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Phylogenetic analysis of the subgenus *Lampetis* (*Spinthoptera*) (Coleoptera: Buprestidae) of North and Central America, and the West Indies

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Abstract

Phylogenetic relationships between species of *Lampetis* (*Spinthoptera*) of North and Central America and the West Indies were analysed by cladistic methods, based on 65 characters from the external morphology and male genitalia. Eleven species of different generic groups of the subtribe Dicercina were considered as outgroups, including also species of *Lampetis* (*Lampetis*) and one South American species of *L.* (*Spinthoptera*). The monophyly of *Lampetis* (*Spinthoptera*) is supported by two synapomorphies, but this subgenus appears to be more closely related to species of *Psiloptera* rather than to Old World species of *Lampetis* (*Lampetis*), suggesting that *Lampetis* (*Spinthoptera*) may be segregated from *Lampetis* as a different genus. The species of *Lampetis* (*Spinthoptera*) from North and Central America and the West Indies do not represent a monophyletic taxon, because *L.* (*S.*) *tucumana* (South American outgroup) is nested within them. Comparison of these results with a previous panbiogeographic analysis indicate that several generalized tracks possess species from different clades, thus suggesting an ancient radiation of this taxon in Mesoamerica and the Mexican Transition Zone.

Keywords: *Biogeography, cladistics, evolution, Mexican Transition Zone, Nearctic, Neotropical*

Introduction

The buprestid genus *Lampetis* Dejean, 1833 is placed in the subtribe Dicercina (Chrysochroinae: Dicercini), according to Bellamy (2003). *Lampetis* comprises two subgenera, *Lampetis* Dejean, 1833 and *Spinthoptera* Casey, 1909, and ca 251 species distributed in the Afrotropical, Andean, Nearctic, Neotropical, Oriental, and Palearctic regions. *Lampetis* (*Spinthoptera*) was recognized for more than 100 species from the New World (Kurosawa 1993). The systematics of some species of *Lampetis* (*Spinthoptera*) has

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been reviewed by Nelson (1986) and Corona (2004, 2005), who recognized 31 species in Central America, North America, and the West Indies. Corona and Morrone (2005) analysed their biogeographic patterns, but there are no hypotheses regarding their phylogenetic relationships.

Our objective is to present a cladistic analysis of the species of *Lampetis* (*Spinthoptera*) of North and Central America, and the West Indies, using characters from the external morphology and male genitalia. We suspect that the studied group is paraphyletic, but we were not able to include all the South American species in the analysis; however, we hope it may provide a phylogenetic basis for further studies.

