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Phylogeny of *Dasyophthalma* butterflies (Lepidoptera, Nymphalidae, Brassolini)

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Abstract. This study provides a species-level phylogeny and morphological characterization for the Neotropical brassoline genus *Dasyophthalma* Westwood, 1851. A revised generic definition is given, and two species groups are proposed. Diagnoses and illustrations of habitus and genitalia are provided for all species. Wing color, male scent organs, and male and female genitalic morphology are characterized and discussed.

Key words. *rusina*, *geraensis*, *creusa*, *vertebralis*, genitalia

Introduction

Butterflies in the genus *Dasyophthalma* Westwood, 1851 are conspicuous members of the Atlantic Forest fauna of Brazil. Brassolines are usually active at dawn and dusk, flying occasionally during the daytime (e.g., Fruhstorfer 1912). Nonetheless, *Dasyophthalma* butterflies are active during the day, especially in the afternoon hours (Brown 1992, Casagrande and Mielke 2000, 2003), and species that have iridescent blue patches on the wings are highly visible (pers. obs.). According to Casagrande (2004), *Dasyophthalma* includes four species: *D. rusina* (Godart, 1824) type species of the genus, *D. geraensis* Rebel, 1922, *D. creusa* (Hübner, 1821) and *D. vertebralis* Butler, 1869. Together, the conspicuous transverse band across the center of the wings, the oval forewing shape of *D. creusa* and *D. vertebralis*, and the pubescent eyes, grant these butterflies a distinctive appearance (Fig. 1). Owing to these unique characters, it is understandable that early workers did not associate *Dasyophthalma* with any particular brassoline genus (e.g., Stichel 1904, 1909; Fruhstorfer 1912). In fact, Miller (1968) created the *Dasyophthalma*-series for this genus alone.

A phylogenetic analysis by Penz (2007) examined two species of *Dasyophthalma* and supported the monophyly of the genus. That study suggested that *Dasyophthalma* may be closely related to *Opoptera* Aurivillius, 1882 based on one character: the distal edges of mid- and hind-leg segments and tarsomeres are light-colored, forming rings that contrast the dark brown overall color of the legs (character 14:1 in Penz 2007; Fig. 1L). Among all brassolines sampled, this character was present only in *Dasyophthalma* and *Opoptera*. However, it is absent in the syme-group of *Opoptera* (Penz 2007, 2009). Furthermore, when this character is excluded from the matrix, *Dasyophthalma* groups either with *Opoptera*, or it appears as sister genus to *Opoptera* + (Caligo-clade + Opsiphanes-clade) (Penz 2007). Therefore, future studies should re-examine the relationships between *Dasyophthalma* and *Opoptera* using additional characters.

Perhaps due to the small size of the genus, early catalogs did not contain an infra-generic classification for *Dasyophthalma* (e.g., Stichel 1909, 1932; Fruhstorfer 1912). Wing coloration conceivably suggests two groups: *D. rusina* and *D. geraensis* have blue iridescence at the postmedial areas of both wings, while *D. creusa* and *D. vertebralis* do not. This study examines new characters in addition to those considered by Penz (2007) to assess relationships of all species of *Dasyophthalma*, and determine whether two species groups can be supported within this genus.

Material and methods

Species sampled. Appendix 1 provides information on the materials used here (species, specimen locality data). The ingroup included the four recognized *Dasyophthalma* species in accordance with the

taxonomic checklist by Casagrande (2004). The Species Identification section includes a diagnosis for each species. Geographical distributions are estimated based on published records and collection specimens.

Dynastor darius (Fabricius, 1775) and *D. napoleon* Doubleday, 1849 were selected as outgroups based on Penz (2007). The genitalic morphology and wing color pattern of *Dynastor* Doubleday, 1849 better represent the brassoline groundplan than those of *Opoptera*, the putative sister genus of *Dasyophthalma*. Therefore, the noticeably divergent brassoline clade *Opoptera* was not included in this analysis.

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 21 characters and associated character matrix. The analysis included both structural and wing coloration characters, as was done in Penz (2008). Terminology for genitalia 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 *Dasyophthalma*. All 21 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 excluding uninformative characters. MacClade 4 (Maddison and Maddison 2000) was used for tracing character changes and tree editing. Terms used to indicate character status in Fig. 2 follow MacClade 4.

Results

Parsimony analysis yielded a single most parsimonious tree with 21 steps (CI excluding uninformative characters=1, RI=1; Fig. 2). This tree indicates that *Dasyophthalma* is monophyletic and includes two species groups, the rusina- and creusa-groups. *Dasyophthalma* species groups are distinctive and completely consistent in their character change combinations, including differences in wing scale morphology. Some of the character changes in Fig. 2 appear as 'ambiguous' optimizations because tree topology is completely symmetrical, with the outgroup and two species groups showing different characters states. Character changes that support each node are indicated in Fig. 2, and illustrated in Fig. 1 and 3. Below I characterize the genus *Dasyophthalma* and its species groups based on these characters, plus others that were not included in the analysis because the subtle or continuous variation was difficult to code (e.g., overall FW shape).

