

Cladistics and biogeography of the assassin bug genus *Rasahus* Amyot & Serville (Heteroptera: Reduviidae: Peiratinae)

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Key words: Cladistics; biogeography; *Rasahus*; Heteroptera.

The assassin bug genus *Rasahus* Amyot & Serville (Heteroptera: Reduviidae: Peiratinae) comprises 26 Neotropical species. A cladistic analysis of the genus was carried out using 63 characters from external morphology, body vestiture, and male and female genitalia, with the species considered as terminal taxa. The analysis yielded 149 equally parsimonious cladograms, each with 206 steps, CI = 0.35, and RI = 0.60; the successive weighting procedure resulted in eight cladograms (CI = 0.79 and RI = 0.91). In the strict consensus cladogram, two major clades are delimited: one comprising the species *R. rufiventris*, *R. hamatus*, *R. arcitenens*, *R. arcuiger*, *R. amapaensis*, *R. thoracicus*, *R. biguttatus*, *R. argentinensis*, *R. limai*, *R. grandis*, and *R. angulatus*; and the other with *R. castaneus*, *R. aeneus*, *R. scutellaris*, *R. maculipennis*, *R. brasiliensis*, *R. sulcicollis*, *R. surinamensis*, *R. albomaculatus*, *R. guttatipennis*, *R. atratus*, *R. peruensis*, *R. costaricensis*, *R. bifurcatus*, *R. flavovittatus*, and *R. paraguayensis*. A cladistic biogeographic analysis of the provinces of the Neotropical subregion, considering distributional data of the species of *Rasahus* and three other genera of Peiratinae (*Eidmannia*, *Melanolestes*, and *Thymbreus*) was carried out. Four general area cladograms were obtained applying programs COMPONENT 2.0 and TASS. The most parsimonious general area cladogram (= implying fewer items of error) was obtained with COMPONENT 2.0 minimizing the number of leaves added, and shows the sequence (Desierto, (Caatinga, (Cerrado, (Chacoan, (Caribbean, Amazonian), (Paranaense, Atlantic)))). This sequence of area relationships is congruent with the history previously hypothesized for the subregion, where the development of an open vegetated diagonal (comprising the Chacoan, Cerrado, and Caatinga provinces) due to the aridification induced by the gradual uplift of the Andes, separated the former Amazonian forest in a northwestern part (Caribbean plus Amazonian provinces) and a southeastern part (Paranaense plus Atlantic provinces).

Introduction

The assassin bug genus *Rasahus* Amyot & Serville (Heteroptera: Reduviidae: Peiratinae) is widespread throughout the Neotropical subregion, with two species extending into the Nearctic (Morrone & Coscarón, 1996). The 26 species of the genus have been revised (Coscarón, 1983, 1986a; Coscarón & Maldonado-Capriles, 1988). Although other genera of Peiratinae have been cladistically analyzed (Coscarón, 1989, 1994, 1997; Coscarón & Morrone, 1995, 1997), a phylogenetic hypothesis of *Rasahus* is still lacking.

In a recent parsimony analysis of endemism (PAE) of the Neotropical Peiratinae, we (Morrone and Coscarón, 1996) hypothesized that the gradual development of an open vegetated diagonal, comprising the Chacoan, Cerrado, and Caatinga provinces, separated the former Amazonian forest in a northwestern part (Caribbean plus Amazonian provinces) and a southeastern part (Paranaense plus Atlantic provinces). PAE does not constitute a strict cladistic biogeographic method (but could be useful for

identifying areas of endemism; see Morrone and Crisci, 1995), so the availability of four area cladograms of peiratine genera allowed us to test our former hypothesis.

Our objectives are to undertake a cladistic analysis of the species of *Rasahus*, and to relate their distributional patterns to those of other taxa using a cladistic biogeographic approach, to test our previous hypothesis (Morrone and Coscarón, 1996).

