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PHYLOGENETIC SIGNAL OF SUBSETS OF MORPHOLOGICAL CHARACTERS: A CASE STUDY IN THE GENUS *ERYTHEMIS* (ANISOPTERA: LIBELLULIDAE)

Señal filogenética de subgrupos de caracteres morfológicos: un estudio de caso en el género *Ertyhemis* (Anisoptera: Libellulidae)

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ABSTRACT
Erythemis Hagen, 1861 shows a considerable variation in genitalic characters, body coloration and wing venation. Since it is known that these traits are affected by different kinds of selection that probably blur their phylogenetic signal, we chose the genus *Erythemis* as a model taxon to analyze and compare the phylogenetic signal of these and other morphologic characters. A cladistic analysis was performed using ten species of the genus plus another seventeen species of Libellulidae as outgroup. Characters were defined following standard criteria and were managed using the software DELTA. Tree search was performed with the software NONA. Partitioned and combined analyses were conducted. Character tracking of characters with ri=100 was used to identify synapomorphies. In agreement with the literature, color characters provided strong phylogenetic signal, meanwhile, genitalia characters offered no synapomorphies. We did not find any character that could support the monophyly of *Erythemis*. The only clade that has strong support from the morphologic set of characters is (*E. vesiculosa*, (*E. simplicicollis, E. collocata*)). Contrary to the results found in other Odonata, wing characters offered synapomorphies for some *Erythemis* clades.

Key words. Odonata, dragonfly, phylogenetic signal, male genitalia, body coloration.

RESUMEN
Erythemis muestra una considerable variación en caracteres de genitalia, coloración del cuerpo y venación alar. Estos caracteres están afectados por diferentes tipos de selección, lo que puede desdibujar su señal filogenética, por lo que nosotros elegimos el género *Erythemis* como taxón modelo para analizar y comparar la señal filogenética

de éstos y otros caracteres morfológicos. Un análisis cladístico se realizó con las diez especies del género más otras 17 especies de Libellulidae como grupo ajeno. Los caracteres se definieron siguiendo criterios de estandarización y fueron manejados con el software DELTA. La búsqueda de árboles fue ejecutada con el software NONA. Se adelantaron análisis particionados y análisis combinados. El rastreo de caracteres con ri=100 se usó para identificar las sinapomorfías. En coincidencia con la literatura, los caracteres de color proveen fuerte señal filogenética mientras que los caracteres de genitales no ofrecieron sinapomorfías. No se encontró ningún caracter que soporte la monofilia del género. El único clado con fuerte soporte es (*E. vesiculosa*, (*E. simplicicollis, E. collocata*)). Contrario a lo reportado para otros Odonata, la venación alar arrojó sinapomorfías para algunos clados de *Erythemis*.

Palabras clave. Odonata, libélula, señal filogenética, genitales del macho, coloración corporal.

INTRODUCTION

The genus *Erythemis* Hagen, 1861, is composed by ten species distributed in the Neotropical and Neartic regions, which are found from sea level to 2300 masl. Some species within the genus show territorial behavior and tolerate high temperatures (McVey, 1981), males exhibit continuous signals of interspecific aggression during mating and hunting (Baird & May, 2003). Several authors have studied the phylogenetic relationships in Odonata using different data sets; of these, only a few have included *Erythemis* in their analysis, but no more than one species of the genus has been included (e.g. Ware *et al*., 2007; Pilgrim & Von Dohlen, 2008). Specific studies on phylogenetic relationships among *Erythemis* species, were conducted by Kennedy (1923) and Pinto (2008). Kennedy (1923) established a relationship among *E. vesiculosa, E. collocata* and *E. simplicicollis* based on the absence of the posterior lobe of the vesica espermalis. Likewise, this author proposed the grouping of *E. peruviana*, *E. mithroides*, and *E. attala*, separating them from the group *E. plebeja*, *E. carmelita* and *E. haematogastra* considering the narrower abdomen of this last group. Unfortunately, the data of Pinto (2008) have not been published and the characters worked by him are not known.

The phylogenetic signal of a character has been an important topic in systematics, which began for the interest on the evolutionary phenomena that may affect it (Wilson, 1975). Currently, the phylogenetic signal is a topic used to describe the tendency of related organisms to resemble each other without implications about the mechanisms that might cause it (Blomberg, *et al*., 2003), and it can be described as the number of homologies that may be found in a particular character set. The amount of phylogenetic signal that provides different systems of characters may depend on the selection pressures and evolutionary rates that the character experiences. For example, some studies on genital characters, across several groups of insects, suggests that their evolution could have been faster due to sexual selection (Córdoba-Aguilar, 2005), and this phenomenon may blur the phylogenetic signal of these characters in comparison with other characters that are not under those selective pressures.

The phylogenetic signal of a character set (a group that includes all the characters of a particular corporal region, i.e. wings or thorax) can be analyzed in two ways: 1. A separate analysis of each character set can be conducted and the consensus analysis between the trees obtained may indicate the level of congruency between each proposal; it has

been argued that in this way the properties and the selective pressures of each character set are included in every analysis and are shown by the tree that better reflects the information in each analysis (Kluge, 1989). For instance, odonate wings are under natural selection, related to the aerodynamics of the flight (Kesel, 2000) while odonate genitalia and coloration may be under the selective pressures of species recognition processes and sexual selection (Córdoba-Aguilar & Cordero, 2008), thus, the phylogenetic behavior of those character sets may be different. 2. A combined analysis can be performed and the behavior of each character set is compared; it is believed that this approach maximizes the explanatory power of the characters and may conduct a more rigorous test of homology for the characters (Nixon & Carpenter, 1996). In addition, given the phylogenetic signal of different character sets may add to the solution of conflicts in these analyses, polytomies may become less frequent (Kluge, 1989; Kluge & Wolf, 1993).

A priori down weighting or character removal is frequently used (Wiens, 1995). However, it has been proven that supposedly unreliable characters (i.e. genitalia or coloration) may provide phylogenetic signal, meanwhile character sets traditionally considered reliable, may provide lower phylogenetic signal (Areekul & Quicke, 2006, Song & Bucheli, 2010). In the present study a phylogenetic analysis of the genus *Erythemis* was conducted to: 1) compare the phylogenetic signal of genitalia and color characters with those of other groups of characters, 2) test whether *Erythemis* is a monophyletic taxon, and 3) propose a phylogenetic hypothesis of relationships among *Erythemis* species.

MATERIALS AND METHODS

Taxa

The analysis included 27 species, the ten currently recognized species of *Erythemis* as ingroup, and 17 species as outgroup, those species were selected according to previous phylogenetic hypotheses (e.g. Pilgrim & Von Dohlen, 2008) and to include representatives of other Libellulidae subfamilies. The species included in this study were: Subfamily Sympetrinae *Erythemis attala* (Selys *in* Sagra), *E. carmelita* Williamson, *E. collocata* (Hagen), *E. credula* (Hagen), *E. haematogastra* (Burmeister), *E. mithroides* (Brauer), *E. peruviana* (Rambur), *E. plebeja* (Burmeister), *E. simplicicollis* (Say), *E. vesiculosa* (Fabricius), *Rhodopygia cardinalis* (Erichson), *R. geijskesi* Belle, *R. hinei* Calvert, *R. hollandi* Calvert, *R. pruinosa* Buchholz; Subfamily Leucorrhininae *Brachymesia herbida* (Gundlach); Subfamily Libellulinae *Garrisonia aurindae* Penalva & Costa, 2007, *Libellula herculea* Karsch; Subfamily Palpopleurinae *Perithemis lais* (Perty), *Perithemis mooma* Kirby, *Perithemis thais* Kirby, *Perithemis tenera* (Say); Subfamily Trameinae *Miathyria marcella* (Selys), *Pantala flavescens* (Fabricius), *Tramea calverti* Muttkowski, and *T. rustica* De Marmels and Racenis. Considering the work of Pilgrim & Von Dohlen (2008) *Rhodothemis rufa* Rambur was used for rooting purposes.

In order to record character variation a total of 3,000 specimens from the following entomological collections were studied. Their acronyms follow Evenhuis & Samuelson (2004) and are provided within brackets: Colección de Entomología, Universidad de los Andes, Bogotá, Colombia (ANDES), Laboratorio de Colecciones Entomológicas de la Universidad de Antioquia (CEUA), Colección Nacional de Insectos, Universidad Nacional Autónoma de México, México D. F., México (CNIN), Florida State Collection of Arthropods, Gainesville, Florida, USA (FSCA), Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá D.C. (ICN), Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ), Museo de Entomología Francisco

Luis Gallego, Universidad Nacional de Colombia, Medellín, Colombia (MEFLG), Museu Nacional, Universidade do Rio Janeiro, Rio de Janeiro, Brazil (MNRJ), Museo de Entomología de la Universidad del Valle, Cali, Colombia (MUSENUV), Rosser W. Garrison personal collection, Sacramento, California, USA (RWG), Museo de Colecciones Biológicas-Universidad del Atlántico Región Caribe (UARC), and Museum of Zoology, University of Michigan, Ann Arbor, Michigan, USA (UMMZ).