GENUS *Dasyophthalma* Westwood, 1851

Dasyophthalma species are medium size butterflies with slight differences between males and females. Eyes heavily pubescent in both sexes (character 1:1, Fig. 1H). General color of body scales and setae dark brown dorsally and ventrally. Mid- and hind legs dark brown; segments and tarsal subsegments with light-colored distal edges forming rings that contrast the dark color of the legs (Fig. 1I, character 14:1 in Penz 2007). In males, FW anal margin bowed and tornus slightly (*D. rusina*, *D. geraensis*) or strongly truncated, producing a nearly oval-shaped FW outline (*D. creusa*, *D. vertebralis*). Dorsal wing background color dark brown. Basal to submedial areas of both wings opaque (*D. creusa*, *D. vertebralis*) or with strong blue iridescence (*D. rusina*, *D. geraensis*; character 3, Fig. 1C, E). Well-developed transverse postmedial bands running across both wings (weak on the HW of *D. creusa*), varying in color from white, pale yellow, dark yellow, or orange. On the FW, the posterior portion of this band may extend towards the submedial area, reaching the anal margin near the wing base (*D. creusa*, *D. vertebralis*; character 5:1, Fig. 1A). In females, the proximal arm of the postmedial band is visible, such that the band is Y-shaped (a clear pattern in *D. rusina*, Fig. 1F). Ventral wing background with prominent ripple-pattern. Ventral HW with large eyespots in cells Sc+R1 and Cu1, and sometimes also in cell M1 (character 15, Fig. 1A, E).

Males with a dorsal androconial patch at the HW Rs-M1 fork (character 13, Fig. 1C), and a hairpencil at base of HW discal cell that projects over the androconial patch (character 11, Fig. 1C). This hairpencil being pale yellow (*D. creusa*, *D. vertebralis*) or brown (*D. rusina*, *D. geraensis*; character 12, Fig. 1C, G).