Material and methods

Data were taken from the most recent revisions (Coscarón, 1983, 1986a; Coscarón and Maldonado-Capriles, 1988) and from material provided by the following collections: American Museum of Natural History, New York (USA); The Natural History Museum, London (United Kingdom); California Academy of Sciences, California (USA); Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa (Canada); Fundación e Instituto Miguel Lillo, San Miguel de Tucumán (Argentina); Instituto Oswaldo Cruz, Rio de Janeiro (Brazil); Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires (Argentina); Museo de La Plata, La Plata (Argentina); Museu Paranaense Emílio Goeldi, Belém (Brazil); Museum National d'Histoire Naturelle, Paris (France); Museu de Zoologia de São Paulo, São Paulo (Brazil); Naturhistoriska Riksmuseet, Stockholm (Sweden); Nationaal Natuurhistorisch Museum, Leiden (The Netherlands); Snow Entomological Museum, Kansas (USA); United States National Museum, Washington, D.C. (USA); Universidad Central de Venezuela, Maracay (Venezuela); Universitetets Zoologiske Museum, Copenhagen (Denmark); Zoological Museum, University of Helsinki, Helsinki (Finland); Zoologisches Museum der Humboldt Universität zu Berlin, Berlin (Germany); and private collection of Mr. A. Martínez, Salta (Argentina).

Rasahus forms a monophyletic group that is distinguished from other Peiratinae genera by the spongy fossa occupying more than half the length of the tibia, the non-accuminated scutellum, and female tergite X lacking a projection. The 26 species of the genus (Coscarón, 1983, 1986a; Coscarón and Maldonado-Capriles, 1988) are considered as terminal taxa. Table 1 lists the species and their geographical distribution.

A total of 63 characters were derived from external morphology, male and female genitalia, and body vestiture (table 2). Multistate characters 39-47 were treated as nonadditive. Characters for which information was not available were assigned a missing data code. Table 3 contains the data matrix used, which was analyzed with Hennig86 version 1.5 (Farris, 1988), applying the *mhennig** and *bb** options for calculating trees. Cladograms were rooted with the genus *Peirates* (Coscarón and Morrone, 1995; Coscarón, 1997). Consistency (Kluge and Farris, 1969) and retention (Farris, 1989) indices were calculated excluding autapomorphies. In order to reduce the number of trees and to raise the consistency index we used the successive weighting procedure implemented in Hennig86 (Farris, 1989). The strict consensus tree was calculated with the *nelsen* option of Hennig86. CLADOS version 1.1 (Nixon, 1992) was used for examination of character distributions.

Cladistic biogeographic methods are detailed in Morrone and Carpenter (1994) and Morrone and Crisci (1995). The areas of endemism considered as terminal units are eight out of the nine biogeographical provinces of the Neotropical subregion (*sensu* Morrone, 1996): Caribbean, Amazonian, Paranaense, Atlantic, Desierto, Caatin-

ga, Cerrado, and Chacoan (fig. 2). We lack data for Peiratinae from the Guyanan province, so this area was not included in the analysis.

In order to analyze the generality of the geographical patterns of *Rasahus*, the cladograms of three other genera of Neotropical Peiratinae were considered: *Eidmannia* Teuber (Coscarón, 1986b, 1989), *Melanolestes* Stål (Coscarón and Carpintero, 1993; Coscarón and Morrone, 1997), and *Thymbreus* Stål (Coscarón, 1994). Area cladograms (fig. 3a-d) were constructed by replacing the name of the species of the four taxon cladograms with the name of the area(s) in which they occur.

Two different programs were used to obtain the general area cladograms. COMPONENT 2.0 (Page, 1993) was applied mapping the area cladograms onto the general area cladograms and measuring their fit by minimizing the number of leaves added, losses, and duplications needed to reconcile them. TASS (Nelson and Ladiges, 1995) was used to reduce the area cladograms to paralogy-free subtrees (see Nelson and Ladiges, 1996) and obtain a data matrix under assumption 2 (table 4), which was later analyzed with Hennig86 (Farris, 1988) with the implicit enumeration (ie*) option. In order to select the most parsimonious general area cladogram, items of error (Nelson and Platnick, 1981) were calculated with option FIT of COMPONENT 1.5 (Page, 1989).

