PROC. ENTOMOL. SOC. WASH.
99(1), 1997, pp. 55–59

CLADISTICS AND BIOGEOGRAPHY OF THE ASSASSIN BUG GENUS *MELANOLESTES* STÅL (HETEROPTERA: REDUVIIDAE)

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Abstract.—Melanolestes Stål is a monophyletic genus of nine species, two Nearctic and seven Neotropical. A cladistic analysis of the genus was carried out using 28 characters. The cladograms were rooted with the genus *Peirates* Serville. The analysis yielded 20 equally parsimonious cladograms, with 34 steps, CI = 0.52, and RI = 0.44. A successive weighting procedure resulted in one cladogram with 77 steps, CI = 0.84, and RI = 0.87. The distribution of *Melanolestes* coincides in part with a previous study on Peiratinae, that showed that the former continuous Amazonian forest was separated into two parts by a diagonal line of open areas. In addition, the two Nearctic species *M. picicornis* and *M. picipes* are sister-taxa, so a single dispersal event accounts for the presence of *Melanolestes* in the Nearctic.

Key Words: Peiratinae, Reduviidae, cladistics, biogeography

The New World assassin bug genus *Melanolestes* Stål (Heteroptera: Reduviidae: Peiratinae) is known from southeastern Canada to northern Argentina. The nine species belonging to this genus have been recently revised (Coscarón and Carpintero 1994). Two of these species, *M. picicornis* Stål and *M. picipes* (Herrich-Schaeffer), are restricted to the Nearctic Region, whereas the remainder are Neotropical. Within the Neotropics, *M. goiasensis* Coscarón and Carpintero, *M. lugens* Coscarón and Carpintero, *M. minutus* Coscarón and Carpintero, and *M. picinus* Stål have very small distributional areas within the Amazonian and Chacoan domains. In a previous biogeographic study (Morrone and Coscarón 1996), we analyzed distributional patterns of the Neotropical Peiratinae, concluding that these patterns have been basically caused by the gradual development of a diagonal line of open areas (Chaco-Cerrado-Caatinga), which separated the former continuous tropical forest into two parts.

In this paper we provide a cladistic analysis of *Melanolestes*, and discuss its biogeographic patterns.

Material and Methods

This study is based on the revision of *Melanolestes* by Coscarón and Carpintero (1994), and the examination of specimens borrowed from the following collections: American Museum of Natural History, New York, USA; The Natural History Museum, London, United Kingdom; Instituto Nacional de Pesquisas Amazonicas, Manaus, Brazil; Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; Museo de La Plata, La Plata, Argentina; Museu de Zoologia de Sâo Paulo, Sâo Paulo, Brazil; Naturhistoriska Riksmuseet, Stockholm, Sweden; Zoologisches Museum der Humboldt Universität zu Ber-

Table 1. Data matrix and characters of the species of *Melanolestes* used in the analysis. 0 = plesiomorphic character states; 1, 2 = apomorphic character states; ? = missing data.

Peirates	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
M. argentinus	0 0 1 0 0 1 1 0 0 0 0 1 0 0 1 1 1 1 1 1 0 0 0 0 1 0 1 1
M. degener	0 2 1 0 0 1 1 0 0 0 0 1 ? 0 1 1 1 1 1 1 1 0 0 ? ? ? 1 ?
M. goiasensis	0 2 1 1 0 1 1 0 1 0 0 1 ? 1 1 1 1 1 1 1 1 0 0 ? ? ? 1 ?
M. lugens	0 2 1 0 1 1 0 1 2 1 0 1 1 0 1 1 0 1 0 0 0 0 0 0 1 1 1 0
M. minutus	0 2 1 0 0 1 1 0 1 1 1 1 0 0 1 1 0 1 0 0 0 0 0 ? ? ? 1 ?
M. morio	0 2 1 0 0 1 1 0 1 0 0 1 0 ? 1 1 1 1 1 1 0 0 0 0 1 0 1 0
M. picicornis	0 0 1 0 0 1 1 1 1 1 1 1 1 1 0 1 1 1 1 1 1 0 0 0 0 0 1 1 0
M. picinus	1 1 0 0 0 1 0 0 1 0 0 1 0 1 1 1 1 1 1 1 1 0 1 1 1 1 1 1 1
M. picipes	0 2 1 0 0 1 1 1 1 1 1 0 1 0 0 1 1 1 1 1 1 0 0 0 0 1 0 1 1

