Phylogeny and biogeography of the genus *Pelinoides* Cresson (Diptera-Ephydridae)

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Abstract

A phylogenetic analysis of the 21 species of genus *Pelinoides* using 44 discrete morphological characters is presented. From the previous proposed three groups, *pallipes*, *sulcatus* and *cyclocerus*, the first is recovered. The *sulcatus* group appears as paraphyletic in terms of *cyclocerus*. *Pelinoides* is present in the Neotropical and Andean Regions and in the Transitional South American Zone. Four areas of maximum endemicity were found. Eleven vicariant events are described and discussed, using the areas of endemisms and biogeographic provinces where *Pelinoides* occurs.

Key words: *Pelinoides*, Phylogeny, Biogeography, Andean and Neotropical Regions

Resumen

Se presenta un análisis filogenético de las 21 especies del género *Pelinoides*, usando 44 caracteres morfológicos discretos. Se recupera al grupo *pallipes* de una propuesta anterior que definía tres grupos: *pallipes*, *sulcatus* y *cyclocerus*. El grupo *sulcatus* resulta parafilético en términos de *cyclocerus*. *Pelinoides* está presente en las Regiones Biogeográficas Neotropical y Andina y en la Zona de Transición de América del Sur. Se determinan cuatro áreas de máximo valor de endemidad. Se describen y discuten once eventos vicariantes usando las áreas de endemismo y las provincias biogeográficas donde está presente el género *Pelinoides*.

Palabras clave: *Pelinoides*, Filogenia, Biogeografía, Regiones Andina y Neotropical

Introduction

The shore-fly genus *Pelinoides* Cresson 1931 is placed in the subfamily Ilytheinae Cresson, tribe Hyadinini Phillips et al. (Mathis & Zatwarnicki, 1995). This group is appropriate for cladistic and biogeographic analysis because it is clearly a monophyletic group, with only 21 species that are distributed in very restricted areas — biogeographic provinces, ecoregions— of the Andean and Neotropical Regions and Transitional South American Zone (Morrone, 2004). Although the alpha taxonomy is fairly accurate (Cresson, 1934; Wirth, 1968; Lizarralde de Grosso, 1981, 1989; Mathis, 1977, 1985), relationships between the species are still unknown, and nothing has been published regarding the sequence of vicariant events in this genus. The only statement on the internal relationships in *Pelinoides* was given by Mathis (1985), who divided the genus in 3 species groups: the *pallipes* group, with two species (*P. pallipes* and *P. andinus*) distributed on both sides of the Andes in Perú, Ecuador and Colombia and, in Central America below 1000 m of altitude; the *cyclocerus* group, with a single
species, from the O’ Higgins Province in Chile; and the sulcatus group with the 18 remaining species (P. ambly, P. andinus, P. australis, P. chilensis, P. chiloensis, P. colerus, P. flavipalpus, P. flinti, P. fuscus, P. nigrihalteratus, P. obscurus, P. opacus, P. penai, P. phaeopleurus, P. pruinosus, P. pullus, P. sulcatus, P. unctus) spread from the Navarino Island through temperate zones in Argentina and Chile to the highest areas in Perú and Ecuador. This is the first attempt to analyze relationships among the 21 species of Pelinoides according the morphological characters classically used in the taxonomy of this group.

Objectives of this work are to propose the first cladistic analysis for the 21 species of Pelinoides, to test the validity of species groups previously proposed, and to identify possible vicariant events, that requires not only the phylogenetic hypothesis of the group in question but also the units of study (the areas) identified. Geographic units of study were analyzed using formal and quantitative methods.

Material and methods

Cladistic Analysis

Cladistic analysis was carried out using parsimony criteria under equal weights, as implemented in the program TNT ver. 1.0 (Goloboff et al., 2005; see reviews of the program in Giribet, 2005, Hovenkamp, 2004, Meier & Ali, 2005). The tree search algorithms used here were forty replications of a random addition sequence Wagner tree, each followed by tree bisection reconnection (TBR) branch-swapping. The group support was measured using relative Bremer Support (Goloboff & Farris, 2001) and jacknifing (symmetric re-sampling of Goloboff et al., 2003).