Character coding and cladistic analyses

The definition of the characters follows the parameters proposed by previous authors (Vogt *et al*., 2010); in most cases, the functional components of the character follows Sereno (2007) considering characters as properties of the species observed in the organisms expressed as independent variables with exclusive states. The "absent" state was only considered for neomorphic characters in the sense of a "substance" which is either present or absent in any structure (Sereno, 2007). Morphological terminology follows Borror (1942), Riek & Kukalová-Peck (1984), and Garrison *et al*. (2006). The characters were recorded in a matrix (Supplementary Material) using the DELTA package (Descriptive Language for Taxonomy) (Dallwitz, 2000). Specimens were examined using stereomicroscope and Scanning Electron Microscopy at low voltage (25-30kV). Gold-coated structures were observed using a Scanning Electron FEI Quanta200 microscope.

Diagnostic characters should be synapomorphies as they should be restricted to the species belonging to a specific taxon (i.e. genus); once a diagnostic character is present in other taxa, its value is questionable. The diagnosis of the genus *Erythemis* (Garrison *et al*., 2010) was based on a combination of characters and none of them are unique to *Erythemis* species. Three of these characters were coded with minor adjustments, to fulfill with character definition criteria described above, these were: origin of CuP in HW attached to posterior angle of triangle (character 93), posterior border of vulvar lamina rounded or acute or truncated (119), and posterior hamule bifid (122). Body color was alternatively coded as presence/absence of pigments (coding 1, Table 1), or as presence/absence of color patterns such as spots or stripes on the skeleton (coding 2, Table 1). Partitioned analyses were conducted to test the effect of these coding schemes. The character posterior femur widened and with 3-4 robust spines located at the external angle of the distal region, as described by Garrison *et al*. (2010), generates several non-exclusive character states violating the exclusivity principle defined by Sereno (2007). Thus, we proposed seven characters considering separate qualities in each such as femur width, spines thickness, number, size, distribution pattern, and location of spines (characters 69-71, 73, 74, 76, 77).

A total of 131 characters were coded (Table 1): 15 characters belong to the abdomen, thorax, and legs, 34 to the wing venation, 15 to the genitalia (vesica spermalis; vulvar lamina, and cerci), and 67 were color characters. Due to high intraspecific variation, the following five characters were not included in the phylogenetic analyses: Number of postnodal veins between costa and radio veins, previous to first postnodal vein between radio and M1 veins in FW (100), Number of postnodal veins between costa and radio veins previous to first postnodal vein between radio and M1 veins in HW (101), Number of cells between A_1 and anal angle in HW (102), Number of rows of cells between MA and Mspl in FW (103), and Number of cells in the anal keel bifurcation in HW (107). Williamson (1923) proposed the character widening of the abdominal basal region with different states to separate some species in his key, however, such definition of the character did show high overlapping between states and no species separation,

for this reason this character was recoded (character 80). Some characters correspond to alternative coding strategies to test their effect on the phylogenetic analysis (see table 1).

Table 1. List of characters used in the study. The characters were grouped into the following sets: body coloration (0-66), thorax-legs-abdomen (67-81), genitalia (82-84, 119-130), and wing venation (85-118). *Color pigment character coding strategy 1, **color pattern coding strategy 2, *** Characters not included in the phylogenetic analyses.

0. *Yellow on labrum*: present (1), absent (2)*.
1. *Black on labrum*: present (1), absent (2)*.
2. *Yellow spots on labrum*: present (1), absent (2)**.
3. *Red on labrum*: present (1), absent (2)*.
4. *Dark longitudinal stripe in the middle region of the labrum*: present (1), absent (2)**.
5. *Red on frons*: present (1), absent (2)*.
6. *Yellow on frons*: present (1), absent (2)*.
7. *Black on frons*: present (1), absent (2)*.
8. *Green on frons*: present (1), absent (2)*.
9. *Violet overtones on frons*: present (1), absent (2)**.
10. *Brown stripe in the posterior region of the frons*: present (1), absent (2)**.
11. *Greenish-yellow stripe in the anterior region of the frons*: present (1), absent (2)**.
12. *Spots on the frons*: present (1), absent (2)**.
13. *Metallic blue spot in the anterior region of the frons*: present (1), absent (2)**.
14. *Brown spots in the anterior region of the frons*: present (1), absent (2)**.
15. *Red on vertex*: present (1), absent (2)*.
16. *Yellow on vertex*: present (1), absent (2)*.
17. *Green on vertex*: present (1), absent (2)*.
18. *Black on vertex*: present (1), absent (2)*.
19. *Black stripe in the anterior edge of the vertex*: present (1), absent (2)**.
20. *Brown stripe in the anterior edge of the vertex*: present (1), absent (2)**.
21. *Violet overtones on vertex*: present (1), absent (2)**.
22. *Vertex with brown on the anterior region and green on the posterior region*: yes (1), no (2)**.
23. *Vertex with a brown stripe in the anterior and posterior regions*: yes (1), no (2)**.
24. *Black on thorax*: present (1), absent (2)*.
25. *Red on thorax*: present (1), absent (2)*.
26. *Yellow on thorax*: present (1), absent (2)*.
27. *Green on thorax*: present (1), absent (2)*.
28. *Pruiniscence on thorax*: present (1), absent (2)*.
29. *Pale stripe in the dorsal region of the thorax*: present (1), absent (2)**.
30. *Yellow on femur*: present (1), absent (2)*.
31. *Red on femur*: present (1), absent (2)*.
32. *Black on femur*: present (1), absent (2)*.
33. *Color on the anterior region of the femur*: similar to posterior region (1), different to posterior region (2)*.
34. *Color on the internal region of the femur*: similar to external region (1), different to external region (2)*.
35. *Green on femur*: present (1), absent (2)*.
36. *Red on tibia*: present (1), absent (2)*.
37. *Black on tibia*: present (1), absent (2)*.
38. *Yellow on tibia*: present (1), absent (2)*.
39. *Red on abdomen*: present (1), absent (2)*.
40. *Black on abdomen*: present (1), absent (2)*.
41. *Yellow on abdomen*: present (1), absent (2)*.
42. *Green on abdomen*: present (1), absent (2)*.
43. *Pruiniscence on abdomen*: present (1), absent (2)*.
44. *Black on epiproct*: present (1), absent (2)*.
45. *Red on epiproct*: present (1), absent (2)*.
46. *Yellow on epiproct*: present (1), absent (2)*.
47. *Green on epiproct*: present (1), absent (2)*.
48. *Black in the epiproct apical region*: present (1), absent (2)*.
49. *Lower and upper regions of the epiproct with different colors*: yes (1), not (2)*.
50. *Epiproct with anterior and posterior regions with different colors*: yes (1), not (2)*.
51. *Basal coloration in HW*: present (1), absent (2)*.52. *Yellow on basal coloration in HW*: present (1), absent (2)*.
53. *Red on basal coloration in HW*: present (1), absent (2)*.
54. *Black on basal coloration in HW*: present (1), absent (2)*.
55. *Basal coloration in HW*: not reaching the cubito-anal crossvein (1), reaching beyond of the cubito-anal crossvein (2)*.

Table 1 continuation. List of characters used in the study. The characters were grouped into the following sets: body coloration (0-66), thorax-legs-abdomen (67-81), genitalia (82-84, 119-130), and wing venation (85-118). *Color pigment character coding strategy 1, **color pattern coding strategy 2, *** Characters not included in the phylogenetic analyses.