Results and discussion

The analysis of the data matrix (table 3) using equal weights yielded 149 equally parsimonious cladograms, each with 206 steps, a consistency index of 0.35, and a retention index of 0.60. When successive weighting was applied, eight minimum-length cladograms resulted, with length 362, a consistency index of 0.79, and a retention index of 0.91. The strict consensus tree for these cladograms is shown in fig. 1. Two major clades are delimited: one comprising the species *R. rufiventris*, *R. hamatus*, *R. arcitenens*, *R. arcuiger*, *R. amapaensis*, *R. thoracicus*, *R. biguttatus*, *R. argentinensis*, *R. limai*, *R. grandis*, and *R. angulatus*; and the other with *R. castaneus*, *R. aeneus*, *R. scutellaris*, *R. maculipennis*, *R. brasiliensis*, *R. sulcicollis*, *R. surinamensis*, *R. albomaculatus*, *R. guttatipennis*, *R. atratus*, *R. peruensis*, *R. costarricensis*, *R. bifurcatus*, *R. flavovittatus*, and *R. paraguayensis*.

The area cladograms of *Rasahus*, *Eidmannia*, *Melanolestes*, and *Thymbreus* are presented in fig. 3a-d. COMPONENT 2.0 allowed to obtain a single general area cladogram minimizing the number of leaves added (fig. 4a) and two general area cladograms minimizing the number of losses (fig. 4b, c). When minimizing duplications + leaves added and duplications + losses, the limit of 1000 cladograms that can be stored by the program was reached, so the search was interrupted. Applying TASS, a data matrix (table 4) was produced. Analysis of this data matrix with Hennig86 led to a single general area cladogram (fig. 4d) with 19 steps, CI= 0.73, and RI= 0.78.

Items of error were calculated for the four general area cladograms. The first general area cladogram (fig. 4a), obtained with COMPONENT 2.0, has the lowest value (300), so it was selected as the best hypothesis to explain the data. The other general area cladograms obtained with COMPONENT (fig. 4b,c), as well as the cladogram obtained with TASS (fig. 4d), have more items of error (352, 362, and 430, respectively).

The chosen general area cladogram (fig. 4a) shows the following sequence of area relationships: (Desierto, (Caatinga, (Cerrado, (Chacoan, ((Caribbean, Amazonian), (Paranaense, Atlantic))))) In this general area cladogram, the "open vegetated" provinces (Desierto, Caatinga, Cerrado, and Chacoan) are basal, whereas the "forest" provinces (Caribbean, Amazonian, Paranaense, and Atlantic), although now widely separated in two disjunct areas, form a monophyletic group.

The relationships of the provinces in the general area cladogram are in general agreement with the previously hypothesized scenario (Morrone and Coscarón, 1996). The gradual uplift of the Andes, which began in the late Oligocene and underwent its major uplift until Pliocene, cut off the Pacific wind drift and induced aridity to vast areas in South America. By middle Miocene, subtropical environments were shifted to the North and extensive open-country environments developed (Pascual and Ortiz Jaureguizar, 1990). The openly vegetated diagonal is hypothesized to be the vicariant event that separated the former continuous forest into two "blocks" (Caribbean + Amazonian, and Paranaense + Atlantic). Future studies are needed to determine which are the vicariant events that subdivided the open vegetated provinces, the Caribbean and Amazonian provinces, and the Paranaense and Atlantic provinces.