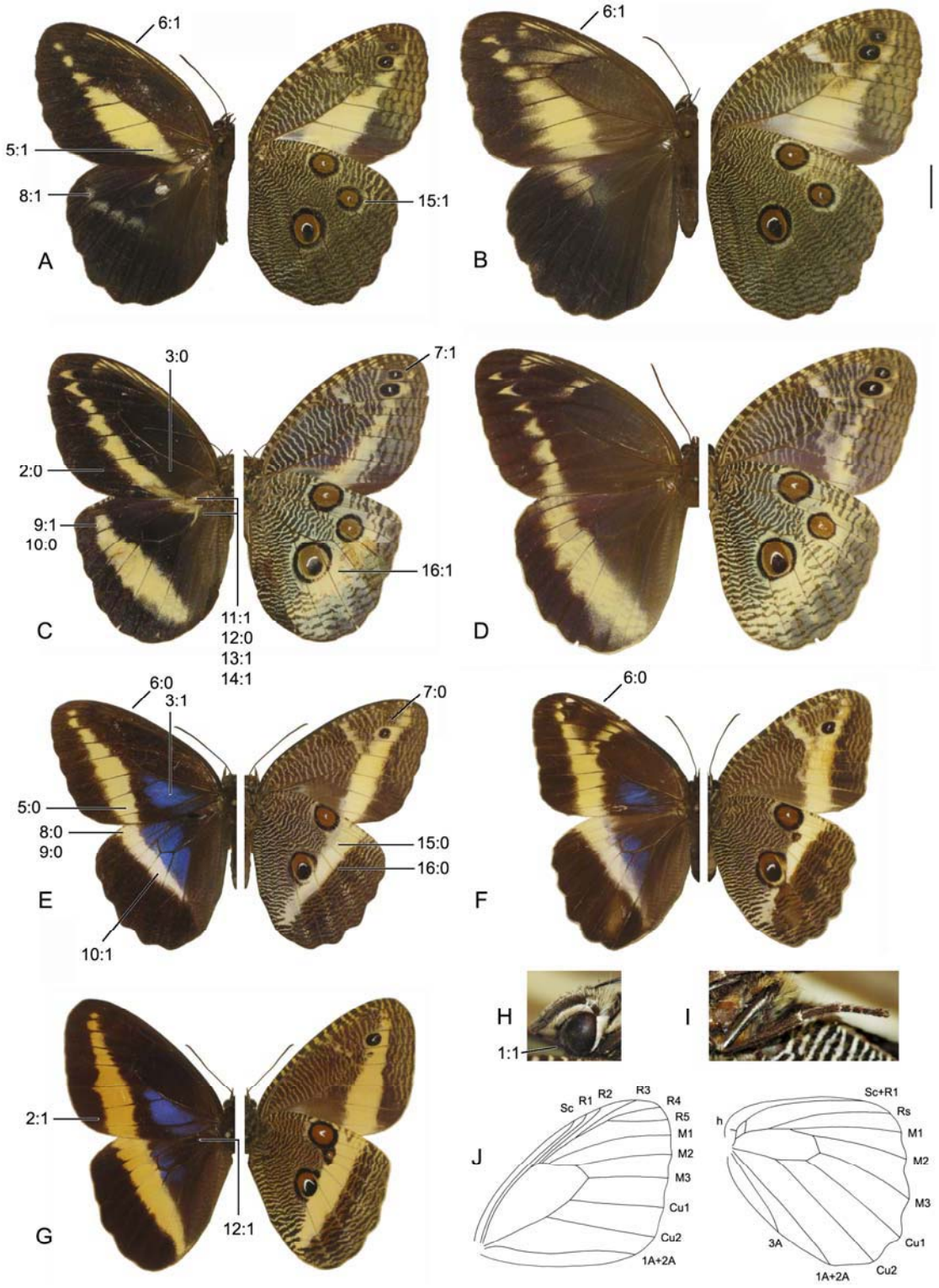

Figure 1. *Dasyophthalma* adults. Habitus with dorsal side on the left, ventral side on the right. Scale bar next to B = 1cm. **A)** *D. creusa* male, Brazil, Santa Catarina, São Bento do Sul. **B)** *D. creusa* female, Brazil, Santa Catarina, São Bento do Sul. **C)** *D. verebralis* male, Brazil, Espírito Santo. **D)** *D. vertebralis* female, [Brazil] East Amazonas. **E)** *D. rusina* male, South Brazil. **F)** *D. rusina* female, South Brazil. **G)** *D. geraensis* male, [Brazil] Minas Gerais. **H)** Detail of the head of *D. rusina*. **I)** Detail of the hindleg of *D. rusina*. **J)** Venation pattern of *D. rusina*, vein thickness is not shown.

The presence of the androconial patch at the fork of HW Rs-M1 is associated with the bowed FW vein 1A+2A, and also the shapes of the FW anal margin and tornus.

Male valva elongate with a long dorsal row of large spines. Overall valva shape is diagnostic of the genus; proximal half broad, straight, relatively flat in ventral view, while the distal half is conspicuously narrow, cylindrical, forming a broad and evenly rounded arch (characters 17 and 18, Fig. 3E, G). Female sterigma well developed posteriorly, but lacking anterior sclerotization. Corpus bursae lacking signa. Intersegmental sac between sternite 7 and sterigma with conspicuous, broken ribs (character 19, Fig. 3F), diagnostic of the genus but similar to that seen in *Selenophanes* Staudinger, 1887.

Species Groups

creusa-group

Dasyophthalma creusa and *D. vertebralis* form a monophyletic group supported by the following character states (Fig. 2): male dorsal FW postmedial band reaches cell 3A near wing base (character 5:1, Fig. 1A); dorsal FW yellow markings across costal margin present in both sexes (6:1, Fig. 1A-B); presence of an eyespot in ventral FW cell R5 (7:1; Fig. 1C); male dorsal HW postmedial band fading towards the costal margin (9:1, Fig. 1C); dorsal HW hairpencil at base of discal cell pale yellow (12:0, Fig. 1C); androconial patch at the fork of HW veins Rs-M1 pale yellow (14:0, Fig. 1C); posterior portion of sterigma extended towards midline nearly enclosing the ostium bursae (20:0, Fig. 3B).

rusina-group

Dasyophthalma rusina (type-species of the genus) and *D. geraensis* form a monophyletic group supported by the following character states (Fig. 2): presence of dorsal FW blue iridescence below discal cell (character 3:1, Fig. 1E), and also at the submedial area of the HW; dorsal FW yellow scales located inside cell R5 with bifid edge (4:0); absence of dorsal FW yellow markings across costal margin in males (6:0, Fig. 1E; but present in some individuals of *D. rusina*); dorsal HW hairpencil at base of discal cell brown (12:1, Fig. 1G); androconial patch at the fork of HW veins Rs-M1 brown (14:1); ventral HW postmedial band with well-defined edges (16:0, Fig. 1E); presence of a small midline extension on the posterior portion of sterigma (21:1, Fig. 1F; but note that *D. geraensis* females were not available for examination).

Species Identification

Below I provide a diagnosis for currently recognized *Dasyophthalma* species, following the Brassolini checklist by Casagrande (2004). References to the original descriptions of all taxa listed here can be found in Lamas et al. (1995).

Dasyophthalma creusa (Hübner, 1821)

(Fig. 1A-B, 3A-B)

Type locality. Brazil.

Diagnosis. Dorsal FW postmedial band pale yellow, broadening in cells Cu1 and Cu2, reaching the edge of discal cell inside cell Cu1. Dorsal HW postmedial band faded, reduced in both sexes. Ventral HW with homogeneous ripple-pattern, and a pale yellow halo around eyespots.

Distribution. Brazil, from Bahia to Rio Grande do Sul (D'Abrera 1987, Brown 1992, Brown and Freitas 2000, Testón and Corseuil 2002, Iserhard and Romanowski 2004, Uehara-Prado et al. 2004).

Remarks. The fourth and fifth instar larvae and pupa of *D. creusa creusa* were described by Casagrande and Mielke (2003), reared on the palm *Geonoma schottiana* (Arecaeae). Females were reported to oviposit on "taquara" (Gramineae) and "palm tree" by Hoffmann (1936), and larvae were also found on *Astrocaryum aculeatum* / *vulgare*? (Arecaceae) (Schmith and Hoffmann 1931) and *Bactris* sp. (Arecaceae) (Brown 1992).