Characters used in this study (Appendix 1) were observed in types and additional material from the Instituto-Fundación Miguel Lillo, and/or taken from the literature (Cresson 1931, 1934; Hendel 1930, Lizarralde de Grosso, 1981; Mathis, 1977, 1985; Zatwarnicki, 1992).

All characters are discrete. Stripe pattern of mesonotum, which has eight conditions (Figs.1–8), was coded in two ways: (1) as a lineal additive character with eight states, and (2) the trait was divided into six characters (see Appendix 1 for a full description). Results of both codification types are compared and discussed.

Nostima elegantula Hendel 1930 was chosen as the outgroup, and all species of Pelinoides were included in the study (see Appendix 2).

Biogeographic analysis

To identify areas we used the formal method of areas of endemism (Szumik et al., 2002; Szumik & Goloboff, 2004); implemented in the programs NDM and VNDM ver. 2.5 (Goloboff, 2005). A data matrix for this analysis consisted of a cell grid of 2º where presence/absence of each species of Pelinoides was recorded for each cell of the grid. The method evaluates, with an index, areas (group of cells) according to how well the distribution of a species to each area is adjusted. Then, those areas with maximum values are retained. One hundred records from the 21 species were analyzed (binary data matrix in Appendix 3). When the species were not part of any area of endemism, distribution was replaced by the biogeographic provinces equivalent (following Morrone, 2001; 2004). The resulting areas were scored as a unique unordered character and mapped using a down pass Fitch optimization (following Ronquist, 1994). Those nodes, that separated two or more disjunct areas, are then considered as evidence of a vicariant event.

Results and discussion

Phylogeny

Optimal trees from both types of codification of mesonotum stripes have some resolution in common (see
consensus Fig. 9): the monophyly of the *pallipes* group and the paraphyly of the *sulcatus* group. Almost all the synapomorphies that define the *Pelinoides* non “pallipes” are not homoplastic (Figs. 10 and 11), namely, the absence of dorsally branching rays onto the arista (character 5), the dorso-apical angle of the first flagellomere angulated (character 6) and blackish brown femora and tibia (character 31). There is also some agreement on the apical section of the cladograms (Fig. 9): (1), the group of *P. pullus* and *P. chilensis* being supported by having a scutum with blackish stripes (character 19, Figs. 10 and 11) and the abdominal tergum less microtomentose than the mesonotum (character 34, Figs. 10 and 11), and (2) the species *P. cyclocerus*, *P. sulcatus*, *P. amblys*, *P. phaeonotus*, *P. chiloensis*, *P. nigrihalteratus* and *P. australis* by sharing the sparsely microtomentose mesonotum (character 16) and the abdominal tergum more microtomentose than mesonotum (character 34, Figs. 10 and 11).

Four optimal trees (with 155 steps, CI: 50, RI: 56) are obtained when the stripes of the mesonotum are analyzed as a unique and additive character, which appears as a synapomorphy of several groups (see consensus Fig. 10). However, it is not very concordant (15 extra steps) and has some parallelisms (e.g. the state 0 present in *P. pullus* and the group of *P. amblys* and *P. phaeonotus*, or the state 1 in *P. andinus* and *P. obscurus*). Six optimal trees (149 steps longer, CI: 52, RI: 57) with the alternative codification of the mesonotum stripes (characters 39 to 44 in Appendix 1) are found. Characters 41 and 42 are the only informative ones. The partial stripes (character 41) appear perfectly adjusted to the trees and supporting the group of *P. punctus* and *P. pruinosis*. The absence of stripes on the dorsal tracks (character 42) defines the sister group of *P. flavipalpus* (Fig. 11) but the presence of this condition reappears independently three times in *P. pruinosis*, *P. phaeopleurus*, and *P. nigrihalteratus*.

There are many optimal alternatives for the position of the species *P. phaeopleurus*, *P. colerus*, *P. flinti*, *P. fuscus* and *P. penai* in the trees in both analyses, but this group is well supported, according to the Bremer support in the alternative codification (Fig.12). There are a few nodes that have a median support like the *pallipes* group (Fig. 12) and some other nodes in the apical section of the cladogram with two supports (Figs. 12 and 13). Then some relationships remain unresolved (position of *P. phaeopleurus*, *P. colerus*, *P. flinti*, *P. fuscus* and *P. penai* and position of *P. flavipalpus*, *P. opacus*, *P. punctus*, *P. pruinosis*). Species groups proposed by Mathis (1985) are recovered in part: in our study, the *pallipes* group is recovered, and *sulcatus* group appears as paraphyletic in terms of *cyclocerus*.