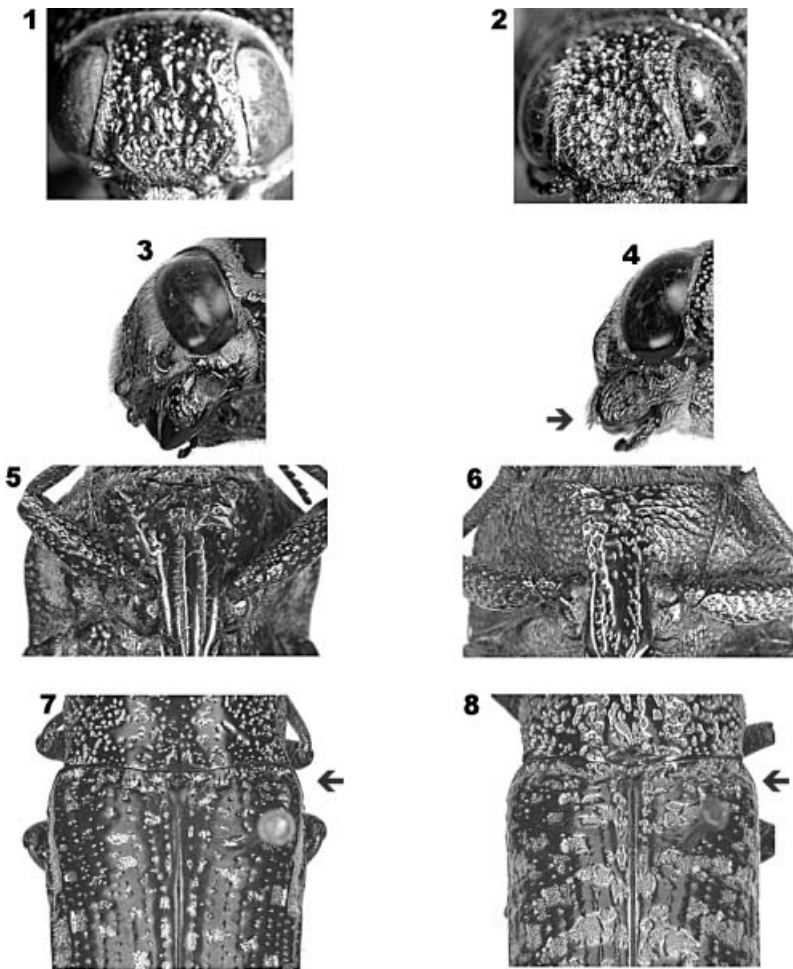
Material and methods

We examined 2433 specimens of the 31 species of *Lampetis* (*Spinthoptera*) of North and Central America, and the West Indies: *L. aurata* (Saunders, 1871), *L. aurifera* (Olivier, 1790), *L. auropunctata* (Kerremans, 1893), *L. bahamica* (Fisher, 1925), *L. chalconota* (Waterhouse, 1882), *L. chamela* Corona, 2005, *L. chiapaneca* Corona, 2004, *L. christophi* Théry, 1923, *L. colima* Corona, 2005, *L. cortesi* (Laporte and Gory, 1837), *L. cupreopunctata* (Schaeffer, 1905), *L. cyanitarsis* Corona, 2005, *L. dilaticollis* (Waterhouse, 1882), *L. drummondi* (Laporte and Gory, 1836), *L. geniculata* (Waterhouse, 1889), *L. granulifera* (Laporte and Gory, 1837), *L. guildini* (Laporte and Gory, 1836), *L. hirtomaculata* (Herbst, 1801), *L. hondurensis* Corona, 2005, *L. lesnei* (Kerremans, 1910), *L. mexicana* Théry, 1923, *L. monilis* (Chevrolat, 1834), *L. obscura* Thomson, 1879, *L. simplex* (Waterhouse, 1882), *L. srdinkoana* (Obenberger, 1924), *L. straba* (Chevrolat, 1867), *L. tigrina* Corona, 2005, *L. torquata* (Dalman, 1823), *L. viridicolor* Corona, 2005, *L. viridimarginalis* Corona, 2005, and *L. webbii* (LeConte, 1858). Eleven species, which correspond to different generic groups, were considered as outgroups: *Perotis unicolor* (Olivier, 1790), *Ectinogonia pulverea* Kerremans, 1919, *Capnodis tenebrionis* (Linnaeus, 1758), *Oedisterna bisulcata* (Laporte and Gory, 1836), *Polybothris (Polybothris) sumptuosa* (Klug, 1833), *Psiloptera bicarinata* (Thunberg, 1789), *Lampetis (Lampetis) amaurotica* (Klug, 1855), *L. (L.) viridimarginata* (Boheman, 1851), *L. (L.) fastuosa* (Fabricius, 1774), *L. (L.) rugosa* (Palisot de Beauvois, 1807), and *L. (Spinthoptera) tucumana* (Guérin-Méneville and Percheron, 1835).

The following 65 characters and character states were derived from the external morphology and male genitalia.