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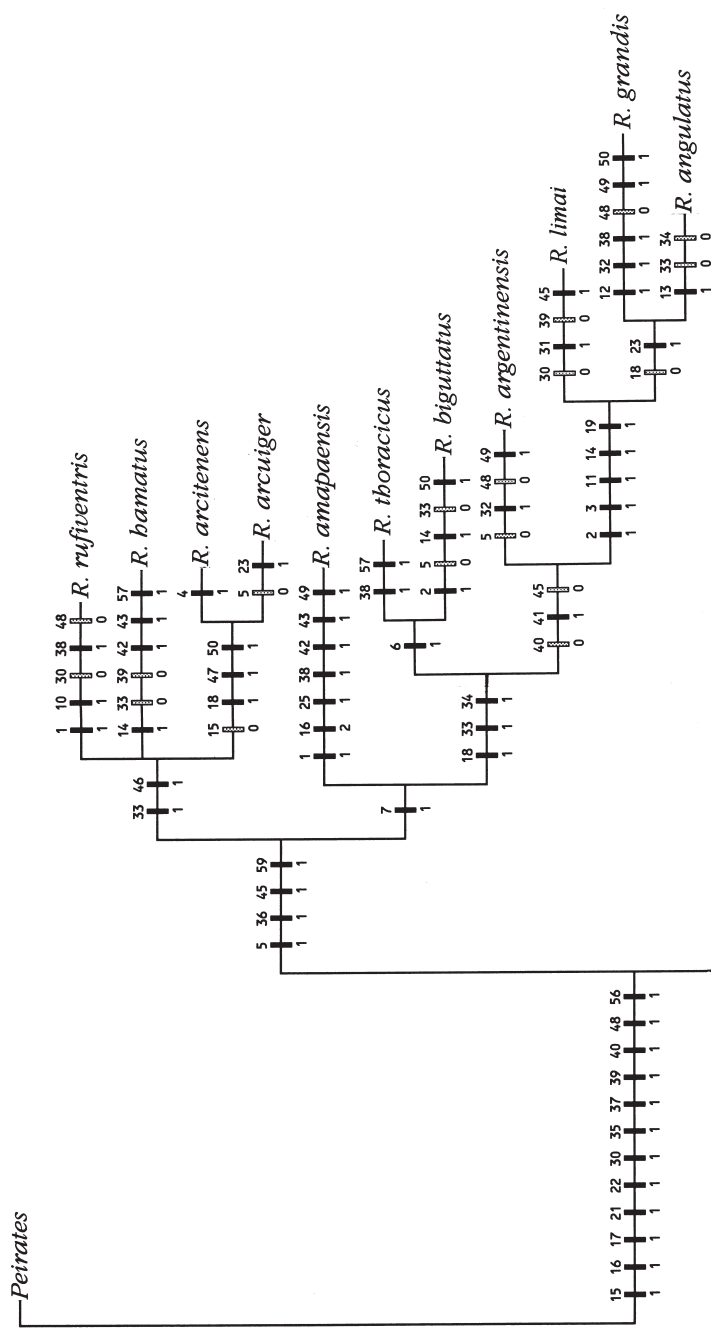
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Fig. 1. Strict consensus of the eight cladograms obtained after successive weighting. Black squares= synapomorphies; dotted squares = homoplastic changes.