Hence, we propose two species groups, *pallipes*, like Mathis 1985, and *sulcatus*, for all other species (Fig. 9–13):

a) *pallipes* group: *P. pallipes* and *P. andinus*. Distribution: Panamá, Honduras, Guatemala, Colombia, Ecuador and Perú.

b) *sulcatus* group: the other 19 species. Distribution: Ecuador, Perú, Argentina, Uruguay, Chile to Navarino Island.

Biogeography

*Pelinoides* is distributed from Mesoamerica to the extreme south of South America. The *pallipes* group is distributed from Guatemala to Perú, and the *sulcatus* group from Ecuador to the south of Chile. The groups overlap only in Ecuador and Perú.

Eight species are found in a single locality: *P. cyclocerus* (Río Claro, O’Higgins Province, Chile), *P. pullus* (Abra Pampa, Jujuy, Argentina), *P. amblys* (Parral Linares, Chile), *P. chiloensis* (Chepu, Chiloé, Chile), *P. phaeonotus* (Río Orosmayo, Jujuy Province, Argentina), *P. opacus* (Tucumán, Argentina), *P. pruinosis* (Escoipe, Salta Province, Argentina) and one in a very restricted area: *P. nigrihalteratus* (Osorno Province, Chile) (all of them of *sulcatus* group).

Four areas with maximum values of endemicity were found with NDM (Figs. 14). Area (A) is equivalent to the combined biogeographic provinces Puna / Prepuna and is defined by five species: *P. fuscus*, *P. opacus*, *P. phaeonotus*, *P. pruinosis* and *P. pullus*. Area (B) is the combination of the provinces of Coquimbo / Maule
and is defined by three species *P. chilensis*, *P. flavipalpus* and *P. penai*. Area (C) is the combination of Maule / Valdivian Forest, where two species gave the endemicity score: *P. penai* and *P. phaeopleurus*. Area (D) is the Valdivian Forest defined by three species: *P. chiloensis*, *P. cyclocerus* and *P. nigrihalteratus*. We replaced the distributions of the twelve species of *Pelinoides* that do not give any endemicity score by the biogeographic provinces they occupy (Appendix 4). An unordered character of 14 states representing those provinces was mapped onto the ten optimal trees in the morphological analysis.

FIGURES 1–9. 1–8, Conditions of stripes of mesonotum. 9, Consensus of all trees obtained in both analyses.
FIGURES 10–11. 10, Consensus with the synapomorphies common to the four optimal trees. (mesonotum stripes’ codification I). 11, Consensus with the synapomorphies common to the six optimal trees. (mesonotum stripes’ codification II).

Vicariant events common to the 10 cladograms (Fig.9, 15–25) are: A (Fig.15) (Peruvian Puna + Napo + Western Ecuador + Western Panamanian Isthmus + Chiapas) and (Argentinean Puna + Prepuna + Atacama + Coquimbo + Santiago + Maule); B (Fig.16) (Peruvian Puna + Napo) and (Western Ecuador + Western Pana
FIGURES 12–13. 12, Relative Bremer supports (from 5000 trees 6 steps longer) and Symmetric Resampling (P=33) for codification I. 13, Relative Bremer supports (from 5000 trees 6 steps longer) and Symmetric Resampling (P=33) for codification I.

manian Isthmus + Chiapas); C (Fig.17) (Argentinean Puna + Prepuna) and (Atacama + Coquimbo + Santiago + Maule); D (Fig.18) (Argentinean Puna + Prepuna) and (Maule + Valdivian Forest). The following vicariant event present in both groups of cladograms, even though the relationships among the species are not the same. Such an event (Figs.10–11, 15–25) is represented by E (Fig.19) (similar to C but present in the basal section of the cladograms) between (Atacama + Coquimbo + Santiago + Maule) and (Puna + Prepuna). Other events are present only in one cladogram group like (Figs.10-11): F (Fig.20) (Monte + Pampa) and (Norandean Paramo + Puna + Prepuna + Magellanic Forest); G (Fig.21) (Norandean Paramo + Peruvian Puna) and (Argentinean Puna + Prepuna + Magellanic Forest); H (Fig. 22) (Argentinean Puna + Prepuna) and (Magellanic Forest); I
(Fig23), which is similar to F, (Monte + Pampa) and (Puna + Prepuna); J (Fig.24) (Puna + Prepuna + Atacama + Coquimbo + Santiago + Maule) and (Valdivian Forest); K (Fig.25) (Puna + Prepuna + Maule) and (Valdivian Forest).