56. *Yellow on pterostigma*: present (1), absent (2)*.
57. *Black on pterostigma*: present (1), absent (2)*.
58. *Red on pterostigma*: present (1), absent (2)*.
59. *Black in the costal edge of the pterostigma*: present (1), absent (2)*.
60. *Red in the costal edge of the pterostigma*: present (1), absent (2)*.
61. *Brown in the costal edge of the pterostigma*: present (1), absent (2)*.
62. *Wing apex color*: hyaline (1), tinged with brown (2), yellow (3), tinged with yellow (4)*.
63. *Color in the abdominal S1-2*: similar to S3-10 (1), different to S3-10 (2)*.
64. *Extension of the basal coloration in HW*: to supplementary anal vein (1), to A1 (2), to triangle (3), not reaching the A1 (4)*.
65. *Basal coloration in HW extended to first antenodal vein*: yes (1), not (2)*.
66. *Basal coloration in HW extension to anal angle region*: covering the last row of cells (1), covering the penultimate row of cells (2)*.
67. *Number of spines in the external angle of the median tibia*: eight or less (1), nine or more (2).
68. *Median femur thickened*: yes (1), not (2).
69. *Long spines in the posterior femur*: thickened (1), thin (2).
70. *Disposition of the spines in the external angle of the posterior femur*: long spines followed by short spines (1), long spines followed by medium spines and short spines (2), only long spines present (3), spines gradually decreasing in size (4).
71. *Size of the short spines in the posterior femur*: variable (1), similar (2).
72. *Number of spines in the external angle of the posterior tibia*: eleven or less (1), twelve or more (2).
73. *Spines in the external angle of the posterior femur*: present (1), absent (2).
74. *Size of the spines in the external angle of the posterior femur*: similar (1), different (2).
75. *Number of long spines in the external angle of the medial femur*: least than three (1), three (2), four (3), more than four (4).
76. *Posterior femur*: thickened (1), not thickened (2).
77. *Number of long spines in the external angle of the posterior femur*: least than three (1), three (2), four (3), more than four (4).
78. *Dorsal carina of the tenth abdominal segment in males*: present (1), absent (2).
79. *Dorsal carina of the tenth abdominal segment in males*: widened (1), not widened (2).
80. *Narrowing from the fourth abdominal segment*: present (1), absent (2).
81. *Posterior lobe of the prothorax*: narrowed at base (1), not narrowed at base (2).
82. *Posterior extension of ventral teeth on cerci of male*: about the same level as apex of epiproct or not that far (1), three or more teeth beyond level of apex of epiproct (2).
83. *Dorsal edge of the epiproct in lateral view*: bent (1), straight (2).
84. *Posterior edge of the epiproct in lateral view*: bent (1), truncated (2), acute (3).
85. *Length of the costal side respect to the proximal side in the FW triangulus*: half or more (1), 1/3 or less (2), more than 1/3 and less than half (3).
86. *Pterostigma shape*: parallelogram (1), trapezoid (2).
87. *Distal edge of the discoidal field in FW*: parallel and narrow (1), widened (2).
88. *Supplementary anal vein to anal keel*: with marked curve (1), without marked curve (2).
89. *R_3 vein*: without marked curve (1), with marked curve (2).
90. *Number of bridge crossing veins in FW*: one (1), two (2), three (3), four (4), five (5).
91. *Number of cubito-anal veins in HW*: one (1), two (2), three (3).
92. *Stalk in the sector near to FW arculus*: present (1), absent (2).
93. *Origin of Cup in HW*: attached to posterior angle of the triangulus (1), separated from posterior angle of the triangulus (2).
94. *Number of rows of the cells in anal field in FW under the proximal region of the subtriangulus*: one (1), two (2).
95. *Number of cells in the subtriangulus in FW*: one (1), two (2), three (3), four (4), five (5), six (6), seven (7), eight (8).
96. *Number of cells between the basis and subtriangulus*: three (1), four (2), five (3), six (4), seven (5), eight (6).
97. *Number of crossing veins of the triangulus in FW*: one (1), two (2), three (3), zero (4).
98. *Crossing veins of the triangulus in FW*: present in the two wings (1), present in one wing (2), absent (3).
99. *Number of rows of cells between MA and Mspl in FW*: one (1), two (2).
***100. *Number of posnodal veins between costa and radio veins previous to first posnodal vein between radio and M1 veins in FW*: two (1), three (2), four (3), five (4).
***101. *Number of posnodal veins between costa and radio veins previous to first posnodal vein between radio and M1 veins in HW*: one (1), two (2), three (3), four (4), five (5).
***102. *Number of cells between A_1 and anal angle in HW*: three (1), four (2), five (3), six (4), seven (5), eight (6), eleven (7).
***103. *Number of rows of cells in the discoideal field region in FW*: one (1), two (2).
104. *Double cells in the medial planate in HW*: absent (1), present (2).
105. *Double cells in the radial planate in HW*: absent (1), present (2).
106. *Number of transversal veins under pterostigma*: one (1), two (2), three (3), four (4), five (5).
***107. *Number of cells in the anal keel bifurcation in HW*: two (1), three (2), four (3), five (4), six (5), seven (6), eight (7), nine (8).
108. *Individual cells in discoidal field of the HW*: present (1), absent (2).

Table 1 continuation. List of characters used in the study. The characters were grouped into the following sets: body coloration (0-66), thorax-legs-abdomen (67-81), genitalia (82-84, 119-130), and wing venation (85-118). *Color pigment character coding strategy 1, **color pattern coding strategy 2, *** Characters not included in the phylogenetic analyses..

109. *Number of simple cells in anterior region of discoidal field in HW*: one (1), two (2), three (3), four (4), five (5), zero (6).
110. *Cells in the anterior region of the discoidal field in HW*: with simple and double cells (1), with simple and triple cells (2), with simple, double and triple cells (3), double cells only (4), simple cells only (5), with double and triple cells (6).
111. *Disposition of cells in the anterior region of the discoidal field in FW*: alterning columns and rows of cells (1), rows of cells only (2).
112. *Rows of two cells in the anterior region of the discoidal field in FW*: present (1), absent (2).
113. *Columns of two or three cells in the anterior region of the discoidal field in FW*: present (1), absent (2).
114. *Position of the arculus in FW*: near to first antenodal vein (1), near and anterior to second antenodal vein (2), near and posterior to second antenodal vein (3).
115. *Number of intermedial crossveins above hindwing supertriangle*: one (1), two (2).
116. *Position of the first intermedial vein above HW supertriangle*: in the distal third (1), in the medial third (2), in the proximal third (3).
117. *Number of trasverse veins on the above triangle in FW*: one (1), two (2), three (3), four (4).
118. *Position of the inferior angle of the triangle respect to the inferior angle of the subtriangle*: previous (1), to same distance (2).
119. *Posterior border of the vulvar lamina*: rounded (1), acute (2), truncated (3), forked (4).
120. *In lateral view, vulvar lamina protrudes of the abdominal ventral region*: yes (1), no (2).
121. *Number of lobes in the vulvar lamina*: one (1), two (2), three (3), four (4).
122. Posterior hamule bifid: yes (1), no (2).
123. *Cornual lobes to apex*: separate (1), fused (2).
124. *Cornual orientation respect to vesica spermalis tranversal axis*: parallel (1), perpendicular (2), diagonal (3).
125. *Posterior lobe of vesica spermalis*: present (1), absent (2).
126. *Posterior lobe of vesica spermalis*: covered by lateral lobe (1), no covered by lateral lobe (2).
127. *Posterior extension of lateral lobe of vesica spermalis respect to medial lobe*: less extended into posterior region (1), more extended into posterior region (2).
128. *Posterior edge of vesica spermalis hook*: acute (1), rounded (2), truncated (3).
129. *Cornua of vesica spermalis in lateral view*: covered by lateral lobe (1), exposed (2).
130. *Shape of the vesica spermalis hook*: triangular (1), finger-shaped (2), rectangular (3), trapezoidal (4), suboval (5).

All the characters were coded as non-additive. Missing data were indicated by a question mark ("?") and inapplicable data were indicated by a hyphen mark ("-"). Phylogenetic analyses were done using the parsimony software NONA under the WinClada package10.00.08 (http://www.cladistics.com/). Given the number of taxa (27), heuristic search based on the Ratchet algorithm (Nixon, 1999) with 10% of characters resampled was applied. Ten trees were retained per replicate and tree-bisection-reconnection (TBR) and branch swapping with the default options of the software were used.

For an assessment of tree search thoroughness, we repeated tree search increasing repetitions up to 100,000. Once every search was completed the number of fundamental trees, their length, Ci and Ri were recorded. If the number of fundamental trees did not increase with replications, this was considered as an indication of exhaustively sampled space tree. However, since the number of fundamental trees may increase as replication increases, due to some clades where no further resolution can be reached with the current data set, we identified these cases by comparing the strict consensus trees of every replicate (Table 2). Strict consensus trees were used in every analysis as a summary of the congruent information obtained from the fundamental trees (Nixon & Carpenter, 1996). We only used characters with retention index of 100 as support for specific clades. This value appears if no trace of homoplasic interpretations can be observed in a character (Patterson, 1982; Farris, 1989a). A flowchart of the procedure described here is presented in figure 1.

