5G (MGCL); 1M Peru, Pasco, Chuchurras, no date (MGCL); 1M, Chuchurras, Peru, no date, Fig. 1G (MGCL); 1M, Peru, Huanuco, ca. 15 kms. N of Tingo Maria on Rio Huallaga, 15-22 August 1981 (MGCL); 1M, Peru, Huanuco, ca. 15 kms. N of Tingo Maria on Rio Huallaga, August 1981 (MGCL); 1M Peru, Tingo Maria, 19-24 July 1978 (LACM); 1M*, Peru, Huánuco, Tingo Maria, 860 m, December 1984, 08-29 Dissected by C.M. Penz (LACM); 1M, Peru, Huánuco, Tingo Maria, 860 m, December 1984 (LACM); 2 M, Bolivia, no date (LACM); 2 M no data (LACM); 1M, Peru, Juanjui, Iquitos, 7-19 May 1961 (MGCL); 4M, Chanchamayo, Peru, no date (AMNH)

**Opoptera bracteolata**

1M*, Bolivia, no date, 01-59 Dissected by C.M. Penz, Fig. 1H, 4H, 5H (MPM); 1M, Bolivia, Cochabamba, Chapare, Alto Palmar 110 m, December 1956 (MGCL)

**Dasyophthalma creusa**

1M*, South Brazil, no date 01-17 Dissected by C.M. Penz (MPM)

1F*, South Brazil, no date, 01-16 Dissected by C.M. Penz (MPM)

**Dasyophthalma rusina**

1M*, Brazil, Santa Catarina, 26 December 1957, 01-18 Dissected by C.M. Penz (MPM)

1F*, Brazil, Santa Catarina, São Bento do Sul, 25 January 1986, 01-19 Dissected by C.M. Penz (MPM)

**Appendix 2. Character list**

1. Eye pubescence: absent (0), present (1). Character 1 in Penz (2007).

2. FW apex: rounded (0); mildly pointed (1); angular, projected at M1 (2). Adapted from Stichel (1909). Fig. 1A, D, F.

3. Dorsal surface of wings: brown background nearly homogeneous from base to outer margin (0), basal to medial areas lighter than those closer to outer margin (1). Fig. 1A, G.

4. Dorsal FW, proximal arm of postmedial band: narrow (0), broad (1). Fig. 1A–B.

5. Dorsal FW broad proximal arm of postmedial band: reaching the edge of discal cell (0), not reaching the edge of discal cell (1). Fig. 1B–C.

6. Dorsal FW, proximal arm of postmedial band: continuous (0), broken (1). Fig. 1H.

7. Dorsal FW, proximal arm of postmedial band: yellow (0), orange (1), white (2). Fig. 1B–C.

8. Dorsal FW, distal arm of postmedial band: well developed (0), reduced (1). Fig. 1B–C.

9. Prominent HW tail at M3: absent (0), present (1). Character 7 in Penz (2007). Fig. 1E–F.

10. Undulations of HW outer margin: deep (0), shallow (1). Fig. 1C–D, F–G.

11. Dorsal HW, marginal band: continuous (0), broken at veins (1). Fig. 1B, D, F.

12. Male dorsal HW, thin hairpencil in discal cell that extends over crossvein cu1-cu2: absent (0), present (1). Fig. 1I.

13. Male dorsal HW, hairs in discal cell: sparse (0); dense, forming a broad hairbrush (1). Fig. 1K.

14. Male dorsal HW, hairs in cell Cu2: sparse (0); dense, forming a long hairbrush (1). Fig. 1J.

15. Male dorsal HW, scent organ in cell Cu1 associated with vein Cu2: absent (0); present, shallow, open depression on wing membrane (1); present, infolded ‘pocket’ on wing membrane (2). Fig. 1K–L.

16. Mid- and hindlegs, dorsal spines: long (0), short (1). Adapted from Casagrande (1982).

17. Mid- and hindlegs, color of distal edge of each segment and tarsal subsegment: similar to the color of the segment/subsegment (0); lighter, forming rings that contrast the color of the segment/subsegment (1). Character 14 in Penz (2007).