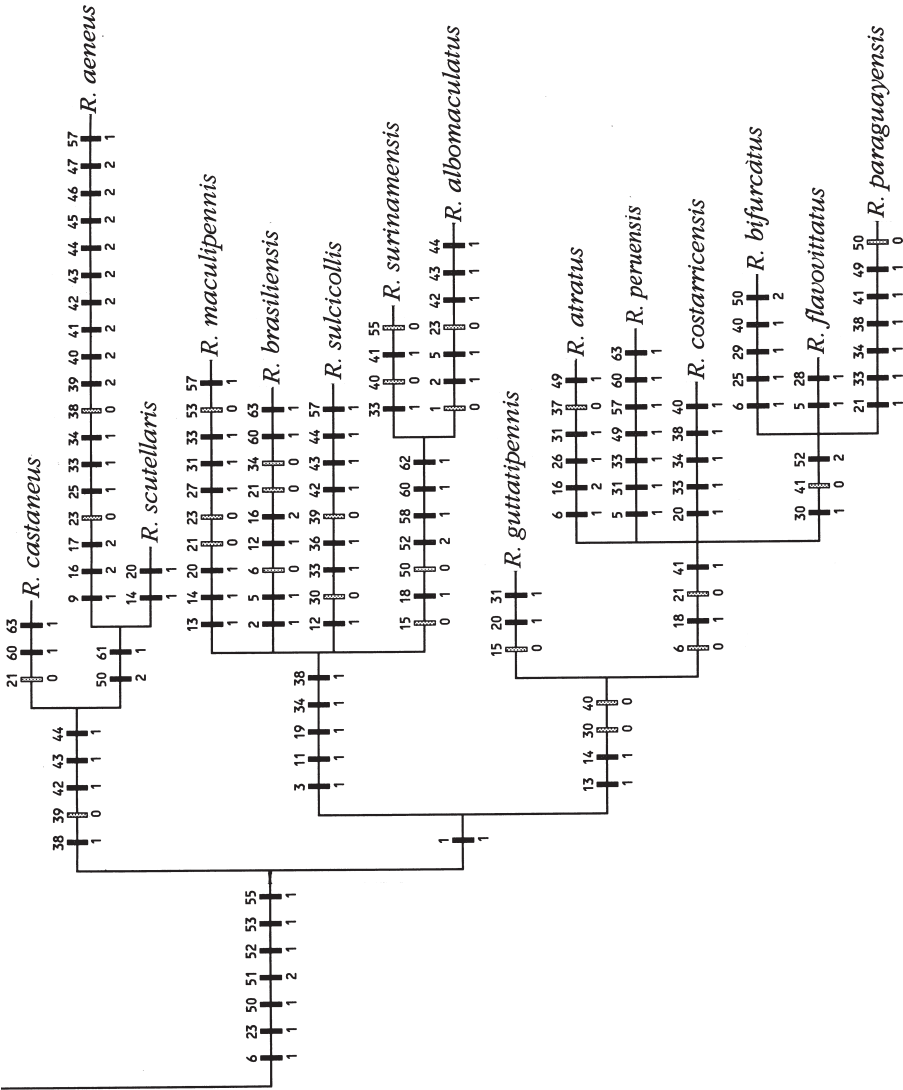




Fig. 2. Map of South America with the biogeographic provinces (Morrone, 1996) considered in the analysis. AMA = Amazonian; ATL = Atlantic; CAA = Caatinga; CAR = Caribbean; CER = Cerrado; CHA = Chacoan; DES = Desierto; PAR = Paranaense.