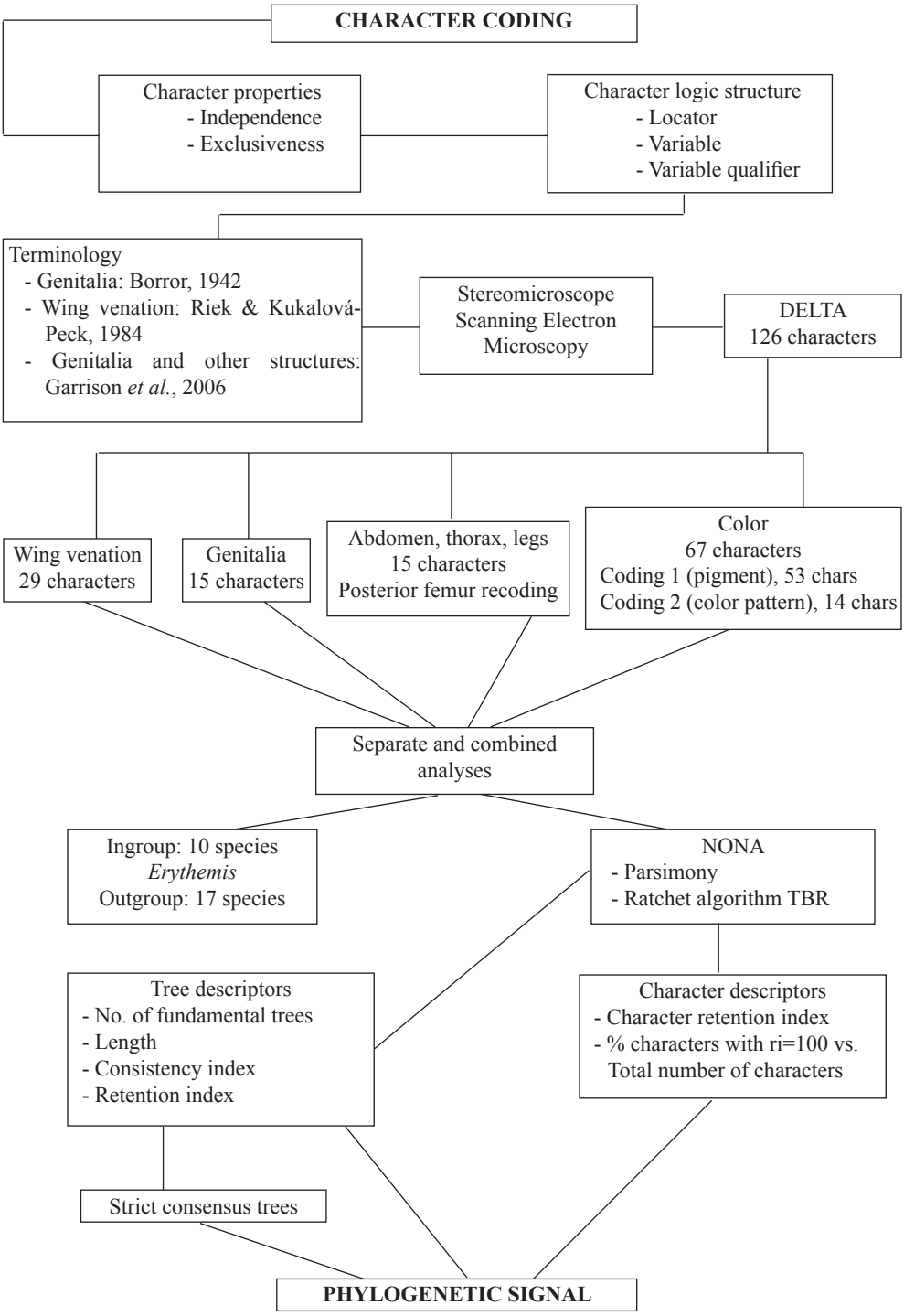

Figure 1. Flowchart of the methods followed in this study.

Comparison of the phylogenetic signal of different character sets

Characters were grouped into the following sets: wing venation, thorax-legs-abdomen, genitalia, and body coloration. These character sets may be susceptible to different selection pressures. For example, the wing venation is exposed to aerodynamic conditions and thus to natural selection pressures (Kesel, 2000), while genitalia and coloration may be subject of sexual selection (Córdoba-Aguilar & Cordero, 2008). Separate and combined or simultaneous phylogenetic analyses were conducted. The strict consensus tree from the combined analysis using the pigment coding strategy (coding 1) was used as reference, given that a higher number of characters provided a more severe test of homology (Kluge, 1989; Kitching *et al*., 1998) and in some cases these allowed the recovery of hidden homologies within a character subset (Nixon & Carpenter, 1996). In addition, as it is shown in the results section below, this tree presented higher resolution and retention index

The phylogenetic signal of a character set was analyzed by looking at the retention index of each tree. This index has been traditionally used as a general descriptor of the phylogenetic signal in a tree as this is not affected by matrix size (Farris, 1989a; Farris, 1989b; Kitching *et al*., 1998; Klingenberg & Gidaszewski, 2010). In this study the character sets ranged in size from 15 characters in the genitalia set up to 112 characters in the combined evidence analysis using the color pigment coding strategy. We also traced each character with retention index of 100 on both, its own subset tree, and on the combined analysis tree. In the latter, their assignation of a character subset was recorded; this strategy identifies the phylogenetic signal of that subset in the context of a more stringent dataset (Farris, 1989a; Song & Bucheli, 2010). A third approach to quantify the informativeness of each character set was recording the percentage of homologies with retention 100, respect to the total number of characters in both partitioned and combined analyses.

RESULTS AND DISCUSSION

Tree search

The analyses with the abdomen-legs-thorax character subset and the combined data set reached a maximum of trees that did not changed after 10,000 and 5,000 replications respectively (Table 2). In the analyses with the character subsets genitalia, wings, and color, the number of trees always increased with the number of replications (Table 2); however, the topology of the strict consensus trees of each replication were identical within these character subsets, indicating that the changes in the number of fundamental trees of each replication were the result of polytomies, where no characters allow subtree resolution. These results lead us to conclude that tree search was thorough in all the character subsets and in the total evidence analyses.

Character coding

The consensus tree from the combined pattern presence/absence coding strategy (coding 2, Fig. 2) presented lower resolution than that of the tree from the combined pigment presence/absence coding strategy (coding 1, Fig. 3). In the latter, several species of *Erythemis* appear in a single clade, the genus *Rhodopygia* appeared as monophyletic, and it is the sister group of a large clade that includes species of several genera. Nine characters with retention of 100 appeared on this tree. Similarly, when comparing both color dataset codifications, there was a large difference between the two strategies; the tree from the pattern coding was highly unresolved, and with a single clade (*E. vesiculosa*, (*E. simplicicollis*, *E. collocata*)) (Fig. 4) that is also present in the tree from the pigment coding (Fig. 5). The latter was a more resolved tree. The retention index of both coding strategies was very similar (Table 3).

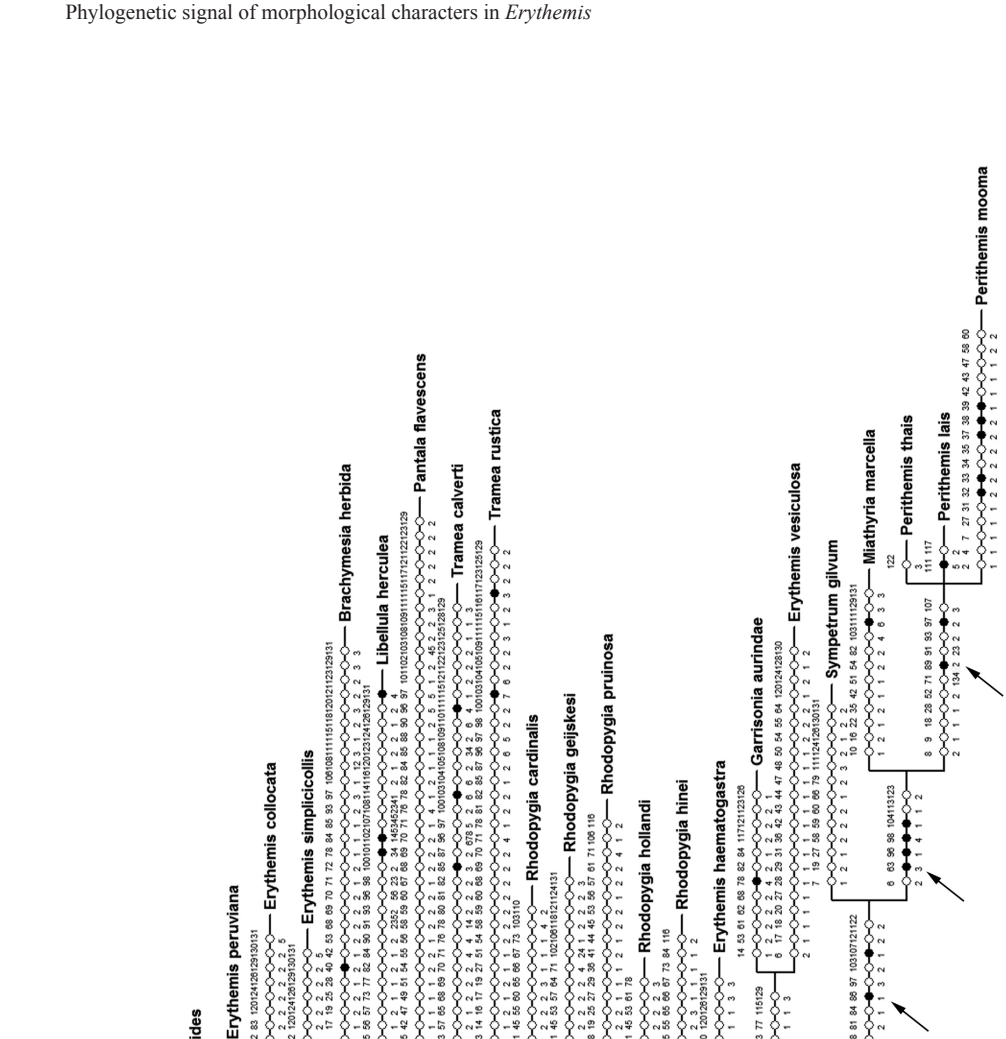

Figure 2. Strict consensus tree of the combined evidence analysis using the pattern presence/absence coding strategy (coding 2). Quantitative descriptors of the fundamental trees are indicated in table 3. Character numbers above and character state numbers below follow table 1. Two or three digit numbers under a character points to polymorphisms. Arrows highlight to characters with ri=100.