18. In lateral view, tegumen outline: flat (0), slightly raised (1), markedly raised (2). Fig. 4B, E–F.

19. In dorsal view, outline of the anterior edge of the tegumen: slightly concave (0), markedly concave (1). Fig. 5C, F.

20. In ventral view, valvae: narrowed at base (0), not narrowed at base (1). Note: Other changes associated with the narrowing of the valvae include the shape of the juxta (anterior edge concave), and the saccus (broad unsclerotized region anterior to the base of valvae). Fig. 5D.

21. Heavier sclerotization of the dorsal edge of valva: does not extend to the valva tip (0), extends just to the valva tip (1), encircles the valva tip (2). Character 26 in Penz (2007). Fig. 4A.

22. Heavily sclerotized portion of the dorsal edge of valva: with minute ribbed serrations (0), with even-shaped spines (1), with uneven-shaped spines or projections (2). Character 28 in Penz (2007). Fig. 4I.

23. Heavier sclerotization that encircles the valva tip (=sclerotized carena): fan-shaped (0); prong-shaped (1). Fig. 4A, D.

24. Fan-shaped sclerotization that encircles the valva tip (=sclerotized carena): forming a raised crest anteriorly to edge (0), not forming a raised crest anteriorly to edge (1). Fig. 4A, I–K.
25. Fan-shaped sclerotization that encircles the valva tip (=sclerotized carena): straight (0), twisted (1). Fig. 4A, I–K.
26. Setose portion of valva tip (immediately proximal to sclerotized carena): bulbous, narrow (0), flattened, palmate (1).
   Fig. 4A, D, F.
27. In ventrolateral view, palmate valva tip: ventral (inner) edge strongly projected (0); ventral (inner) edge weakly
   projected (1). Note: Fig. 4 shows a lateral view that lessens the height of the projection. Fig. 4A–C.
28. Lateral uncus wings, as they expand posteriorly into uncus process: vanishing gradually (0); merging to form a
   single, prominent dorsal keel (1); forming two dorsolateral keels (2). Character 39 in Penz (2007). Fig. 5A, D, H.
29. Gnathos, outer portion: flat (0), raised to form a keel (1). Fig. 5I–J.
30. Gnathos, anterior expansion of proximal region: absent (0), present (1). Character 49 in Penz (2007). Fig. 4A.
31. Gnathos, edge of distal region: smooth (0), jagged (1). Fig. 5J.
32. Diaphragm, region around phallus that bears setae: membranous (0), with partly sclerotized patches (1). Character 25
   in Penz (2008). Fig. 5G.
33. Anterior section of sterigma: continuous (0), interrupted by a gap at midpoint (1), absent (2). Character 65 in Penz
   (2007).
34. Creased, mildly sclerotized swelling associated with the posterior edge of sterigma: absent (0), present (1). Fig. 6A,
   D–E.
35. Projected ‘flaps’ on lateral, posterior edges of sterigma: absent (0), present (1). Fig. 6D–F.
36. Posterior edge of sterigma: projected at midline (0), retracted at midline (1). Fig. 6B, E.
37. Intersegmental sac between seventh abdominal sternite and sterigma: rounded (0), with two lateral pockets (1).
   Character 59 in Penz (2007). Fig. 6A, F.

Appendix 3. Character matrix

| creusa  | 1000?10000 ?000001101 11????0?000 0020000 |
| rusina  | 1000?10000 ?000001101 11????0?000 0020000 |
| syme    | 0010?01000 1100200101 2001010001 0000000 |
| sulcius | 0011101000 1100200101 2001010001 0000000 |
| fruhstorferi | 0001002100 1100200101 2001011000 0000000 |
| stauningeri | 0100?01101 0010211011 200010?010 0000101 |
| arsippe | 0200?01111 0010101211 200010?210 110???? |
| bracteolata | 0200?11110 1100201211 200010?210 110???? |
| aorsa   | 0200?01110 1001201200 201???2000 0001111 |
| hilaris | 0200?01110 1001201210 201???2000 0001111 |