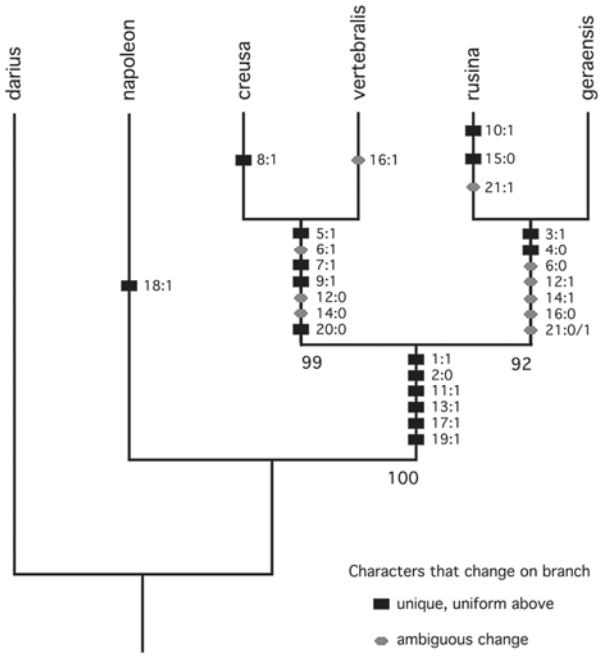

Figure 2. Most parsimonious tree from the analysis of 21 morphological characters. Character numbers correspond to list in Appendix 2. Legend for character status follows MacClade 4. Ambiguous changes were traced given that they represent some important characters that define species-groups. Gray numbers below branches are jackknife values.

Casagrande (2004) listed two subspecies; nominal *D. c. creusa* from 'Brazil' and *D. c. baronesa* Stichel, 1904 from Brazil, Espírito Santo.

***Dasyophthalma vertebralis* Butler, 1869**
(Fig. 1C-D, 3C-D)

Type locality. Brazil.

Diagnosis. Dorsal FW postmedial band pale yellow, narrow, not reaching discal cell inside cell Cu1. Dorsal HW postmedial band well developed. Ventral HW with a broad, diffuse, pale yellow postmedial band across entire wing that masks the ripple-pattern.

Distribution. Brazil, Minas Gerais, Espírito Santo. This species is known from Santa Leopoldina (Espírito Santo) and from Alto Rio Mucuri (Espírito Santo) near Teófilo Otoni (Minas Gerais) (A.V.L. Freitas pers. comm.). The records "Bahia ?, Pará" in Stichel (1932) are probably erroneous (see also Appendix 1).

Remarks. Immature stages unknown. This species mostly inhabits the interior forests of Minas Gerais state (A.V.L. Freitas pers. comm.) and it is currently listed as critically endangered in the Lista Oficial da Fauna Brasileira ameaçada de extinção (http://www.biodiversitas.org.br/f_ameaca/p_fauna.asp, consulted on 26 January, 2009).

***Dasyophthalma rusina* (Godart, 1824)**
(Fig. 1E-F, H-J, 3E-F)
Type species of the genus by original designation.

Type locality. Brazil.

Diagnosis. Transverse postmedial bands have different colors on FW and HW. FW postmedial band pale or darker yellow. HW band completely or mostly white, extended to anal margin or fading at cell Cu2. HW blue iridescence more conspicuous in males than in females. Male genitalia indistinguishable from *D. geraensis*. In females only, dorsal FW postmedial band with a proximal branch, ventral HW with a small eyespot in cell M1, and ventral HW postmedial band interrupted by eyespot in cell Cu1.

Distribution. Brazil, from Bahia to Santa Catarina (D'Abrera 1987, Brown 1992, Brown and Freitas 2000, Uehara-Prado et al. 2004).

Remarks. d'Araújo e Silva et al. (1968) reported immature stages of *D. rusina* on "palmito" (*Euterpe edulis*, Arecaceae) and *Bambusa* sp. (Gramineae), and Brown (1992) found it on "bamboos" and "palms", but a larval description was not provided by these authors. The fifth instar larva of *D. rusina rusina* was found to feed on the palm *Geonoma schottiana* (Arecaeae) , and both larva and pupa were described by Casagrande and Mielke (2000). Casagrande (2004) listed three subspecies of *D. rusina*; nominal *D. r. rusina* from 'Brazil', *D. r. delanira* Hewitson, 1862 from 'Brazil', and *D. r. principesa* Stichel, 1904 from Espírito Santo, Brazil. In the Lista Oficial da Fauna Brasileira ameaçada de extinção, *D. delanira* is considered a separate species from *D. rusina*, and it is listed as critically endangered (http://www.biodiversitas.org.br/f_ameaca/p_fauna.asp, consulted on 26 January, 2009). This butterfly inhabits high altitude areas (~1200 m) in the vicinities of Nova Friburgo, Rio de Janeiro State, and its taxonomic status should be verified.

***Dasyophthalma geraensis* Rebel, 1922**
(Fig. 1G, 3G)

Type locality. Brazil, Minas Gerais, Passa Quatro.