**FIGURE 14.** Areas of endemism obtained with NDM/VNDM: (A): Puna + Prepuna; (B): Coquimbo / Maule; (C): Maule + Valdivian Forest; (D): Valdivian Forest.
According to Morrone’s Biogeographic Regions (2004) *Pelinoides* is present in the Neotropical and Andean Regions, and also in the Transitional South American Zone. In this study we describe four areas of endemism: one corresponding to Transitional South American Zone, and three to the Andean Region. The eleven vicariant events described here involved only the Transitional Zone (one event); the Transitional Zone and the Andean Region (6 events); the Transitional Zone and the Neotropical Region (3 events); and the Transitional Zone, and the Neotropical and the Andean regions (one event). Morrone (2004) commented on the relevance of the biotic components that are present in transitional zones. That is the case in event F (Fig. 20) that involved almost all the South American Transitional Zone plus the biogeographic province of Pampa (in part) of the Neotropic Region.

Areas of endemism are restricted to the Transitional Zone (Argentinean Puna and Prepuna) and the Andean Region (Coquimbo, Maule and Valdivian Forest), except for the province of Santiago that is between them. (Fig. 27).

Our results are mainly coincident with other works using arthropods (Morrone 1994; Morrone et al, 1997; Roig Juñent & Coscarón 2001; Roig Juñent & Flores 2001; Roig Juñent et al 2003; Marino et al 2001); some disagreement between them can probably be ascribed to different methods and taxonomy groups treated in each research project.

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References


Appendix 1. List of characters used in the cladistic analysis. Characters 1, 2, 4, 7, 9, 10, 12, 13, 15, 20, 21, 24, 25, 30, 35, 36 and 37 are uninformative; they are included here to show on the cladograms the list of autapomorphies of Pelinoides. Characters are codified as additive.

Head:
0. Vestiture of Mesofrons. (0) very sparsely microtomentose; (1) mostly sparsely microtomentose; (2) densely sparsely microtomentose; (3) moderately densely microtomentose; (4) densely microtomentose.
1. Mesofrons with a large bare area. (0) no; (1) yes.
2. Fronto-orbital bristles conspicuous. (0) no; (1) yes.
3. Antenna coloration. (0) black to dark brown; (1) same to 0 but first flagellomere yellowish to orange; (2) orange yellowish.
4. Arista bearing small hairs. (0) yes; (1) no, with long hairs.
5. Arista with dorsally branching rays. (0) long; (1) short; (2) absent.
6. Dorso-apical angle of first flagellomere. (0) broadly rounded; (1) angulated.
7. Face beyond anterior margin. (0) flat; (1) convex.
8. Midface coloration. (0) bluish grey; (1) white silvery; (2) shiny white; (3) brownish white (4) yellowish.
9. Epistomal margin of face broadly emarginate medially. (0) yes; (1) no.
10. Clypeus. (0) conspicuous; (1) inconspicuous.
11. Gena coloration. (0) yellowish white; (1) silvery white; (2) white to grey (3) brownish white.
12. Eyes prominent. (0) yes; (1) no.
13. Eyes. (0) glabrous; (1) pilose.
14. Palpus coloration. (0) black brownish; (1) yellowish brown; (2) yellow to orange; (3) yellow.

Thorax:
15. General coloration. (0) brown to nearly black; (1) pale grey yellowish.
16. Vestiture of the mesonotum. (0) very densely microtomentose; (1) moderately densely microtomentose; (2) sparsely microtomentose; (3) very sparsely microtomentose to bare.
17. Mesonotum coloration. (0) brown to mostly black; (1) mostly brown (2) mostly brown to grayish brown; (3) olivaceous to brown; (4) grey to golden brown.

Stripes of scutum:
18. Stripes of the scutum. (0) absent; (1) present.
19. Stripes of scutum coloration. (0) golden brown; (1) dark brown; (2) greyish; (3) brownish; (4) blackish.
20. Median stripe. (0) present; (1) absent.
21. Intraalar stripes. (0) present; (1) absent.