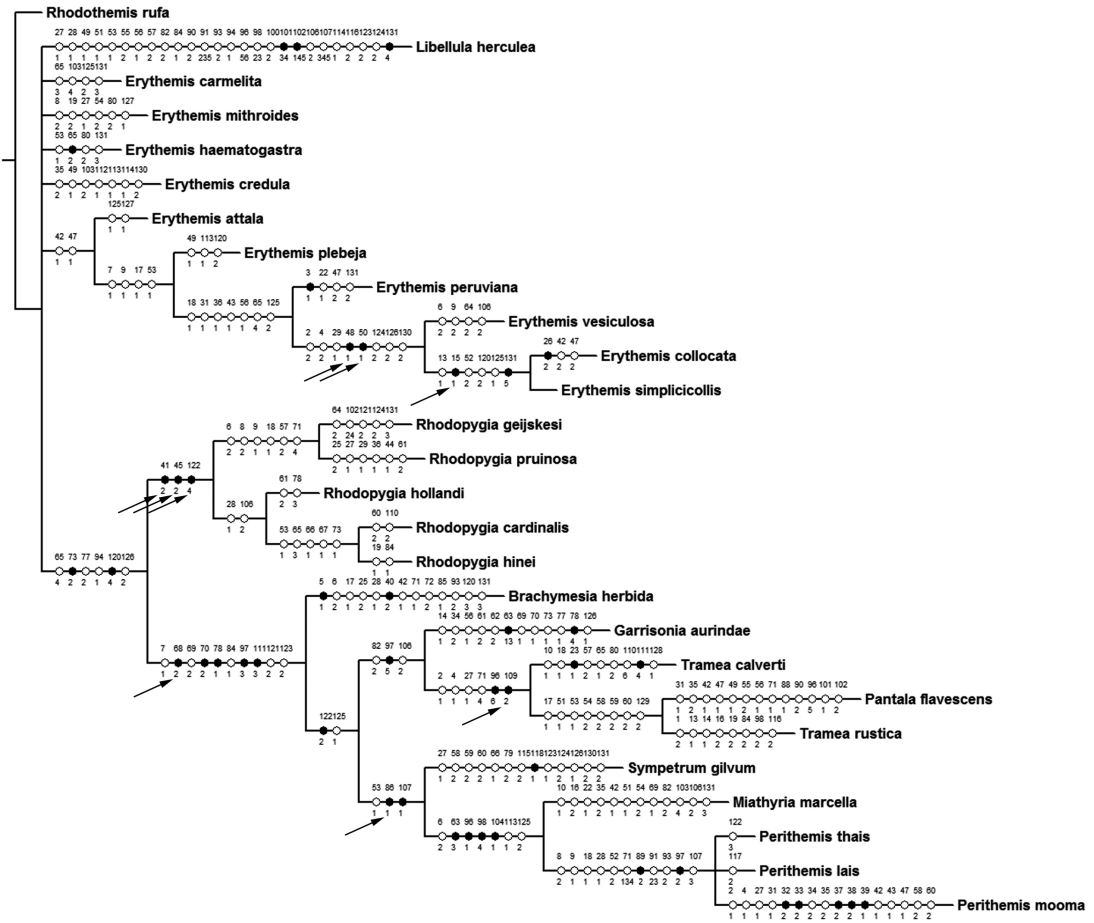

Figure 3. Strict consensus tree of the combined evidence analysis using the presence/absence of pigment coding strategy (coding 1).

Quantitative descriptors of the fundamental trees are indicated in table 3. Character numbers above and character state numbers below follow table 1. Two or three digit numbers under a character point to polymorphisms. Arrows highlight characters with ri=100.

It has been proposed that proper coding of characters is a crucial step in phylogenetic research especially when using morphologic data, and the compliance with basic requirements of character definition, such as independence, exclusivity, and logical standardization, must be addressed (Sereno, 2007; Vogt *et al*., 2010). In this study we found a good example of the importance of these requirements; when coding color characters as pattern, or strategy coding 1, these show lower resolution than the pigment coding, or strategy coding 2, analyzed as separate datasets or in the combined analyses.

Partitioned analyses, combined analyses, and phylogenetic signal

The abdomen-legs-thorax and the genitalia subsets offered higher retention indexes (82 and 64 respectively) while the wing venation subset offered lower retention index (Table 3). The retention index values of the two coding strategies for the color subset were a bit higher than those of

Table 2. Number of trees obtained from each parsimony analyses using a progressive number of ratchet replications and a particular set of characters. All the tree searches have the same length, consistency index value and retention index value within each column.

Number of replications	Genitalia 15 characters	Wings 29 characters	Abdomen-Legs-thorax 15 characters	Color 67 characters	Combined analysis with pigment coding 112 characters
200	363	119	4	30	12
1000	1122	637	52	146	-
5000	5697	1455	60	139	12
10000	40	2449	80	209	-
20000	-	4078	80	248	-
50000	33112	8612	80	270	12
60000	34465	-	80	-	-
70000	46796	-	80	-	-
80000	-	-	80	-	-
100000	52242	9992	80	651	12

Table 3. Quantitative descriptors of the trees obtained from each analysis using a particular set of characters. * Presence or absence of a color pigment, ** Presence or absence of a color pattern. Ci = consistency index, Ri = retention index.

Character set	Number of trees	Length	Ci	Ri
Simultaneous analysis (p/a pigment coding*)	12	397	41	55
Simultaneous analysis (p/a pattern coding**)	1156	423	38	50
Color (p/a pigment coding)	101	133	40	57
Color (p/a pattern coding)	240	147	40	56
Head, thorax, and legs	393	32	56	82
Genitalia	2050	59	40	64
Wing venation	189	478	34	40

the total evidence analyses using the two coding strategies (Table 3). The genitalia subset provided a highly unresolved tree with the single clade (*Erythemis collocata, E. simplicicollis*) (Fig. 6) supported by the character of suboval shape of the vesica spermalis hook (130, ri=100). The extensive analysis of the genitalia of several species through Scanning Electron Microscopy revealed a large complexity of structures not observed before but unfortunately their coding was difficult due to variation. A similar situation occurred with the abdomen-legs-thorax subset, where only a clade (*Erythemis mithroides, E. haematogastra*) was found (Fig. 7). The wing veins subset offered a tree where most of the *Erythemis* species are located in a large basal polytomy and others are in other sections of the tree (Fig. 8). The presence/absence color pigment subset offered a mostly resolved tree with five polytomies, four of these are composed by three branches while one includes seven branches (Fig. 5); the clades are a mixture of species from different genera. Two characters had a 100 ri value and support the clade (*E. vesiculosa*, (*E. collocata, E. simplicicollis*)), these characters refer to the presence of green and red pigment on the epiproct (47 and 49 respectively).

The strict consensus of the 12 fundamental trees found from the combined analysis using the presence/absence of pigment coding strategy presented a basal polytomy composed by *Libelulla herculea*, four species of *Erythemis* and two large clades, one which included the other six species of *Erythemis*, and a large clade with species of several genera (Fig. 3), no characters with 100 ri could be traced at the node of the *Erythemis* species (Fig. 3). A total of nine characters were found with ri = 100, One belong to the color pattern subset (15), four belong to color pigments character subset (41, 45, 48, 50), two to the wing veins subset (86,

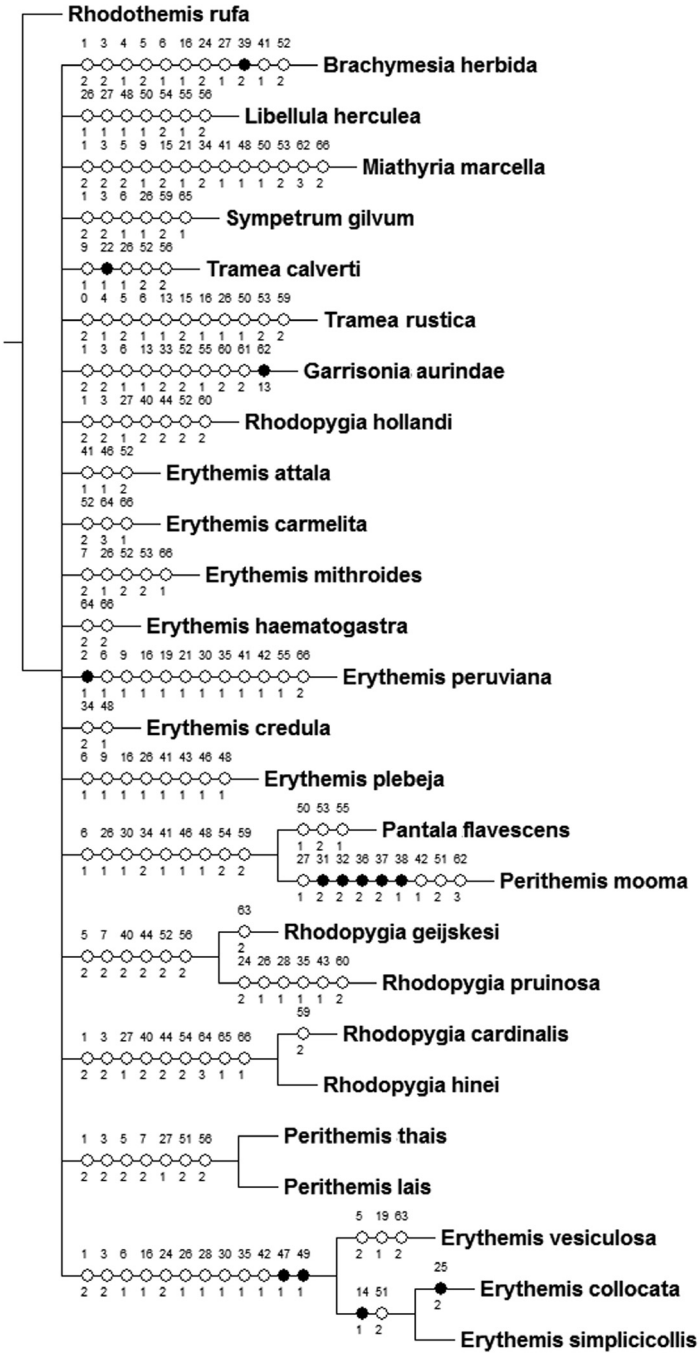

Figure 4. Strict consensus tree of the analysis of color characters subset using the pattern presence/absence coding strategy (coding 2).

Quantitative descriptors of the fundamental trees are indicated in table 3. Character numbers above and character state numbers below follow table 1.