Head

0. Frons sinuate: (0) absent; (1) present.
1. Confluent punctures on frons: (0) scarce (Figure 1); (1) abundant (Figure 2).
2. Strong callosities on frons: (0) absent; (1) present.
3. Frons: (0) as wide as long; (1) 1.6–2.0 times wider than long.
4. Depression behind eyes: (0) absent; (1) present.
5. Punctures on base of mandibles: (0) scarce (Figure 3); (1) abundant (Figure 4).
6. Clypeus margin: (0) emarginate at midline; (1) concave; (2) entire.
7. Third antennal segment: (0) subrectangular; (1) subtriangular.
8. Antennal segments 6th–11th: (0) longer than wide; (1) wider than long.



Figures 1–8. Illustration of some characters and character states. (1, 2) Punctures on frons: (1) *Lampetis* (*Spinthoptera*) *simplex* (scarce); (2) *L. tigrina* (abundant). (3, 4) Punctures on base of mandibles: (3) *L. aurata* (scarce); (4) *Lampetis* (*Lampetis*) *amaurotica* (abundant). (5, 6) Prosternum with punctures confluent laterally: (5) *Oedisterna bisulcata* (scarce); (6) *Perotis unicolor* (abundant). (7, 8) Elytra with transversal depressions on basal surface: (7) *L. auropunctata* (scarce); (8) *L. drummondi* (abundant).

Pronotum

9. Pronotum: (0) wider than long; (1) longer than wide.
10. Concavity along middle and lateral margin: (0) absent; (1) present.
11. Confluent punctures on lateral margins: (0) absent; (1) present.
12. Lateral margins: (0) not parallel; (1) parallel.
13. Lateral margins near anterior margin: (0) not projected outwards; (1) projected outwards.
14. Shape of lateral margin from middle to anterior margin: (0) rounded; (1) convergent.
15. Shape of lateral margin from middle to posterior margin: (0) subparallel; (1) concave.
16. Shape of lobe of posterior margin: (0) rounded; (1) acute.
17. Punctures at middle: (0) absent; (1) present.

18. Circular callosities on surface: (0) absent; (1) present.
19. Sulcus on surface: (0) absent; (1) present.
20. Sulcus and pulverulence along lateral margins: (0) absent; (1) present.
21. Sulcus (sometimes interrupted at middle) along anterior margin: (0) absent; (1) present.
22. Longitudinal median sulci (sometimes interrupted at middle): (0) absent; (1) one; (2) two.
23. Depression like a line along anterior margin from lateral margin to midline: (0) absent; (1) present.
24. Irregular callosities on surface: (0) absent; (1) present.

Elytra

25. Elytral shape: (0) not wider at base than pronotum; (1) wider at base than pronotum.
26. Humeral angles: (0) rounded; (1) slightly acute.
27. Transversal depressions on basal surface: (0) scarce (Figure 7); (1) abundant (Figure 8).
28. Lateral margins: (0) not expanded; (1) expanded.
29. Callosities at lateral margin near anterior margin: (0) absent; (1) present.
30. Strongly impressed longitudinal, punctate striae: (0) absent; (1) present.
31. Striae: (0) separated; (1) close.
32. Several irregular interstitial depressions surrounding callosities laterally: (0) absent; (1) present.
33. Apex: (0) not oblique; (1) oblique.
34. Apex: (0) not dentiform; (1) dentiform.
35. Sutural angles of apex: (0) separated; (1) joined.

Prosternum

36. Shape of anterior margin at middle: (0) flattened; (1) concave; (2) convex (like a lobe).
37. Lateral lobe of anterior margin: (0) absent; (1) present.
38. Punctures confluent laterally: (0) scarce (Figure 5); (1) abundant (Figure 6).
39. Punctures confluent anteriorly: (0) absent; (1) present.

Prosternal process apex

40. Strongly concave behind procoxae: (0) absent; (1) present.
41. Prosternal process: (0) flat; (1) convex.
42. Punctures at middle: (0) absent; (1) present.