1. Body shape. [0] slender; [1] robust.
2. Eyes. [0] not attaining superior edge of head; [1] attaining superior edge of head; [2] surpassing superior edge of head. Treated as additive.
3. Ocelli. [0] not placed on a tubercle; [1] placed on a tubercle.
4. Lateral tubercle on neck. [0] present; [1] absent.
5. Metallic shine in pronotum. [0] absent; [1] present.
6. Pronotal granulations on anterior lobe. [0] absent; [1] present.
7. Pronotal granulations on posterior lobe. [0] absent; [1] present.
8. Pronotal sulci. [0] distinct; [1] not distinct.
9. Pronotal lateral internal sulci. [0] distally united; [1] medially united; [2] not united. Treated as non-additive.
10. Lateral margin of pronotum. [0] carina absent; [1] carina present at entire length.
11. Scutellum coloration. [0] unicolorous; [1] bicolored.
12. Spongy fossa. [0] not occupying distal third of fore and hind tibiae; [1] occupying distal third of fore and hind tibiae.
13. Female hemelytra. [0] macropterous; [1] brachypterous.
14. Hemelytra. [0] surpassing apex of abdomen; [1] not surpassing apex of abdomen.
15. Body color, [0] not uniform; [1] uniform.
16. Hemelytral pale stripe on corium and clavus. [0] present; [1] absent.
17. Color of fore femora. [0] bicolored; [1] unicolorous.
18. Color of hind femora. [0] unicolorous; [1] bicolored.
19. Color of fore tibiae. [0] unicolorous; [1] bicolored.
20. Color of mid tibiae. [0] unicolorous; [1] bicolored.
21. Connexivum. [0] dorsally visible; [1] dorsally not visible.
22. Connexivum color. [0] unicolorous; [1] bicolored.
23. Parameres shape. [0] subrectangular; [1] subtriangular.
24. Gonocoxite IX internal edge hairs. [0] thin; [1] thin and thick.
25. Gonocoxite IX unsclerotized area close to inner margin. [0] absent; [1] present.
26. Shape of IX and X tergites. [0] subquadrangular; [1] subrounded.
27. Intersegmental line of tergites IX and X. [0] not entire; [1] entire.
28. Intersegmental line. [0] not strongly sclerotized; [1] strongly sclerotized.

lin, Berlin, Germany; Zoological Museum, University of Helsinki, Helsinki, Finland; and the private collections of D. Carpintero, Argentina; L. Jirón, Costa Rica; and the late J. Maldonado-Capriles, Puerto Rico.

Melanolestes constitutes a monophyletic group that is distinguished from other Peiratinae by the spongy fossa occupying distal third of fore and hind tibiae, body of uniformly dark color, ocelli placed on a tubercle, pronotal granulations on anterior lobe, hemelytra lacking a pale stripe on the corium and clavus, hind femora unicolorous, and intersegmental line of tergites IX and X entire.

The nine species currently assigned to the genus are considered as terminal taxa: *M. argentinus* Berg, *M. degener* (Walker), *M. goiasensis* Coscarón and Carpintero, *M. lugens* Coscarón and Carpintero, *M. minutus* Coscarón and Carpintero, *M. morio* (Er-