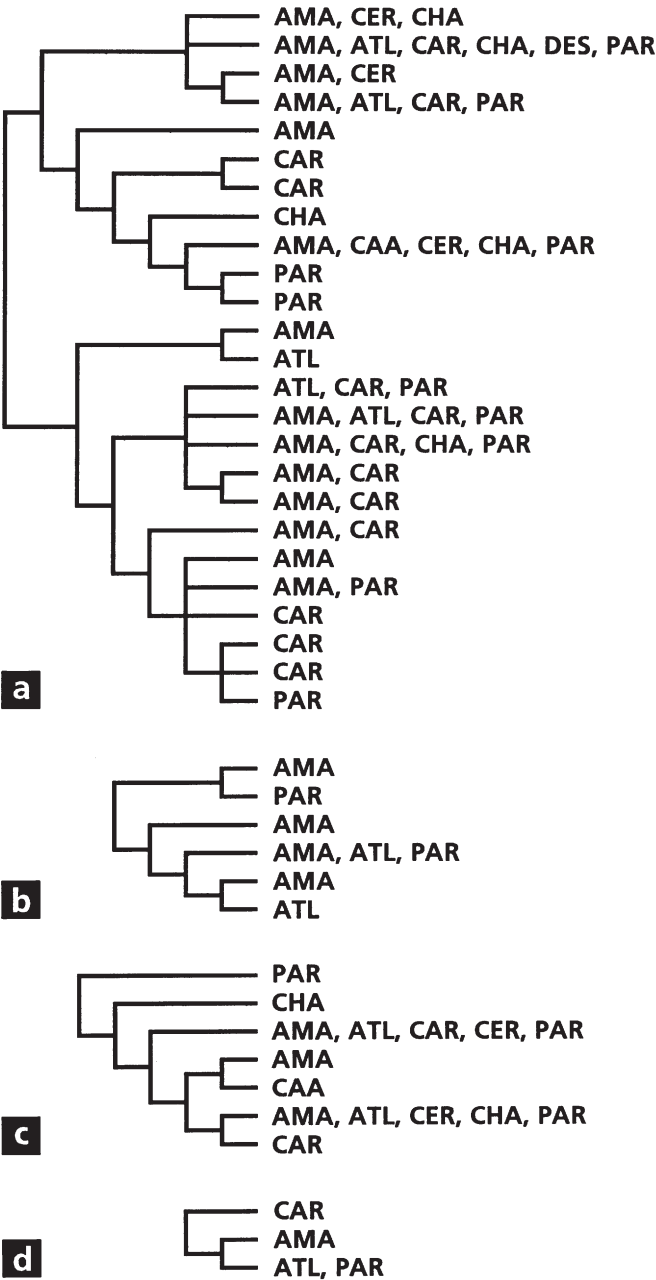


Fig. 3. Area cladograms used in the cladistic biogeographic analysis. a, *Rasahus*; b, *Eidmannia*; c, *Melanolestes*; d, *Thymbreus*. Acronyms as in fig. 2.

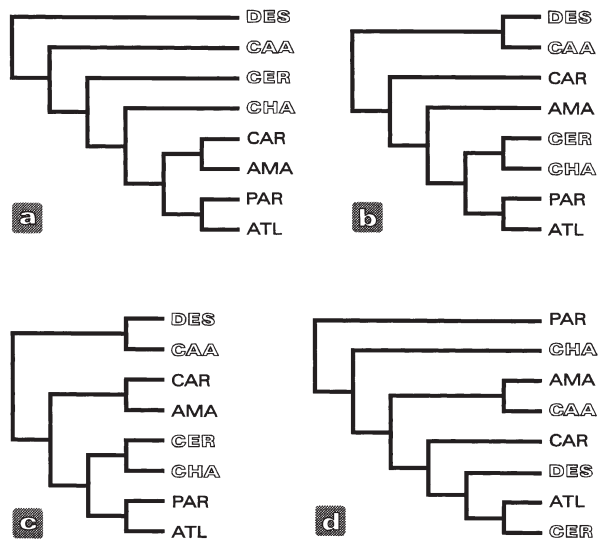


Fig. 4. General area cladograms obtained in the cladistic biogeographic analysis. a, COMPONENT 2.0 minimizing leaves added (300 items of error); b, c, COMPONENT 2.0 minimizing losses (352 and 362 items of error, respectively); d, TASS (430 items of error). Black letters = "forest" provinces; white letters = "open vegetated" provinces. Acronyms as in fig. 2.

Table 1. Species of *Rasahus* and their geographical distribution in the biogeographic provinces of the Neotropical subregion.

Species	Geographical distribution
<i>R. aeneus</i>	Without precise locality.
<i>R. albomaculatus</i>	Amazonian and Caribbean
<i>R. amapaensis</i>	Amazonian
<i>R. angulatus</i>	Amazonian
<i>R. arcitenens</i>	Amazonian, Caribbean, and Cerrado
<i>R. arcuiger</i>	Amazonian, Atlantic, Caribbean, and Paranaense
<i>R. argentinensis</i>	Chacoan
<i>R. atratus</i>	Amazonian
<i>R. bifurcatus</i>	Caribbean
<i>R. biguttatus</i>	Caribbean
<i>R. brasiliensis</i>	Amazonian, Atlantic, Caribbean, and Paranaense
<i>R. castaneus</i>	Amazonian
<i>R. costarricensis</i>	Caribbean
<i>R. flavovittatus</i>	Amazonian and Caribbean
<i>R. grandis</i>	Paranaense
<i>R. guttatipennis</i>	Amazonian and Caribbean
<i>R. hamatus</i>	Amazonian, Atlantic, Caribbean, Chacoan, Desierto, and Paranaense
<i>R. limai</i>	Amazonian, Caatinga, Cerrado, Chacoan, and Paranaense
<i>R. maculipennis</i>	Atlantic, Caribbean, and Paranaense
<i>R. paraguayensis</i>	Paranaense
<i>R. peruensis</i>	Amazonian
<i>R. rufiventris</i>	Amazonian, Cerrado, and Chacoan
<i>R. scutellaris</i>	Atlantic
<i>R. sulcicollis</i>	Amazonian, Caribbean, Chacoan, and Paranaense
<i>R. surinamensis</i>	Amazonian and Caribbean
<i>R. thoracicus</i>	Caribbean

Table 2. Characters and character states used in the cladistic analysis of *Rasahus*.