Mesepisternum and mesepimeron

43. Confluent punctures on surface: (0) absent; (1) present.

Metasternum

44. Concave medially: (0) absent; (1) present.

Legs

45. Metacoxae with three lobes: (0) absent; (1) present.
46. Second lobe of posterior margin of metacoxae: (0) absent; (1) rounded; (2) acute.
47. Pubescence on lateral and posterior margins of metacoxae: (0) scarce; (1) abundant.
48. Confluent punctures forming callosities on metacoxae: (0) absent; (1) present.
49. Apices of metatibiae: (0) rounded; (1) flattened.
50. Pulvillus on third tarsomere: (0) with setae at margin; (1) with teeth at margin.

Abdomen

51. First ventrite: (0) flat; (1) concave.
52. Carina on first ventrite: (0) absent; (1) present.
53. Second ventrite: (0) concave or flattened; (1) convex.
54. Third ventrite: (0) concave; (1) convex.
55. Last male ventrite: (0) rounded; (1) truncate.
56. Lateral circular callosities on surface: (0) absent; (1) present.
57. Punctures on a line on surface: (0) absent; (1) present.

Male genitalia

58. Aedeagus shape: (0) slender, large; (1) wide, small.
59. Median lobe apex: (0) entire; (1) subtriangular; (2) semicircular.
60. Median lobe shape: (0) slender; (1) wide.
61. Parameres of aedeagus from base to middle: (0) parallel; (1) subparallel.
62. Apices of parameres and median lobe: (0) no parallel; (1) parallel.
63. Apices of parameres of aedeagus: (0) rounded; (1) oblique; (2) truncate.
64. Parameres expanded from middle to apices: (0) absent; (1) present.

Multistate characters were treated as non-additive, and characters not observed were coded as “?”. Cladograms were rooted with *Perotis unicolor*. The data matrix (Table I) was analysed with Nona 2.0 (Goloboff 1999) and WinClada 1.00.08 (Nixon 2002). The search strategy used was heuristic search, multiple TBR+TBR, maximum trees to keep (hold)=100, number of replications (mult=N)=20, and starting trees per rep (hold/)=15. In order to assess the confidence of the clades, we undertook a bootstrap analysis (Holmes 2003), with 1000 replications, number of search reps (mult*N)=100, and starting trees per rep (hold/)=10.

Results and discussion

The analysis of the data matrix (Table I) produced two equally parsimonious cladograms, with 250 steps, a consistency index of 0.28, and a retention index of 0.64 (Figure 9). The strict consensus cladogram has 252 steps, a consistency index of 0.28, and a retention index of 0.63, and only two nodes collapsed (Figure 9; Table II). The cladistic sequence is as follows: *Perotis unicolor* (Palearctic), *Oedisterna bisulcata* (Afrotropical), *Capnodis tenebrionis* (Palearctic), *Ectinogonia pulverea* (South American) plus *Polybothris sumptuosa* (Madagascar), *Lampetis rugosa* (Afrotropical), *L. amaurotica* (Afrotropical) plus *L.*

Table I. Data matrix.