Diagnosis. Transverse postmedial bands of same color on FW and HW, both homogeneously yellow. FW and HW blue iridescence patches smaller than in *D. rusina*. HW medial band slightly broader than in *D. rusina* and clearly extended to the anal margin. Male genitalia indistinguishable from *D. rusina*.

Distribution. Brazil, Minas Gerais (Mantiqueira mountain range), Espírito Santo, Rio de Janeiro, São Paulo (Casagrande 2004, A.V.L. Freitas pers. comm., Appendix 1).

Remarks. d'Araújo e Silva (1968) reported "uricana" (*Bactris tormentosa*, Arecaceae) as host plant. This taxon was originally described as a subspecies of *D. rusina* by Rebel (1922), who considered it a 'local form' worthy of a name. The male genitalia are identical to those of *D. rusina*. Females were not available for examination in the collections that were used in this study (Appendix 1). This species higher elevation forests (~1200 m) and it is currently listed as endangered in the Lista Oficial da Fauna Brasileira ameaçada de extinção (http://www.biodiversitas.org.br/f_ameaca/p_fauna.asp, consulted on 26 January, 2009).

Morphology of Male Genitalia

Species of *Dasyophthalma* are remarkably homogeneous regarding their male genitalia, with differences being mostly allometric (Fig. 3). Due to this similarity, only two characters could be scored for phylogenetic analysis (Appendix 2). The tegumen is dome-shaped, and approximately rectangular in dorsal view. In some, but not all specimens of *D. rusina*, *D. geraensis* and *D. vertebralis*, a small 'fenestrula' is visible near the posterior portion of the tegumen, and may or may not be covered by scales that usually detach during KOH treatment for dissection. The fenestrula and scales combination suggests a scent producing function. In lateral view, the uncus is evenly arched or angular, with a sharp and strongly sclerotized tip. The gnathos is a simple, unadorned tube narrowing distally to a point. The *Dasyophthalma* valva has a dorsal row of spines, which are rather large in all species, and vary in number between individuals of the same species. The shape is unique within Brassolini; the proximal half is broad, straight and relatively flat in ventral view, while the distal half is narrow and cylindrical, forming an evenly rounded arch. The broad proximal half bears both setae and scales that usually detach during KOH