109), one to the thorax-legs-abdomen subset (68), and one to the genitalia subset (122). None of these characters were recovered as synapomorphies with ri = 100, in the analyses using the separate subsets of characters. Only three of the six clades observed in the analysis of the color pigment coding subset were present in the combined analysis.

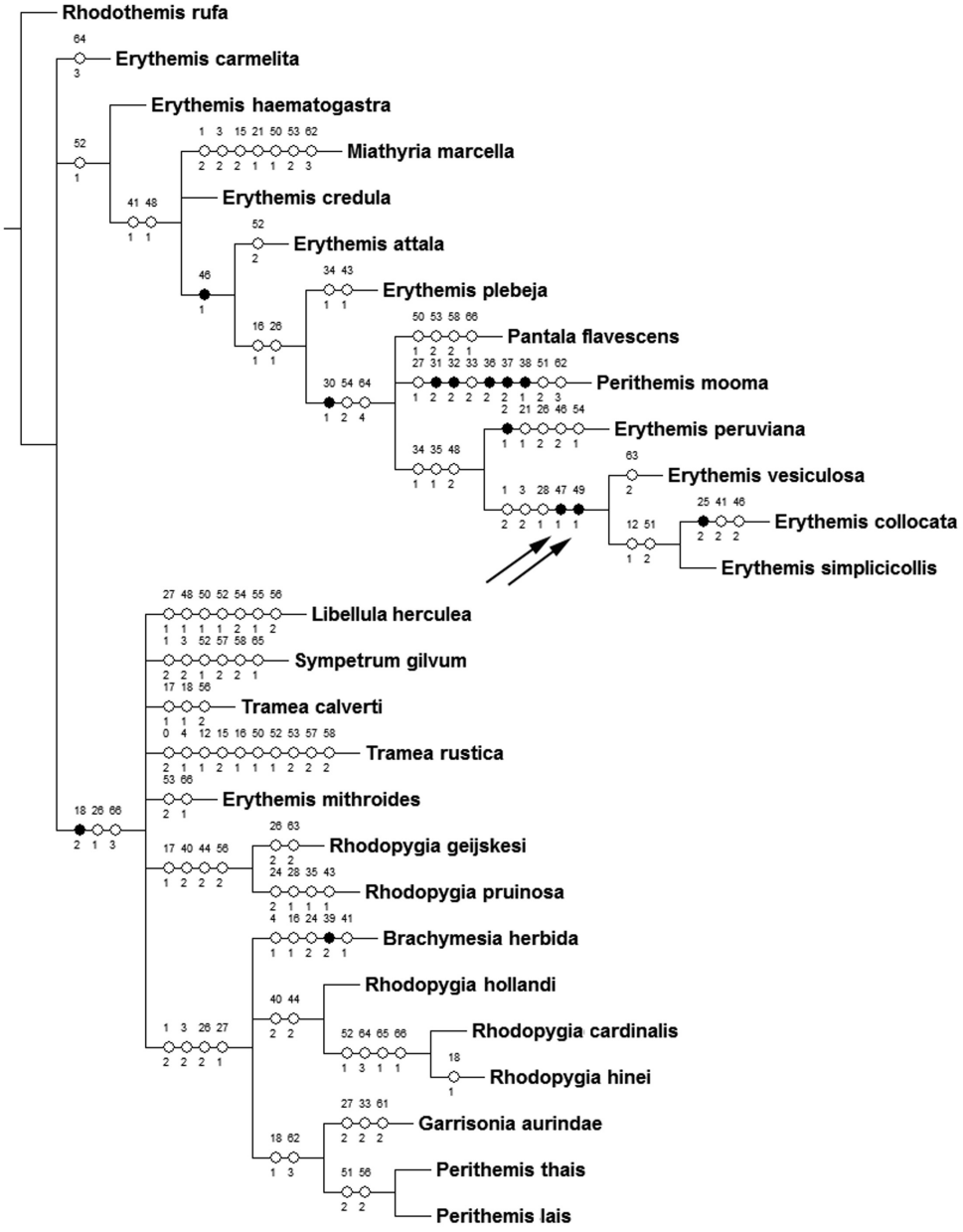

Figure 5. Strict consensus tree of the analysis of color characters subset using the presence/absence of pigment coding strategy (coding 1).

Quantitative descriptors of the fundamental trees are indicated in table 3. Character numbers above and character state numbers below follow table 1. Arrows point to the ri=100 characters described in the results section.

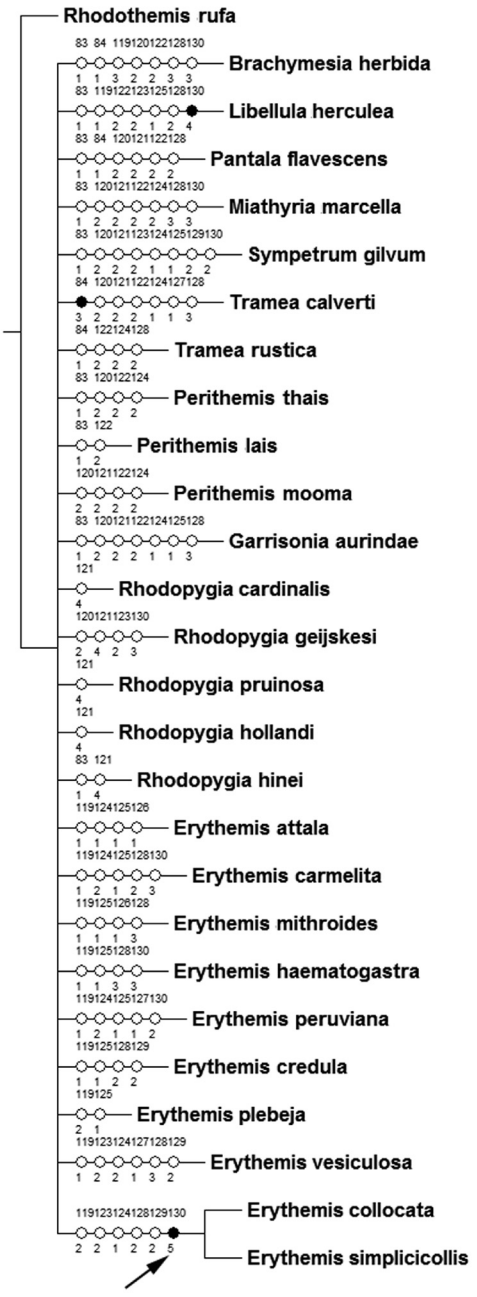

Figure 6. Strict consensus tree of the analysis of genitalia characters subset.
Quantitative descriptors of the fundamental trees are indicated in table 3. Character numbers above and character state numbers below follow table 1. The arrow point to the ri=100 character described in the results section.

The thickened long spines in the hind femur present in *Erythemis*, are also present in the genus *Rhodopygia,* in the species *Libelulla herculea, Rhodothemis rufa* and in *Garrisonia aurindae.* The disposition of the long spines in the external angle of the posterior femur exhibits a large array of variation in the species studied and even variation within species was recorded. The number of long spines in the external angle of the posterior femur also shows large variability and species such as *E. haematogastra* and *E. credula* had specimens with a lower or higher number of long spines to those proposed as diagnostic of the genus. In addition, species of other genera such as *Perithemis*, *Rhodopygia,* and *Libellula* exhibit between 3 and 4 long spines in the hind femur. The widened hind femur is also present in *Libellula herculea* Karsch, 1889 and *Garrisonia aurindae* Penalva & Costa, 2007 (Penalva & Costa, 2007).

Despite the debate about the use of either combined or partitioned analyses in phylogenetic studies (Lecointre & Deleporte, 2004; Nixon & Carpenter, 1996), our analysis is in agreement with the first as the trees of the combined analyses are more informative than these of the partitioned analyses and also present a larger number of synapomorphies. Moreover, the combined analyses uncover nine homologies that were not observed in the partitioned analyses. Another result that agrees with the literature (Wenzel & Siddall, 1999) points out to the lack of additivity of characters in phylogenetic studies; despite that the color characters were the more abundant of the entire data set (58%), that the color characters were five of the nine synapomorphies found in the combined analysis, and that the phylogenetic analysis of the color pigment subset provided the more resolved tree, this tree agreed only in six out of the 19 nodes observed in the combined analysis. In addition, none of the four characters with ri=100 in the subset analyses was observed as such in the combined analysis. Thus, the role