Species	Characters						
		1111111111	2222222222	3333333333	4444444444	5555555555	66666
	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	01234
<i>Perotis unicolor</i>	0001001100	0001000100	0001001000	0100011010	0011012001	0001110010	11001
<i>Ectinogonia pubverea</i>	1010001000	1110000100	0000001000	0100001100	0010000001	0110010000	00120
<i>Cadnodis tenebrionis</i>	0000002110	0001000100	0000100000	0000011100	0110012001	1001110010	11101
<i>Oedisterna bisulcata</i>	0010000100	0101000100	1001000000	0100011100	0100002001	0001110010	11021
<i>Polybothris sumptuosa</i>	1000002001	0010101101	0000010010	0000011100	0010000001	0110000110	00100
<i>Psiloptera bicarinata</i>	0101012100	0200100001	0100001000	1000112010	0000101001	0110010010	01121
<i>Lampetis amaurotica</i>	0101012000	0000100110	0000001000	1000011110	1000012001	0111111010	01021
<i>L. viridimarginata</i>	0101001100	0000100110	0000001000	1000011110	1000012001	0111111010	01021
<i>L. fastuosa</i>	0101001100	0000100100	0000001000	1001002011	1001002101	0101110010	01121
<i>L. rugosa</i>	0101001100	0100100100	0000001000	1000001110	0001002001	0111110010	11101
<i>L. tucumana</i>	0011101100	0000100100	0001000000	1001101110	1001001001	0110110010	11101
<i>L. aurata</i>	0011100100	0000100001	1110000101	1011011111	1100001011	0111110002	01100
<i>L. aurifera</i>	0011100100	0000110001	1110000101	1011101110	1100001011	0110110012	01100
<i>L. auropunctata</i>	1101010100	0100100100	0001001000	1101110010	1001001011	0111110012	11111
<i>L. bahamica</i>	1011101100	0000100001	0100000101	1011101111	1001001011	0111110002	01100
<i>L. chalconota</i>	1101000100	0100100100	0001001000	1011100011	1001001011	0110110010	11111
<i>L. chamela</i>	0101012100	0000100100	0000000100	1011100010	1001001010	0110110012	01100
<i>L. chiapaneca</i>	0101000100	0000100100	0001000000	1001100011	1101001010	0110110010	11111
<i>L. christophi</i>	0101012100	0000100100	0000001000	1011100010	1000001001	0110110010	11101
<i>L. colima</i>	0101012100	0000100100	0000000100	1011110010	1001001011	0111110002	01100
<i>L. cortesi</i>	1101010100	0100100100	0000001100	1011010011	1100001011	0110110001	01111
<i>L. cupreopunctata</i>	1101010100	0100110100	0001001100	1011100011	1100001011	0110110001	01100
<i>L. cyanitarsis</i>	0101012100	0000100100	0001000000	1011110010	1000001001	0110110002	01100
<i>L. dilaticollis</i>	0011000100	0100010000	0001000100	1011010010	1100001100	0100110012	11101
<i>L. drummondi</i>	0011000100	0100010100	0001001100	1011010010	1100001100	0100110012	11101
<i>L. geniculata</i>	0001011100	0100100100	0000001000	1011100010	1000001001	0110110011	01110
<i>L. granulifera</i>	0011010100	0000100100	0000001000	1011100010	1001001011	0110110001	01100
<i>L. guildini</i>	0011000100	0100100100	0000001100	1011100010	1011001001	0111110010	11101
<i>L. hirtomaculata</i>	0001100100	0000100100	0001001000	1001100010	1001001011	0110110001	01100
<i>L. hondurensis</i>	0101011100	0000100100	0001001000	1011100011	1001001011	0110110011	01100
<i>L. lesnei</i>	1101001100	0100100100	0000001000	1011100011	1000001010	01111100??	?????
<i>L. mexicana</i>	0111011100	0100100100	0001001100	1011100010	1101001011	0110110012	01110

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Table I. (Continued).

Species	Characters						
	0123456789	1111111111	2222222222	3333333333	4444444444	5555555555	66666
<i>L. monilis</i>	0101000100	0000100100	0001001000	1001100011	1000001001	0110110001	01100
<i>L. obscura</i>	1101000100	0100110100	0001001100	1011100011	1100001011	0111110001	01101
<i>L. simplex</i>	0101010100	0000100100	0000001000	1011100010	1000001001	0110110001	01110
<i>L. srdinkoana</i>	1011101100	0000100100	0001000000	1001110010	1000001001	0111110010	11101
<i>L. straba</i>	0011011100	0000100001	1120000101	1001111111	1100001011	0001110002	01100
<i>L. tigrina</i>	0101001100	0000110100	0001000000	1011100011	1100001011	0111110011	01110
<i>L. torquata</i>	0011100100	0000110001	0100000101	1011101111	1101001011	0111110002	01100
<i>L. viridicolor</i>	0101010100	0000100100	0001001000	1011100011	1000001011	0111110011	01100
<i>L. viridimarginalis</i>	1101011100	0000110100	0001000000	1011100011	1101001010	0011110001	01100
<i>L. webbii</i>	0011010100	0000110100	0001000000	1011010010	1100001000	0100110012	11101