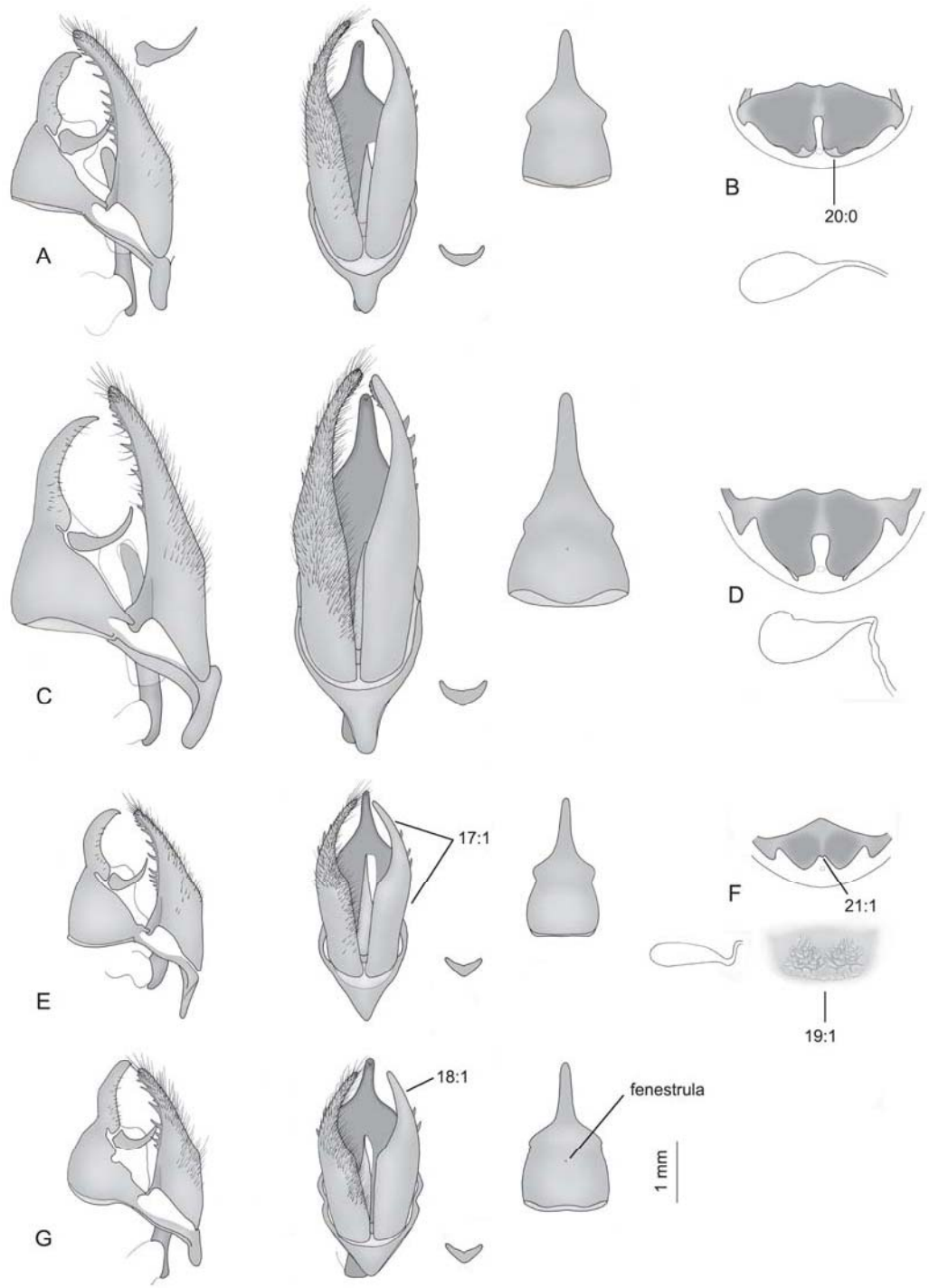

Figure 3. *Dasyophthalma* male genitalia in lateral and ventral views (setae omitted from right side of figure), with detail of the juxta and tegumen + uncus in dorsal view, plus female sterigma and corpus bursae. The line below sterigma represents the shape of the intersegmental sac. Scale bar next to G = 1mm. **A)** *D. creusa* male, South Brazil, 01-17 dissected by C.M.Penz. **B)** *D. creusa* female, South Brazil, 01-16 dissected by C.M.Penz. **C)** *D. vertebralis* male, Brazil, Espírito Santo, 07-170 dissected by C.M.Penz. **D)** *D. vertebralis* female, [Brazil] East Amazonas, no date, 07-171 dissected by C.M.Penz. **E)** *D. rusina* male, Brazil, Santa Catarina, 01-18 dissected by C.M.Penz. **F)** *D. rusina* female (with detail of the intersegmental sac below sterigma), Brazil, Santa Catarina, São Bento do Sul, 01-19 dissected by C.M.Penz. **G)** *D. geraensis* male, Brazil, Minas Gerais, 07-169 dissected by C.M.Penz.

treatment. Members of the rusina-group have the shortest valva within the genus, while *D. vertebralis* has the longest. The juxta has notable apodemes at the dorsolateral edges that appear externally as 'dimples'. The distal opening of the phallus is located dorsolaterally, which is the most common pattern within Brassolini.

Morphology of Female Genitalia

Female genitalia are relatively simple in *Dasyophthalma*, yielding only three characters for phylogenetic analysis (Fig. 3). The corpus bursae is elongated and devoid of a signum in all species. The intersegmental sac between sternite 7 and sterigma has broken ribs. The sterigma lacks sclerotization anteriorly, consisting of a plate located posteriorly to the ostium bursae. In *D. rusina* the anterior edge of this plate is less developed than in *D. creusa* and *D. vertebralis* (compare Fig. 3F and B, D). In the latter two species the inner edges of the sterigma are extended towards the midline nearly enclosing the ostium bursae, and form two projected points (Fig. 3B, D).

Discussion

This study identified two species groups within *Dasyophthalma* (Fig. 2). Although these groups could be intuitively inferred based on the presence (rusina-group) or absence of blue iridescence (creusa-group), several other color and structural characters support the topology in Fig. 2. For example, brassolines share wing pattern elements with basal satyrines, such as the forewing postmedial band (Penz pers. obs., Fig. 1; see Nijhout 1991: 52-53). Males of *D. creusa* and *D. vertebralis* show a displacement of this band towards the base of the wing (Fig. 1A, C), which is also partially the case for female *D. creusa*. In males of both these species the posterior portion of the forewing band is aligned with the hindwing hairpencil that has the same pale yellow color. This shows a correspondence between two color characters from separate wings, and also suggests that the FW band plays a role in male visual sexual displays. Note that among all brassolines the basal displacement of the postmedial band in male *D. creusa* and *D. vertebralis* is unique to these species.

Descriptions and color images of fifth instar larvae and pupae of *D. rusina* and *D. creusa* were provided by Casagrande and Mielke (2000, 2003). Although the fifth instar larvae of both species have a similar overall appearance, that of *D. creusa* has a wider, more conspicuous lemon-yellow dorsal line adorned with a mosaic of black and white dots between abdominal segments 3 and 4, and posterior edge of segments 5-7. In *D. rusina*, the dorsal lemon-yellow line is thinner and a simple white marking is present between abdominal segments 3 and 4. In both species the larval head is rectangular with three pairs of red scoli, the dorsal and laterodorsal pairs being more visible and clearly projected posteriorly over the thorax. The shape of the pupa is quite different between these species. While *D. creusa* has a rounded, unadorned pupa, that of *D. rusina* has projected wing pads with conspicuous white crescent marks, and a small thoracic keel. If and when immature stages of *D. geraensis* and *D. vertebralis* become available, it would be interesting to verify if larval morphology and coloration, and pupa shape are consistent with the species-groups identified here.