- | |
|---|
| 1. Shape: [0] robust; [1] slender. |
| 2. Length: [0] small (< 19 mm); [1] large (> 19 mm). |
| 3. Head: [0] not metallicized; [1] metallicized. |
| 4. White setae on head: [0] scarce; [1] abundant. |
| 5. Eyes: [0] not attaining superior edge of head; [1] surpassing superior edge of head. |
| 6. Ocelli: [0] placed on tubercle; [1] not placed on tubercle. |
| 7. Postocular region: [0] rounded; [1] angular. |
| 8. Anterolateral angles of pronotum: [0] well-developed; [1] not developed. |
| 9. Pronotum: [0] subrounded; [1] subquadrangular. |
| 10. Purple tonalities on pronotum: [0] absent; [1] present. |
| 11. Pronotum: [0] not metallicized; [1] metallicized. |
| 12. Sinuose and punctate band on pronotum lobes: [0] absent; [1] present. |
| 13. Pronotum granulations on anterior lobe: [0] absent; [1] present. |
| 14. Pronotum granulations on posterior lobe: [0] absent; [1] present. |
| 15. Sulci: [0] not distinct; [1] distinct. |
| 16. Lateral internal sulci: [0] absent; [1] present, medially united; [2] present, distally united. |
| 17. Lateral external sulci: [0] absent; [1] present, undivided; [2] present, divided in two. |

18. Scutellum: [0] acuminated; [1] not acuminated.
 19. Scutellum: [0] not metalized; [1] metalized.
 20. Scutellum: [0] uniformly pigmented; [1] not uniformly pigmented.
 21. Scutellum granulations: [0] present; [1] absent.
 22. Pleural pilosity: [0] abundant; [1] scarce.
 23. Metasternum pilosity: [0] abundant; [1] scarce.
 24. Female hemelytra: [0] macropterous; [1] brachypterous.
 25. Hemelytra: [0] surpassing apex of abdomen; [1] not surpassing apex of abdomen.
 26. Hemelytra: [0] multicolored; [1] unicolorous.
 27. Transversal stripe on hemelytra: [0] absent; [1] present.
 28. Longitudinal stripe on hemelytra: [0] absent; [1] present.
 29. X-shape yellow spot on hemelytra: [0] absent; [1] present.
 30. Pale stripe on corium and/or clavum of hemelytra: [0] absent; [1] present.
 31. Area between Pcu + 1A and Cu: [0] bicolorous; [1] unicolorous.
 32. Orange red area between Cu and R+M: [0] absent; [1] present.
 33. Area between Cu and R+M: [0] unicolorous; [1] bicolorous.
 34. Area between R+M and Sc: [0] unicolorous; [1] bicolorous.
 35. Two regular dark dots on membrane: [0] present; [1] absent.
 36. Well-defined dot on Cu: [0] absent; [1] present.
 37. Hemelytra membrane: [0] bicolorous; [1] unicolorous.
 38. Pale dot on membrane: [0] absent; [1] present.
 39. Fore femora color: [0] bicolorous; [1] uniform; [2] with dots.
 40. Mid femora color: [0] uniform; [1] bicolorous [2] with dots.
 41. Hind femora color: [0] bicolorous; [1] uniform; [2] with dots.
 42. Fore tibiae color: [0] uniform; [1] bicolorous; [2] with dots.
 43. Mid tibiae color: [0] uniform; [1] bicolorous; [2] with dots.
 44. Hind tibiae color: [0] uniform; [1] bicolorous; [2] with dots.
 45. Fore coxae color: [0] uniform; [1] bicolorous; [2] with dots.
 46. Mid coxae color: [0] uniform; [1] bicolorous; [2] with dots.
 47. Hind coxae color: [0] uniform; [1] bicolorous; [2] with dots.
 48. Connexivum: [0] dorsally not visible; [1] dorsally visible.
 49. Connexivum: [0] multicolored; [1] unicolorous.
 50. Color of the last abdominal segment: [0] distinct from anterior one; [1] similar to anterior one.
 51. Pygophore: [0] rounded; [1] subrectangular; [2] quadrangular.
 52. Inferior edge of pygophore: [0] straight; [1] sinuose; [2] with evagination.
 53. Median distal region of medial process of pygophore: [0] not curved; [1] curved.
 54. Basal plate: [0] simple; [1] complex.
 55. Parameres: [0] subrectangular; [1] subtriangular.
 56. Edge of gonocoxite VIII: [0] not straight; [1] straight.
 57. Internal edge setae of gonocoxite IX: [0] thin and thick; [1] thin.
 58. Medially sclerotized area of gonocoxite IX: [0] absent; [1] present.
 59. Unsclerotized area close to inner margin of gonocoxite IX: [0] absent; [1] present.
 60. Tergites IX and X: [0] subrounded; [1] subquadrangular.
 61. Tergites IX and X: [0] weakly pigmented; [1] strongly pigmented.
 62. Intersegmental line of tergites IX and X: [0] entire; [1] not entire.
 63. Tergites IX and X: [0] wider than long; [1] as wide as long.
-