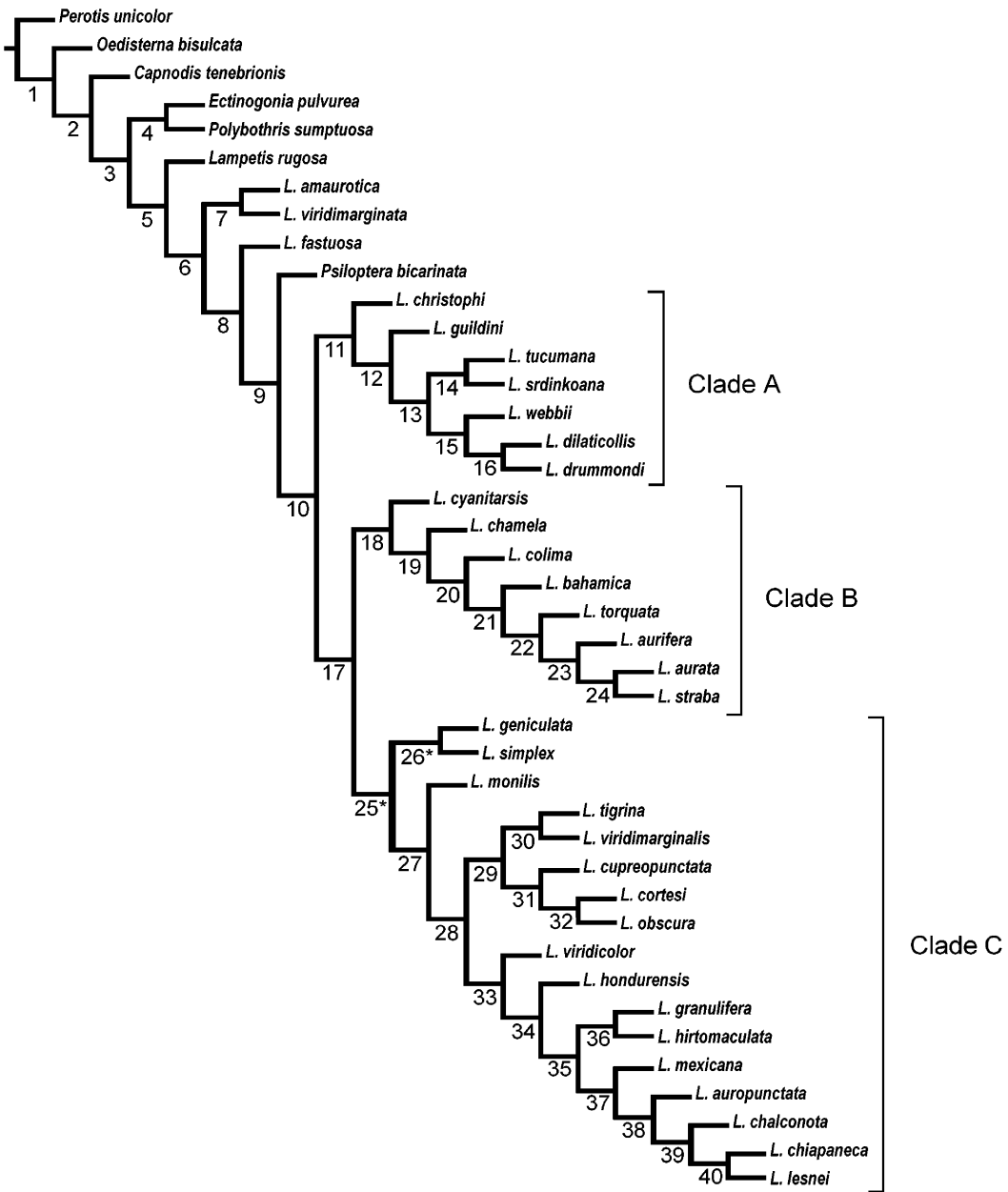


Figure 9. One of the two equally parsimonious cladograms of *Lampetis* (*Spinthoptera*) of North and Central America and the West Indies, and 11 species of different generic groups of the subtribe Dicercina (outgroups). Synapomorphies and homoplastic changes of nodes are listed in Table II. Asterisks indicate the nodes collapsed in the strict consensus cladogram.