Current distribution records suggest that the genus *Dasyophthalma* occurs primarily in the Brazilian Atlantic forest. The dry areas of central Cerrado seem to be unsuitable for these butterflies, despite the fact that several other brassoline genera can be found in that biome (e.g., species of *Narope* Doubleday, 1849, *Brassolis* Fabricius, 1807, *Dynastor* Doubleday, 1849, *Blepolenis* Röber, 1906, *Opsiphanes* Doubleday, 1849, *Catoblepia* Stichel, 1901, *Eryphanis* Boisduval, 1870 and *Caligo* Hübner, 1819 have been recorded near Brasília, DF; Pinheiro and Emery 2006). Individual species distributions are worthy of discussion (see distribution records above). *Dasyophthalma rusina* and *D. creusa* are widespread in the Atlantic forest and reach southern latitudes, but their respective sister species *D. geraensis* and *D. vertebralis* have a narrower distribution. *Dasyophthalma geraensis* ranges from Minas Gerais to Espírito Santo and Rio de Janeiro States, while *D. vertebralis* has only been found in Minas Gerais and Espírito Santo. Both *D. geraensis* and *D. vertebralis* inhabit areas along Mantiqueira mountain range, while *D. rusina* and *D. creusa* seem to flourish in more coastal areas along the Serra do Mar.

A parallel of phenotypic divergence is observed for some species of *Dasyophthalma* and the closely related *Opoptera*. Although *D. rusina* and *D. geraensis* can be distinguished by wing color differences, male genitalia are identical for these two species. A similar situation is found between *Opoptera syme* (Hübner, 1821) and *O. sulcius* (Staudinger, 1887). While males and females can be easily distinguished by wing pattern, male genitalia of *O. syme* and *O. sulcius* are nearly identical, and those of females show only slight differences (Penz 2009). Thus, when comparing the sister pairs *rusina* + *geraensis* and *syme* + *sulcius*, color divergence is more noticeable than structural differences, suggesting recent divergence. Considering the distribution patterns for *D. geraensis* and *D. rusina* (above), plus those of *O. syme* and *O. sulcius* (they overlap in São Paulo), it would be interesting to investigate whether the northern and southern halves of the Atlantic forest constitute sister biogeographical units, as *Dasyophthalma* and *Opoptera* seem to indicate.

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Appendix 1. Examined material with repository collection in parentheses. Dissected specimens are marked with an asterisk. Dissection numbers are provided, and illustrations are cross-referenced. Abbreviations: M, male; F, female; AMNH, American Museum of Natural History; MGCL, Florida Museum of Natural History, McGuire Center for Research on Lepidoptera; MPM, Milwaukee Public Museum; MZUSP, Museu de Zoologia da Universidade de São Paulo.

Dasyophthalma creusa

1 M*, South Brazil, no date, 01-16 dissected by C.M.Penz (MPM) Fig. 3A; 1 M, Brazil, Santa Catarina, São Bento do Sul, 13 February 1966 (MPM) Fig. 1A; 1 M, Brazil, Santa Catarina, São Bento do Sul, 10 February (MGCL); 1 M, Brazil, Santa Catarina, São Bento do Sul, 10 February 1984, Fig. 1A (MGCL); 1 M, Brazil, Rio de Janeiro, December 1943 (MGCL); 1 M*, Brazil, Guanabara [Rio de Janeiro], Jacarepaguá, 20 February 1971, 08-45 dissected by C.M.Penz (MGCL).

1 F*, South Brazil, no date, 01-17 dissected by C.M.Penz (MPM) Fig. 3B; 1 F, Brazil, Santa Catarina, São Bento do Sul, 13 February 1966, Fig. 1B (MPM).

Dasyophthalma vertebralis

1 M*, Brazil, Espírito Santo, no date, 07-170 dissected by C.M.Penz, Fig. 1C, 3C (MZUSP).

1 F*, [Brazil] East Amazonas [likely an erroneous location], no date, 07-171 dissected by C.M.Penz, Fig. 1D, 3D (MZUSP).

Dasyophthalma rusina

1 M*, Brazil, Santa Catarina 26 December 1957, 01-18 dissected by C.M.Penz (MPM) Fig. 3E; 1 M, South Brazil, no date (MPM) Fig. 1E; 1 M* Brazil, Espírito Santo, Santa Teresa, 4-7 March 1973, 08-46 dissected by C.M.Penz (MGCL); 1 M, Brazil, Rio de Janeiro, Petrópolis, Independência, 900 m, 16 January 1972 (MGCL); 1 M, Brazil, Rio de Janeiro, Petrópolis, 900 m, 9-12 January 1971 (MGCL); 1 M*, Brazil, Minas Gerais, Parque Rio Doce, 26 March 1972, 08-36 dissected by C.M.Penz (MGCL); 2 M, Brazil, Santa Catarina, São Bento do Sul, 10 March 1984 (MGCL); 1 M, Brazil, Santa Catarina, 1 January 1968 (MGCL); 1 M [Brazil] Sta. Catharina, no date (AMNH).

1 F*, Brazil, Santa Catarina, São Bento do Sul, 25 January 1966, 01-19 dissected by C.M.Penz (MPM) Fig. 3F; 1 F, South Brazil, no date (MPM). Fig. 1F.