Scutellum:
22. Basolateral margins of scutellum. (0) no microtomentose; (1) slightly velvety microtomentose; (2) densely microtomentose.
23. Posteroblique angle of scutellum appearing velvety black. (0) no; (1) yes.
24. Presutural bristles. (0) conspicuous; (1) inconspicuous.
25. Acrostichal setulae. (0) conspicuous; (1) small, inconspicuous.
26. Dorsocentrals bristles. (0) five; (1) three or four; (2) two; (3) one.

Halters and Wings:
27. Knob of halter. (0) blackish brown; (1) brownish; (2) yellowish slightly brownish; (3) whitish yellowish.
28. Stem of halter. (0) yellowish; (1) yellowish brown.
29. Wing. (0) hyaline; (1) with clouded areas; (2) very lightly infumose.
30. Wing vein 1. (0) rather swollen and black; (1) no swollen and black.

Legs:
31. Femora and tibia. (0) blackish brown; (1) yellowish brown; (2) slightly yellow.

Abdomen:
32. Tergum coloration. (0) mostly blackish; (1) mostly brown.
33. Tergum microtomentose. (0) yes; (1) partially shiny.
34. Tergum microtomentose respect to mesonotum. (0) more; (1) equal; (2) slightly less; (3) less.

Male genitalia:
35. **Epandrium.** (0) distally tapered; (1) distally round.
36. **Gonite.** (0) with reduced setulae; (1) setose.
37. **Long setae inserted at connection of gonite with hypandrium.** (0) present; (1) absent.

Codifications of the mesonotum stripes pattern (Fig. 1–8). Of course when a codification was analysed with the program TNT the other was deactivated.

**Codification I:**
38. (Additive). (0) without stripes; (1) with stripes laterad to acrostichal tracks (2) same as 1 but with partial stripes laterad to dorsocentals tracks; (3) same as 1 but with stripes laterad to dorsocentral tracks; (4) stripes anteriad to either side of acrostichal tracks; (5) stripes through acrostichal tracks and on lateral margin; (6) stripes through acrostichal and dorsocentral tracks; (7) stripes between dorsocentral and intra-alar tracks.

**Codification II:**
39. **Stripes laterad to acrostichal tracks:** (0) absent; (1) present.
40. **Stripes through acrostichal tracks:** (0) present; (1) absent.
41. **Partial stripes laterad to dorsocentral tracks:** (0) present; (1) absent.
42. **Stripes laterad to dorsocentral tracks:** (0) present; (0) absent.
43. **Stripes anteriad on either side of acrostichal tracks:** (0) present; (1) absent.
44. **Stripes on lateral margin:** (0) present; (1) absent.

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Appendix 3. Binary data matrix of presence and absence of species on a cell grid of 26 x 20 (2°x3°). The rows are the grid cells, the numbers indicate the position of the cell in the grid, e.g. cell 0–1 is located in the row 0 and column 1. The columns are the species of *Pelecanoides*: 0, *P. amblys*; 1, *P. andinus*; 2, *P. australis*; 3, *P. chilensis*; 4, *P. chiloensis*; 5, *P. coleru*s; 6, *P. cyclocreus*; 7, *P. flavipalpus*; 8, *P. flii*; 9, *P. fuscus*; 10, *P. nigrihalteratus*; 11, *P. obscurus*; 12, *P. opacus*; 13, *P. pallipes*; 14, *P. penai*; 15, *P. phaeonotus*; 16, *P. phaeopleurus*; 17, *P. pruinosis*; 18, *P. pullus*; 19, *P. sulcatus*; 20, *P. unctus*.

|       | 0-0 | 0-1 | 0-2 | 0-3 | 1-0 | 1-1 | 1-2 | 1-3 | 2-5 | 2-6 | 2-7 | 3-5 | 3-6 | 3-7 | 4-7 | 4-8 | 5-5 | 5-6 | 5-7 | 5-8 | 6-5 | 6-6 | 6-7 | 6-8 | 7-5 | 7-6 | 7-7 | 8-7 | 8-8 | 8-9 | 9-7 | 9-8 | 9-9 | 9-10 | 9-11 | 10-9 |
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