viridimarginata (Afrotropical), *L. fastuosa* (Oriental), *Psiloptera bicarinata* (South American), and the remaining species, all assigned to *Lampetis* (*Lampetis*), arranged in three clades (A, B, and C). Clade A comprises the species *L. christophi* (southeastern Mexican), *L. guildini* (Antillean), *L. tucumana* (South American) plus *L. srdinkoana*

Table II. Synapomorphies and homoplastic changes listed by nodes.

Nodes	Synapomorphies	Homoplastic changes
1	–	37(1) and 41(1)
2	31(0) and 62(1)	23(0)
3	13(0), 14(1), 51(1), 52(1), and 60(0)	26(1), 35(0), and 41(0)
4	12(1), 46(0), and 61(0)	0(1), 7(0), 53(0), 54(0), and 64(0)
5	1(1) and 30(1)	3(1), 38(1), and 42(0)
6	40(1)	63(2)
7	18(1) and 56(1)	35(1), 45(1), and 62(0)
8	33(1) and 36(2)	37(0)
9	34(1) and 46(1)	5(1), 6(0), and 53(0)
10	32(1) and 36(0)	63(0)
11	–	60(1)
12	–	1(0), 2(1), and 5(0)
13	–	23(1), 26(0), and 35(1)
14	–	4(1), 6(1), and 31(0)
15	–	15(1), 34(0), 41(1), 49(0), 52(0), and 59(2)
16	–	11(1), 14(0), 27(1), and 47(1).
17	59(1)	58(0) and 64(0)
18	–	26(0) and 59(2)
19	–	27(1), 43(1), and 48(1)
20	–	53(1)
21	29(1)	1(0), 2(1), 4(1), 5(0), 6(0), 17(0), 19(1), 21(1), 36(1), 37(1), and 39(1)
22	–	15(1) and 41(1)
23	22(1)	20(1) and 43(0)
24	–	15(0) and 35(1)
25*	–	6(0)
26*	–	63(1)
27	–	23(1) and 39(1)
28	–	48(1)
29	–	0(1), 15(1), and 41(1)
30	–	6(1), 26(0), and 53(1)
31	–	11(1) and 27(1)
32	–	64(1)
33	–	58(1)
34	–	43(1)
35	–	39(0)
36	–	1(0) and 58(0)
37	–	11(1), 59(2), and 63(1)
38	–	0(1), 60(1), and 64(1)
39	–	5(0), 39(1), and 59(0)
40	–	49(0)

(Central American), *L. webbii*, *L. dilaticollis*, and *L. drummondi* (North American). Clade B comprises the species *L. geniculata*, *L. simplex* (Central American), *L. cyanitarsis*, *L. chamela*, *L. colima* (Mexican), and *L. bahamica*, *L. torquata*, *L. aurifera*, *L. aurata* plus *L. straba* (Antillean). Clade C comprises the species *L. monilis* (Central American), and two smaller clades: the first one comprises *L. tigrina* (southern Mexican) plus *L. viridimarginalis* (Central American), *L. cupreopunctata* (North American), *L. cortesi* (Central American), and *L. obscura* (central Mexican); whereas the other comprises *L. viridicolor*, *L. hondurensis* (Central American), *L. granulifera* plus *L. hirtomaculata* (Central American), *L. mexicana* (central Mexican), *L. auropunctata* (northern and central Mexican), *L. chalconota* (Central American), *L. chiapaneca* (southern Mexican), and *L. lesnei* (Central American).