Dasyophthalma geraensis

1 M*, Brazil, Minas Gerais 1500 m, no date, 07-169 dissected by C.M.Penz (MZUSP) Fig. 1G, 3G; 1 M*, [Brazil] Minas Gerais , no date, 08-43 dissected by C.M.Penz (AMNH); 1 M Brazil, Espírito Santo, Castello, 21 February 1922 (MGCL); 1 M*, Brazil, Rio de Janeiro, Parque Nacional do Itatiaia, 1000-2000 m, 13-14 January 1973, 08-35 dissected by C.M.Penz (MGCL); 1 M, Brazil, Brazil, Rio de Janeiro, Itatiaia, 21 March 1972 (MGCL).

Dynastor darius

1 M*, Brazil, São Paulo, February 1951, 07-168 dissected by C.M. Penz (MZUSP); 1 M*, Paraguay, 1973, 01-14 dissected by C.M.Penz (MPM); 1 M*, Nicaragua, Managua dept. 7.5 km S Managua, 1858, 07-15 dissected by I.Garzón (MPM).

1 F, Brazil, São Paulo, São Paulo, February 1955 (MZUSP), 1 F*, Brazil, Paraná, Ponta Grossa, November 1947, 01-15 dissected by C.M.Penz (MPM); 1 F, Brazil, Santa Catarina, "Mansa Humbolt" [sic] (MPM).

Dynastor napoleon

1 M*, Brazil, Santa Catarina, November 1954, 06-08 dissected by C.M.Penz (MPM); 1 M*, Brazil, Santa Catarina, September 1964, 06-09 dissected by C.M.Penz (MPM); 1 m, Brazil, Santa Catarina, 1956 (MGCL).

1 F*, Brazil, Rio de Janeiro, 1920, 07-09 dissected by I.Garzón (MPM); 1 F*, no data, 07-10 dissected by I.Garzón (MGCL).

Appendix 2. Character list.

1. Eye pubescence: absent (0), present (1). Fig. 1H. Character 1 in Penz (2007).
2. Male FW anal margin: strongly bowed, distance between veins Cu2 and 1A+2A conspicuously decreasing toward distal margin (0), mildly bowed, distance between veins Cu2 and 1A+2A nearly homogeneous from medial area to distal margin (1). Fig. 1C, G.
3. Dorsal FW blue iridescence below discal cell: absent (0), present (1). Fig. 1C, E.
4. Edge of dorsal FW yellow scales located inside cell R5: bifid (0), trifid (1).
5. Male dorsal FW postmedial band reaching cell 3A: near tornus (0), near wing base (1). Note: Fig. 1 shows that females have a different pattern than males. See Discussion for details. Fig. 1A, E.
6. Dorsal FW yellow markings across costal margin: absent in males, present in females (0), present in both sexes (1). Fig. 1A-B, E-F.
7. Ventral FW eyespot in cell R5: absent (0), present (1). Fig. 1C, E.
8. Dorsal HW medial band: well-developed (0), reduced (1). Fig. 1A, E.
9. Male dorsal HW medial band: fully developed up to the costal margin (0), fading toward the costal margin (1). Fig. 1E.
10. Dorsal HW medial band: same color as dorsal FW medial band (0), lighter color than dorsal FW medial band (1). Fig. 1C, E.
11. Dorsal HW hairpencil at base of discal cell: absent (0), present (1). Fig. 1C.
12. Color of the dorsal HW hairpencil at base of discal cell: pale-yellow (0), brown (1). Fig. 1C, G.
13. Dorsal HW androconial patch at the Rs-M1 fork: absent (0), present (1). Fig. 1C.
14. Color of the dorsal HW androconial patch at the Rs-M1 fork: pale-yellow (0), brown (1). Fig. 1C.
15. Ventral HW eyespot in cell M1: absent (0), present (1). Fig. 1A, E.
16. Ventral HW postmedial band: edges well defined (0); edges diffuse, interspersed by ripple-pattern (1). Fig. 1C, E.
17. In ventral view, distal half of valva: gradually decreasing in width as compared to proximal half (0), strongly decreasing in width as compared to proximal half (1). Fig. 3E.
18. In ventral view, distal portion of valva: strongly arched (0), moderately arched (1). Fig. 3G.
19. Anterior ribs of the intersegmental sac between sternite 7 and sterigma: continuous (0), broken (1). Character 62 in Penz (2007). Fig. 3F.
20. Posterior portion of sterigma: extended towards midline nearly enclosing the ostium bursae (0), further away from midline, not enclosing the ostium bursae (1). Fig. 3B.
21. Posterior portion of sterigma, small midline extension: absent (0), present (1). Fig. 3F.

Appendix 3. Character matrix.

			1		2 2
			0		0 1
Dynastor darius	01010	?	0?0?	0?0?1?0001	0
Dynastor napoleon	01010	?	0???	0?0?1?0101	0
Dasyophthalma rusina	10100	0&1	0001	1111001011	1
Dasyophthalma geraensis	10100	0	0000	111110?0??	?
Dasyophthalma creusa	10011	1	1110	10101?1010	0
Dasyophthalma vertebralis	10011	1	1010	1010111010	0