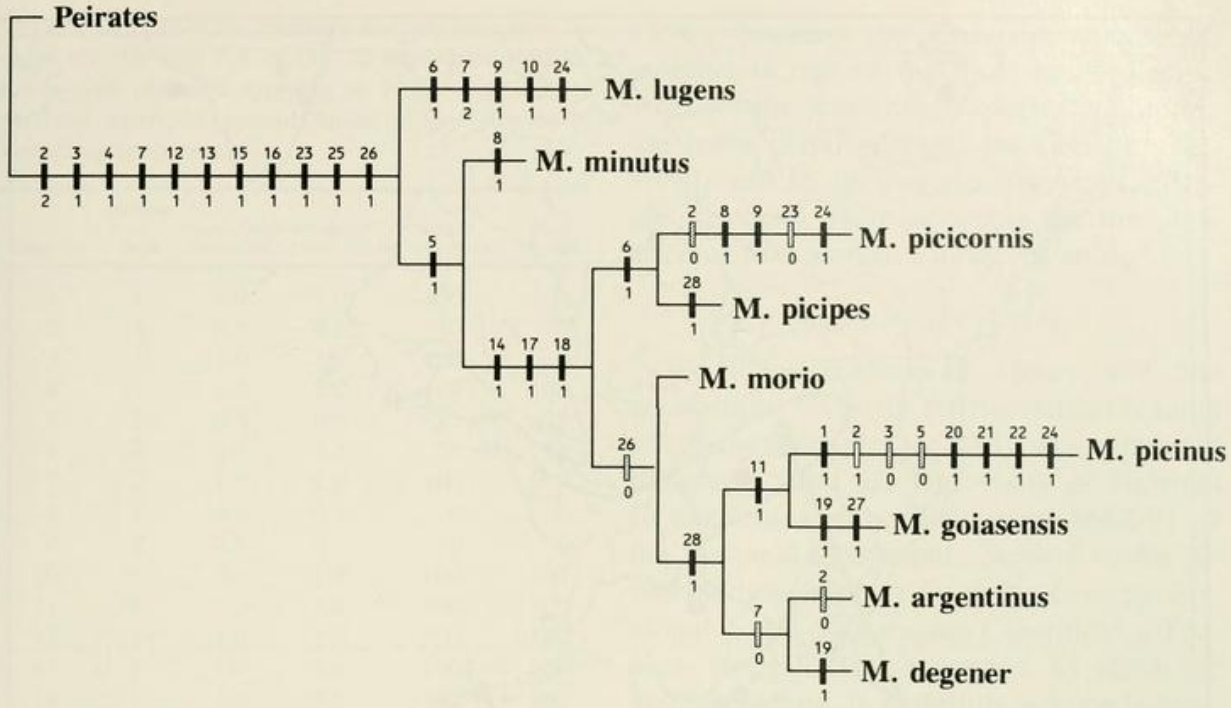

Fig. 1. Cladogram of the species of *Melanolestes*. Synapomorphies = solid black rectangles; homoplasies = dotted rectangles.

ichson), *M. picicornis* (Stål), *M. picinus* Stål, and *M. picipes* (Herrich-Schaeffer).

The data matrix and the 28 characters used in this study are detailed in Table 1. The data were analyzed with Hennig86 version 1.5 (Farris 1988), applying the implicit enumeration (ie*) option for calculating the shortest trees. Consistency (CI) and retention (RI) indices were calculated excluding uninformative characters (autapomorphies and synapomorphies of the genus). We used the successive weighting procedure in Hennig86, that calculates weights from the best fits of the characters on the most parsimonious cladograms using rescaled consistencies (products of the character consistency and the character retention index). These products are scaled in the range 0–10, and the weighting procedure is repeated successively until the cladograms no longer change (Farris 1989). CLADOS version 1.1 (Nixon 1992) was used for examination of character distributions.

Results and Discussion

The analysis using equal weights yielded 20 equally parsimonious cladograms, each with 34 steps, CI = 0.52, and RI = 0.44. When the successive weighting procedure was applied, one minimum-length cladogram was selected from the original ones after the second round of weighting, with 77 steps, CI = 0.84, and RI = 0.87 (Fig. 1). Values for the number of steps, consistency index (ci), retention index (ri), and weight (ri × ci × 100) in the weighted trees are listed in Table 2. The phylogenetic sequence from the basal to the most distal species is as follows: *M. lugens*, *M. minutus*, *M. picicornis* plus *M. picipes*, *M. morio*, *M. picinus* plus *M. goiasensis*, and *M. argentinus* plus *M. degener*.

Several conclusions can be deduced by comparing the cladogram obtained with the areas inhabited by the species of *Melanolestes* (Fig. 2):

(1) the more basal species (M. lugens) is restricted to the Paranaense province of the Amazonian domain;

(2) *M. minutus* is restricted to the Chacoan domain;

(3) the more widespread species *M. morio* and *M. argentinus* are among the most distal species of the cladogram;