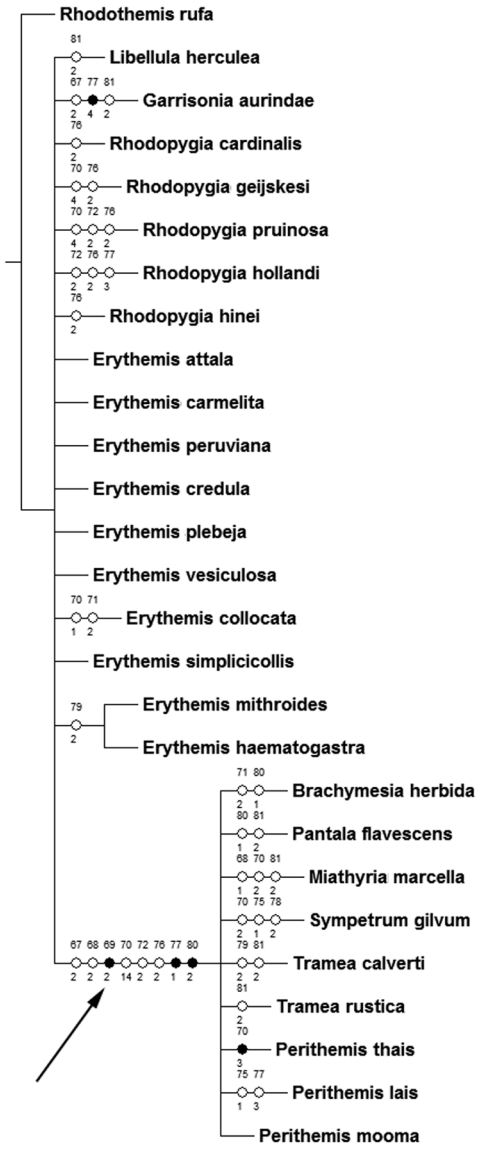

Figure 7. Strict consensus tree of the analysis of the abdomen-legs-thorax characters subset.
Quantitative descriptors of the fundamental trees are indicated in table 3. Character numbers above and character states numbers below follow table 1. Two or three digit numbers under a character indicate polymorphisms. The arrow points out to the ri = 100 character described in the results section.

of a character subset and that of a character can only be understood once the analysis is conducted to detect hidden synapomorphies (Nixon & Carpenter, 1996). A single character from the genitalia subset (122) was recovered as synapomorphy in the combined analysis; this result differs from these found by other authors (e.g., Song & Bucheli, 2010) who surveyed a large number of studies and concluded that genitalia characters can be as useful to phylogenetic analysis as any other character set, but they suggest a careful examination in every study. In the present case, the observed variation is expressed as homoplasy in different lineages, agreeing with the low informativeness of the genitalic region, as a consequence of accelerated and divergent sexual selection pressures (Méndez & Córdoba-Aguilar, 2004; Song & Wenzel, 2008; Song & Bucheli, 2010).

The characters from the abdomen-legs-thorax subset offered a highly unresolved tree; however, one of these characters appeared as a homology supporting a clade in the combined analysis (Fig. 3). Because odonate wing venation is complex and full of autopomorphies (Rehn, 2003), the set of wing characters of *Erythemis* provided a mostly unresolved tree (Fig. 8); however, two characters of this set appeared as homologies in the combined analysis (Fig. 3). Our results do not entirely comply with other authors (e.g., Rehn, 2003; Pilgrim & Von Dohlen, 2008), who proposed that wing venation is a highly variable region and provides very poor phylogenetic information. Despite the strong selection pressures that flight performance exerted over these structures (Kesel, 2000), homologies were recovered from these structures.

Even though Kennedy (1923) proposed the widening of basal region of the abdomen to establish species groups for the genus *Erythemis*, an analysis of body proportions of this region performed by the authors

(unpublished data), showed that its high variation do not allow to recognize the discontinuity and therefore the character states can not be acknowledged. The relation between *E. simplicollis* and *E. collocata* proposed by Kennedy (1923) based on the absence of posterior lobe in the vesica spermalis, was corroborated by this study, but using the shape of the hook of the vesica spermalis.

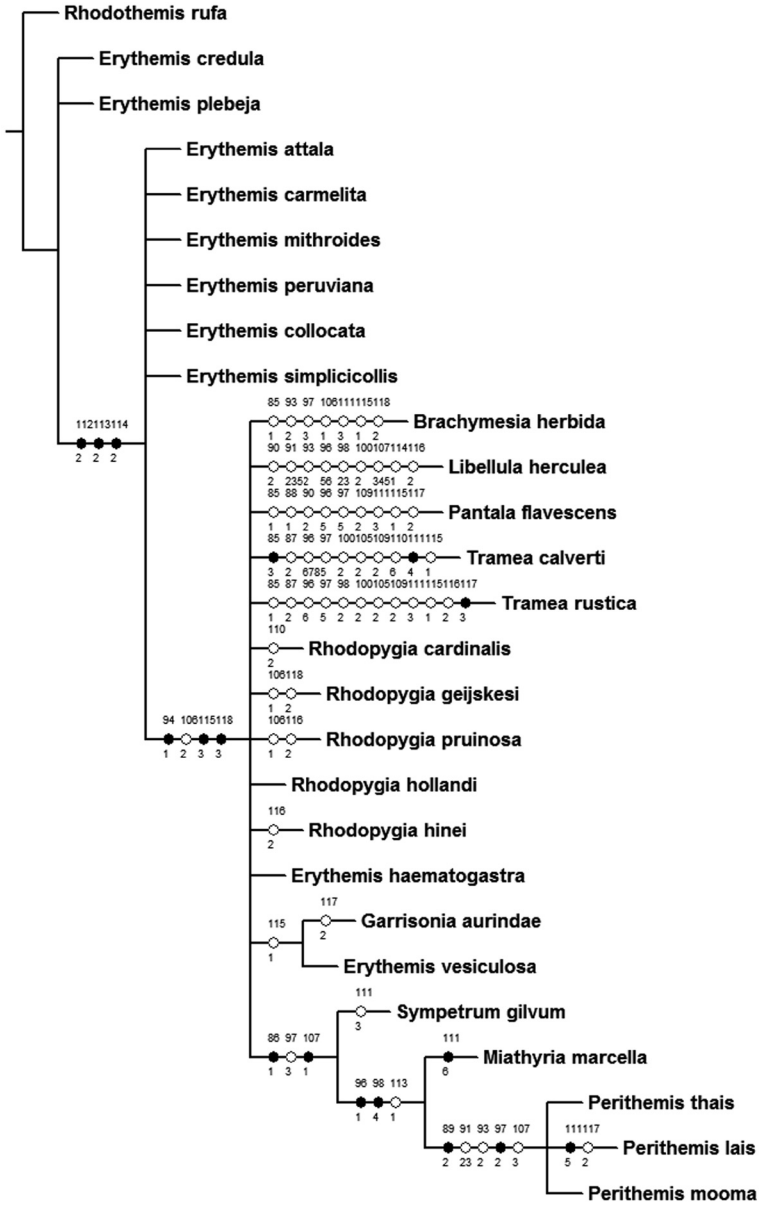

Figure 8. Strict consensus tree of the analysis of wing veins characters.
Quantitative descriptors of the fundamental trees are indicated in table 3. Character numbers above and character state numbers below follow table 1. Two or three digit numbers under a character indicate polymorphisms.

Despite that color varies intraspecifically due to environment, ontogeny, and diet (Winston, 1999), and that museum specimens are often discolored, our results agreed with others who provided evidence that color characters may be useful for phylogenetic analysis in several insect groups (Areekul & Quicke, 2006). These results supports that color characters are involved in strongly conserved patterns (Song & Bucheli, 2010), perhaps as a consequence of their role on sexual recognition in *Erythemis*, doing that color characters may show a strongly structured evolution as a whole, that may lead to a strong phylogenetic signal (Song & Bucheli, 2010). As it was demonstrated above, coding is important when including traits, to avoid violations to logic precepts in the characters such as character interdependence, conjunction of character states, or character correlation (Sereno, 2007). The results on wing and color character subsets also points at the importance of looking at the data before proceeding with preventive subtraction (Wenzel & Siddall, 1999).

As it has happened in other odonate taxa (e.g. Dijkstra & Vick, 2006; Ware et al., 2007; Pilgrim & von Dohlen, 2008; Blanke et al., 2013), *Erythemis* was not found as a monophyletic group due to the extensive homoplasy and structural variability observed in its diagnostic characters (Dijkstra et al., 2014). In *Ertythemis* case, aside from the high intra and interspecific variation that most of the characters showed, a large number of the character states are shared with other genera.

Some authors have approached to the high variation and complexity of Odonate morphology (e.g. Pilgrim & Von Dohlen, 2008) and they have studied wing venation along with many autopomorphies (Rehn, 2003), showing that the developmental process as larvae may influence this variation (Martinov, 1930). In addition it has been proposed that this variation, might respond for the strong differences in the capability of wing flexion among some odonates such as *Aeshna* Fabricius, 1775 and *Pachydiplax* Brauer, 1868 (Combes & Daniel, 2003).

The *Erythemis* morphology may be an example of the interaction between stochastic evolutionary processes altering the genetic homogeneity of the species (Clegg *et al.*, 2002) and the adaptation to habitat heterogeneity inhabited by their species. Studies in other odonates have suggested that selective pressures such as landscape structure (Taylor & Merriam, 1995), food and predation stress (Svensson & Friberg, 2007), wind and high acidification of the larvae biotopes (Marinov & McHugh, 2010), and sexual selection (Outomuro & Johansson, 2011), can affect the evolution of wing and abdomen characters. For example, Johansson & Samuelson (1994) found that the action of predators might influence the length of dorsal and lateral thorns in *Leucorrhinia dubia* (Vander Linden, 1825) larvae. Giacomini & De Marco Jr. (2008) found a relationship among the variation of body length in larvae of several Anisoptera species and the habitat portion used by these. The authors stated that species like *E. peruviana* shows a narrower abdomen associated to the possibility of easy camouflage in macrophytes as a defense against predators. According to Giacomini & De Marco Jr. (2008) the presence and reproduction of the organisms, is related to the variation of their morphology with the environment and its usage that they might do of their habitat.

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Supplementary Material

Morphological data matrix.