Table 4. Data matrix obtained with TASS under assumption 2 for the cladistic biogeographic analysis of the Neotropical subregion. Acronyms as in fig. 2.

root	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AMA	1	1	1	1	1	1	0	1	1	1	1	0	0	1
ATL	0	0	0	0	1	1	1	1	1	0	1	1	1	1
CAA	1	1	1	0	1	1	0	1	1	1	?	0	0	?
CAR	1	0	0	0	1	1	1	1	1	0	?	0	0	0
CER	0	0	0	0	1	1	1	1	1	0	?	1	1	?
CHA	1	1	0	0	1	0	0	1	0	0	?	0	0	?
DES	0	0	0	0	?	?	?	?	?	?	?	1	0	?
PAR	1	1	1	1	0	0	0	0	0	0	0	0	0	1

Appendix

Datafile for COMPONENT 2.0

```
#nexus
[Neotropical Peiratinae]
begin taxa;
dimensions ntax=8;
taxlabels AMA ATL CAA CAR CER CHA DES PAR;
endblock;

begin distribution;
title = 'Rasahus';
ntax=25;
range
rufiventris      :      AMA CER CHA,
hamatus          :      AMA ATL CAR CHA DES PAR,
arcitenens       :      AMA CAR CER,
arcuiger         :      AMA ATL CAR PAR,
amapaensis      :      AMA,
thoracicus       :      CAR,
biguttatus       :      CAR,
argentinensis   :      CHA,
limai            :      AMA CAA CER CHA PAR,
grandis          :      PAR,
angulatus        :      AMA,
castaneus        :      AMA,
scutellaris      :      ATL,
maculipennis     :      ATL CAR PAR,
brasiliensis     :      AMA ATL CAR PAR,
sulcicollis      :      AMA CAR CHA PAR,
surinamensis    :      AMA CAR,
albomaculatus    :      AMA CAR,
guttatipennis    :      AMA CAR,
```

atratus : AMA,
 peruensis : AMA,
 costarricensis : CAR,
 bifurcatus : CAR,
 flavovittatus : AMA CAR,
 paraguayensis : PAR;

tree set1= (((1,2,(3,4)),(5,((6,7),(8,(9,(10,11)))))),((12,13),((14,15,16,(17,18)),
 (19,(20,21,22,(23,24,25))))));

endblock;

begin distribution;

title = 'Eidmannia';

ntax=6;

range

matogrossensis : AMA,
 obscura : PAR,
 guyanensis : AMA,
 attaphila : AMA ATL PAR,
 beniensis : ATL,
 bahiensis : AMA;

tree set2= ((1,2),(3,(4,(5,6))));

endblock;

begin distribution;

title = 'Thymbreus';

ntax=3;

range

ocellatus : CAR,
 crocinopterus : AMA,
 pyrrhopterus : ATL PAR;

tree set3= (1,(2,3));

endblock;

begin distribution;

title = 'Melanolestes';

ntax=9;

range

lugens : PAR,
 minutus : CHA,
 morio : AMA ATL CAR CER PAR,
 picinus : AMA,
 goiasensis : CAA,
 argentinus : AMA ATL CER CHA PAR,
 degener : CAR;

tree set4= (1,(2,(3,((4,5),(6,7)))));

endblock;