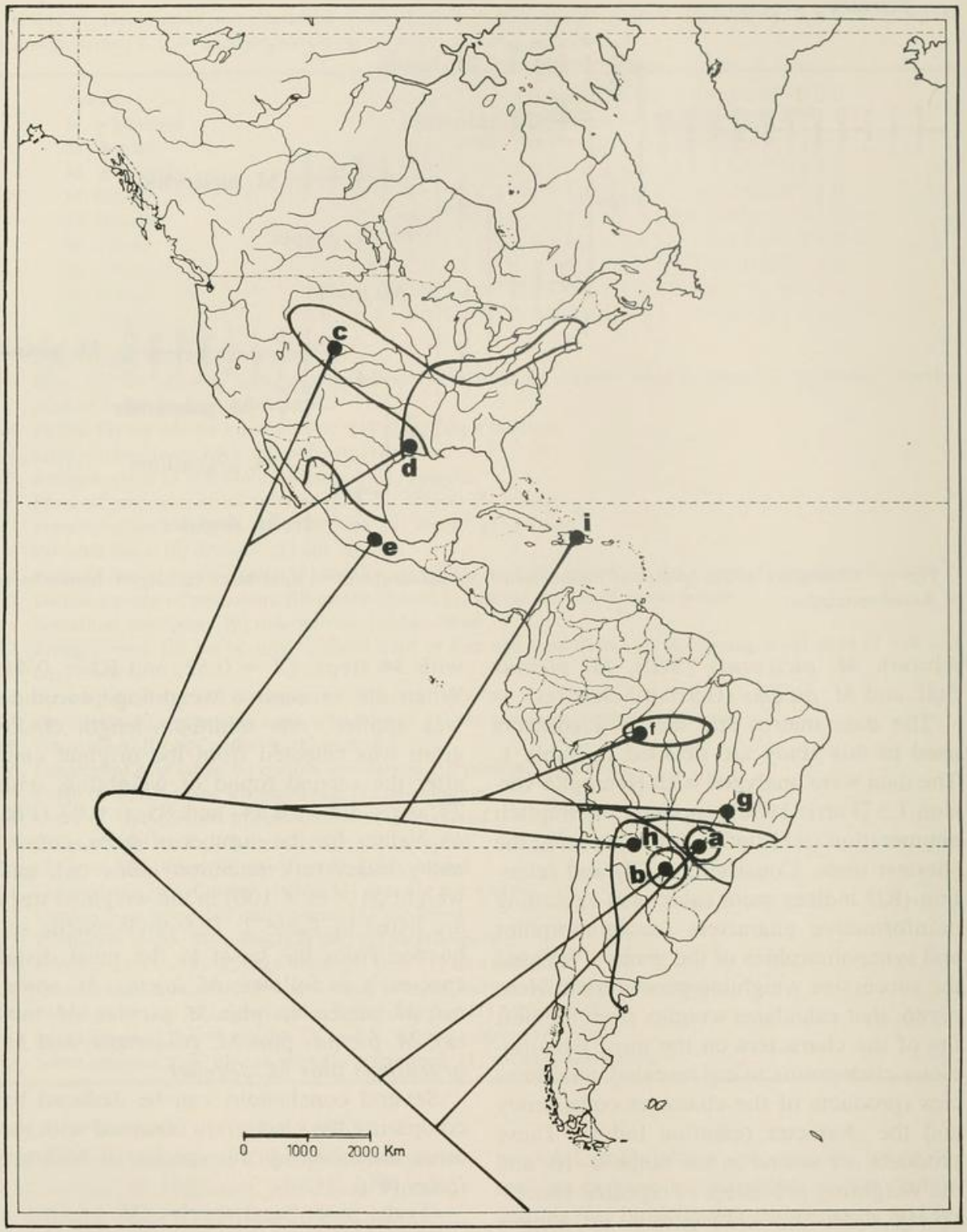

Fig. 2. Geographical distribution of the species of *Melanolestes*, with the cladogram superimposed. a, *M. lugens*; b, *M. minutus*; c, *M. picicornis*; d, *M. picipes*; e, *M. morio*; f, *M. picinus*; g, *M. goiasensis*; h, *M. argentinus*; i, *M. degener*.

Table 2. Character consistencies and retention indices are the best fits of the 20 most parsimonious cladograms obtained applying ie. Final weights were obtained after the second round of the successive weighting procedure.

Character	Number of Steps	Consistency Index (ci)	Retention Index (ri)	Weight (ri × ci × 100)	Final Weight
1	1	1.0	1.0	100	100
2	4	0.5	0.6	30	0
3	1	1.0	1.0	100	0
4	1	1.0	1.0	100	100
5	2	0.5	0.5	25	25
6	2	0.5	0.5	25	25
7	2	1.0	1.0	100	0
8	2	0.5	0	0	0
9	2	0.5	0	0	0
10	1	1.0	1.0	100	100
11	1	1.0	1.0	100	100
12	1	1.0	1.0	100	100
13	1	1.0	1.0	100	100
14	1	1.0	1.0	100	100
15	1	1.0	1.0	100	100
16	1	1.0	1.0	100	100
17	1	1.0	1.0	100	100
18	1	1.0	1.0	100	100
19	1	1.0	1.0	100	100
20	1	1.0	1.0	100	100
21	1	1.0	1.0	100	100
22	1	1.0	1.0	100	100
23	2	0.5	0	0	0
24	2	0.5	0.5	25	0
25	1	1.0	1.0	100	100
26	1	1.0	1.0	100	33
27	1	1.0	1.0	100	100
28	2	0.5	0.5	25	25

(4) the two Nearctic species (*M. picicornis* and *M. picipes*) are sister-taxa.

These results corroborate, in part, our previous study (Morrone and Coscarón 1996), because the Chacoan species *M. minutus* is one of the most basal species, whereas the Amazonian species are among the most distal species. Because *M. picicornis* and *M. picipes* are sister-taxa, a single dispersal event accounts for the presence of *Melanolestes* in the Nearctic.

Acknowledgments

We thank Thomas J. Henry and one anonymous reviewer for the critical reading of the manuscript. Our study was supported by grants from the University of Helsinki to the senior author and grant 4662-91 of the National Geographic Society to the junior author. Support from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina, to which the authors belong, is gratefully acknowledged.

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