	0	10	20	30	40	50	60
Rhodothemis rufa	2121212112	22222122212	2222111222(12)	211(12)(12)21121	1222112222	2121121111	1221(12)(12)(12)121
Brachymesia herbida	1222121122	2222211222	2222212122	2111121122	1122112222	2121121111	1121---222
Libellula herculea	1(12)21212(12)22	22222122(12)2	2222111122	2111121121	1222112212	111(12)212111	(12)12(12)---111
Pantala flavescens	1121(12)(12)1(12)22	(12)222211212	(12)222111222	111(12)221121	1122111121(12)	1112211222	11(24)1421222
Miathyria marcella	1222(12)22121	2222222212	2122112222	2111221121	1122112212	1112121111	1131122212
Sympetrum gilvum	1222211122	2222212222	2222111222	2111121121	1222112222	2111121222	1121413222
Tramea calverti	112121(12)121	2222212112	221(12)1112222	211(12)121121	122(12)1122(12)2	2121122111	11(24)112(13)222
Tramea rustica	2121121122	2211221222	2222111222	2111121121	1222112222	1112121222	112????222
Perithemis thais	122222(12)212	222221(12)(12)(12)2	2222112122	(12)(12)(12)1121121	12221122(12)2	(12)2----211(12)	11(23)1---222
Perithemis lais	1222222212	2222212112	2222112122	2111121121	1222112222	22----2111	1131---222
Perithemis mooma	1121221212	22222(12)(12)1(12)2	2222111122	1222222211	111211121(12)	22112221212	1131---222
Garrisonia aurindae	1222211122	2221212212	(12)22(12)-12222	2112121121	1222112222	2121111111	22(13)1(24)(12)3211
Rhodopygia cardinalis	1222212122	2222212222	2222(12)12122	2111121121	2222212222	211122(12)112	1121311111
Rhodopygia geijskesi	(12)1212222212	22222(12)21(12)2	22221(12)2(12)22	2111121121	222221(12)222	21211(12)2111	1122(24)231(12)1
Rhodopygia hinei	1222212122	2222212212	2222(12)1212(12)	2111121121	2222212222	2111221111	1121311111
Rhodopygia hollandi	12222(12)(12)(12)(12)2	22222(12)2(12)22	2222(12)1212(12)	2111121121	22(12)2212222	212(12)(12)21111	21214231(12)1
Rhodopygia pruinosa	1121222212	2222222122	2222211212	2111111121	2221212222	2(12)21112111	21214231(12)1
Erythemis attala	1121(12)1212(12)	2222212212	2(12)22112222	211(12)(12)21121	11221112(12)2	2121121111	112(12)(13)(12)(123)111
Erythemis carmelita	1(12)2(12)2121(12)2	2222212(12)12	2222112(12)2(12)	211(12)121121	1222112222	2121121111	11(12)13(12)1111
Erythemis collocata	1222211112	(12)(12)1211(12)1(12)2	(12)2(12)1221(12)12	1111(12)11121	121(12)1112121	22----1111	1121---111
Erythemis credula	(12)(12)2(12)21(12)1(12)(12)	(12)(12)2221(12)212	(12)22211(12)2(12)(12)	211(12)221121	1(12)2(12)112212	21(12)1121111	11(12)1(12)2(23)111
Erythemis haematogastra	1121(12)121(12)(12)	2222212(12)1(12)	22(12)2112(12)22	2111(12)21121	122(12)(12)12222	2111121111	112(12)222111
Erythemis mithroides	1121(12)12222	2222212222	2222111222	211(12)121121	(12)222(12)12222	2122121111	11(12)11(12)1111
Erythemis peruviana	1111(12)11111	2222211111	2122(12)1222(12)	111(12)111121	11121112222	2111111111	11(12)(12)422111
Erythemis plebeja	1121(12)11111	2222211212	2222111122(12)	211(12)121121	1121111212	2111121111	1121(12)23111
Erythemis simplicicollis	1222211112	(12)212111112	122(12)211(12)12	111(12)111121	111(12)111121	22----1111	11(12)1---111
Erythemis vesiculosa	1222221122	2222211111	2222211112	111(12)(12)11121	1111111121	2112211111	11(12)2423111

	70	80	90	100	110	120
Rhodothemis rufa	2111222(23)2-	122(12)221211	111223411(12)	(23)(34)81112(45)1(45)	1111211(12)13	131232-111
Brachymesia herbida	1221222111	1111121211	1121233112	3(23)21112(12)11	3222111213	232132-231
Libellula hercúlea	(12)1112(23)1(12)(12)1	(12)211(23)(23)1212	(235)(123)212(56)(456)(23)1(34)	(145)(345)(347)2(12)2(345)(234)(12)1	(14)(12)21(23)21(23)11	1322312221
Pantala flavescens	1121242111	1211121112	1111255111	2(45)21122221	3222112314	2221132-221
Miathyria marcella	21212(12)2111	2211211211	1111213432	(23)411121116	6212111214	222122-231
Sympetrum gilvum	212121212-	2111211111	1112331?2	3(12)21111111	3222211114	2212112212
Tramea calverti	4121242(14)12	221(12)322211	11112(678)511(12)	366222(12)(34)26	42221(12)1314	222112-131
Tramea rustica	4121222111	2212122211	1111265212	3762222621	322212331-	---2122-221
Perithemis thais	3(12)(12)1242(13)11	2111211121	(2345)12(12)(12)(12)243(12)	(23)(234)(15)111(345)(2567)(12)(23)	12121(12)1(23)14	232122-211
Perithemis lais	(14)121212311	2111211121	(23)12121(12)431	2211113314	52121(12)221-	---2-------
Perithemis mooma	(134)(12)21242(1234)11	211(12)(23)11121	(123)12(12)(12)(12)24(23)(12)	(123)(1234)(15)111(234)(234568)1(1234)	(15)(12)121(12)1(23)14	2221122-2(13)1
Garrisonia aurindae	21112(23)141-	1211221211	111123(45)11(12)	(23)(12)2112(12)(34)11	(13)222112(23)14	2221112231
Rhodopygia cardinalis	2111222(23)11	(12)1122211211	111(12)2(34)(45)112	(34)4211(12)2(67)12	12223(12)1(23)14	141132-211
Rhodopygia geijskesi	41(12)1222(23)11	1112221211	1111234112	(24)321112(568)11	1222311214	241232-211
Rhodopygia hinei	2111222211	1111221211	11112(34)4112	(34)(345)21122(5678)11	1222321314	141132-211
Rhodopygia hollandi	(24)(12)21222311	1112221211	1111234112	3321122(456)11	12223(12)1314	141132-211
Rhodopygia pruinosa	41212(12)2(12)11	1112221211	111123(45)11(12)	(13)(34)21112(56)11	1222321314	141132-211
Erythemis attala	(12)(12)11221(23)1(12)	11122(12)1211	111223(345)(12)(12)(12)	(23)(12345)(23)1(12)(12)(123)(23456)1(12)	1(12)222(12)1211	1311111211
Erythemis carmelita	(12)(12)11221211	1112221211	1112234(12)1(12)	(23)42111(23)(2345)11	1222211211	1311212221
Erythemis collocata	1211221211	11222(23)1211	(12)1112234(12)1(12)	(23)(2345)(2)1112(245)11	1(12)2(12)211(12)12	1312212-222
Erythemis credula	(12)(12)112(12)1(12)11	1112221211	1112(12)(23)(45)(14)(123)(12)	(123)2(12589)111(123)(123)1(1234)	(13)111(23)(12)1211	13113122222
Erythemis haematogastra	(12)(12)112(23)1(234)12	1112221211	111(12)23(34)11(12)	(23)(123)211(12)(12)(234567)1(12)	1222(23)(12)(12)(23)11	1311312231
Erythemis mithroides	(12)(12)11221(23)12	(12)11(12)221211	11122341(12)(12)	(23)(234)21112(2345)1(12)	1222(23)11211	1311311231
Erythemis peruviana	(12)(12)11221211	(12)1(12)22(12)1211	1(12)1223411(12)	2(23)(12)1112(2345)1(12)	12222111(12)11	1311212111
Erythemis plebeja	(12)(12)112(12)1211	11(12)2221211	11122341(12)(12)	(123)(123)(124)11(12)(12)(2345)11	1(12)1(12)(23)1(12)212	1311312211
Erythemis simplicicollis	(12)(12)11221211	11(12)22(23)1211	11122341(12)(12)	(23)(123)2(12)112(2345)1(12)	12(12)2211(12)12	1312212-222
Erythemis vesiculosa	(12)(12)11221211	11(12)22(23)1211	111(12)23(45)11(12)	(23)(123)2(12)122(23456)11	1222(12)(12)1(23)11	131222-132

	130
Rhodothemis rufa	1
Brachymesia herbida	3
Libellula herculea	4
Pantala flavescens	1
Miathyria marcella	3
Sympetrum gilvum	2
Tramea calverti	1
Tramea rustica	1
Perithemis thais	1
Perithemis lais	-
Perithemis mooma	1
Garrisonia aurindae	1
Rhodopygia cardinalis	1
Rhodopygia geijskesi	3
Rhodopygia hinei	1
Rhodopygia hollandi	1
Rhodopygia pruinosa	1
Erythemis attala	1
Erythemis carmelita	3
Erythemis collocata	5
Erythemis credula	1
Erythemis haematogastra	3
Erythemis mithroides	1
Erythemis peruviana	2
Erythemis plebeja	1
Erythemis simplicicollis	5
Erythemis vesiculosa	(14)