Psiloptera and *Lampetis* constitute a monophyletic group, supported by one synapomorphy, the last male abdominal ventrite truncate. *Lampetis* appears to be paraphyletic, because *Lampetis* (*Spinthoptera*) is more closely related to *Psiloptera* than to *Lampetis* (*Lampetis*), based on two synapomorphies: the elytral apex dentiform and the second lobe of posterior margin of metacoxae rounded. In *Lampetis* (*Lampetis*), the elytral apex is not dentiform and the second lobe of the posterior margin of the metacoxae is acute.

The subgenus *Lampetis* (*Spinthoptera*) is monophyletic, supported by two synapomorphies: several irregular interstitial depressions surrounding callosities laterally present in the elytra, and the anterior margin of prosternum flattened at middle. The majority of the outgroups present the latter concave, but in *Psiloptera* and *Lampetis* (*L.*) *fastuosa* it is convex (like a lobe), further changing to flattened in *Lampetis* (*Spinthoptera*) and reverting to concave in the Antillean species of the latter. This feature would be a good diagnostic character if *Lampetis* (*Spinthoptera*) is segregated as a distinct genus from *Lampetis*.

Within the subgenus three clades are identified (Figure 9; Table II). The first clade (A) is characterized by the median lobe of male genitalia wide. This character is also present in four species of clade C (*L. auropunctata*, *L. chalconota*, *L. chiapaneca*, and *L. lesnei*). The remaining species of the subgenus have the median lobe of the male genitalia slender. Clades B and C are supported by one synapomorphy, the median lobe apex of male genitalia subtriangular. The median lobe apex is entire in all the outgroups; changing to semicircular in clade A in the North American species (*L. webbia*, *L. dillaticollis*, and *L. drummondi*), in clade B, and in clade C in *L. mexicana*; and reverting to the plesiomorphic state in clade C in *L. auropunctata*, *L. chalconota*, *L. chiapaneca*, and *L. lesnei*. In clade B, the Antillean species present one synapomorphy, the pronotum with callosities at lateral margin near anterior margin; this condition is absent only in *L. guildini*. Characters within clade C are conflicting, because two nodes (25 and 26) are collapsed in the strict consensus cladogram and present several homoplastic changes. Clade C comprises two smaller clades, each one with one North American species among several Central American species. The bootstrap analysis supported strongly the clades (1) *Ectinogonia pukvurea* plus *Polybothris sumptuosa*, (2) *Lampetis amaurotica* plus *L. viridimarginata*, (3) *L. webbia*, *L. dillaticollis* plus *L. drummondi*, and (4) *L. aurata*, *L. aurifera*, *L. bahamica*, *L. straba* plus *L. torquata* (Figure 10).

The cladistic analysis shows that *Lampetis* (*Spinthoptera*) is more closely related to *Psiloptera* than to *Lampetis* (*Lampetis*). This suggests that species of *Lampetis* (*Spinthoptera*) may be segregated from *Lampetis* and recognized as a different genus. We believe that more detailed supraspecific analyses are still needed, including more evidence, such as internal features, and larval and molecular characters, to corroborate this preliminary hypothesis. On the other hand, the analysis revealed that the North and Central American and Antillean *Lampetis* (*Spinthoptera*) do not constitute a monophyletic group, because *L. (S.) tucumana*, from South America (outgroup), is nested within them.

From a biogeographic viewpoint, the species of *Lampetis* (*Spinthoptera*) analysed herein correspond to the Paleoamerican biotic element (Halffter 2003; Morrone 2005), which includes Neotropical taxa that underwent diversification prior to the Pliocene closure of the Isthmus of Tehuantepec. They are restricted to Mexican mountain areas, with ecological preferences for deserts, grasslands, and rain forests; and may also have some species in Central America. Their closest relatives are Old World temperate and tropical taxa (Liebherr 1991, 1994).

If we compare our phylogenetic results with the panbiogeographic analysis of Corona and Morrone (2005), we recognize that nine of the 15 generalized tracks appear once in the

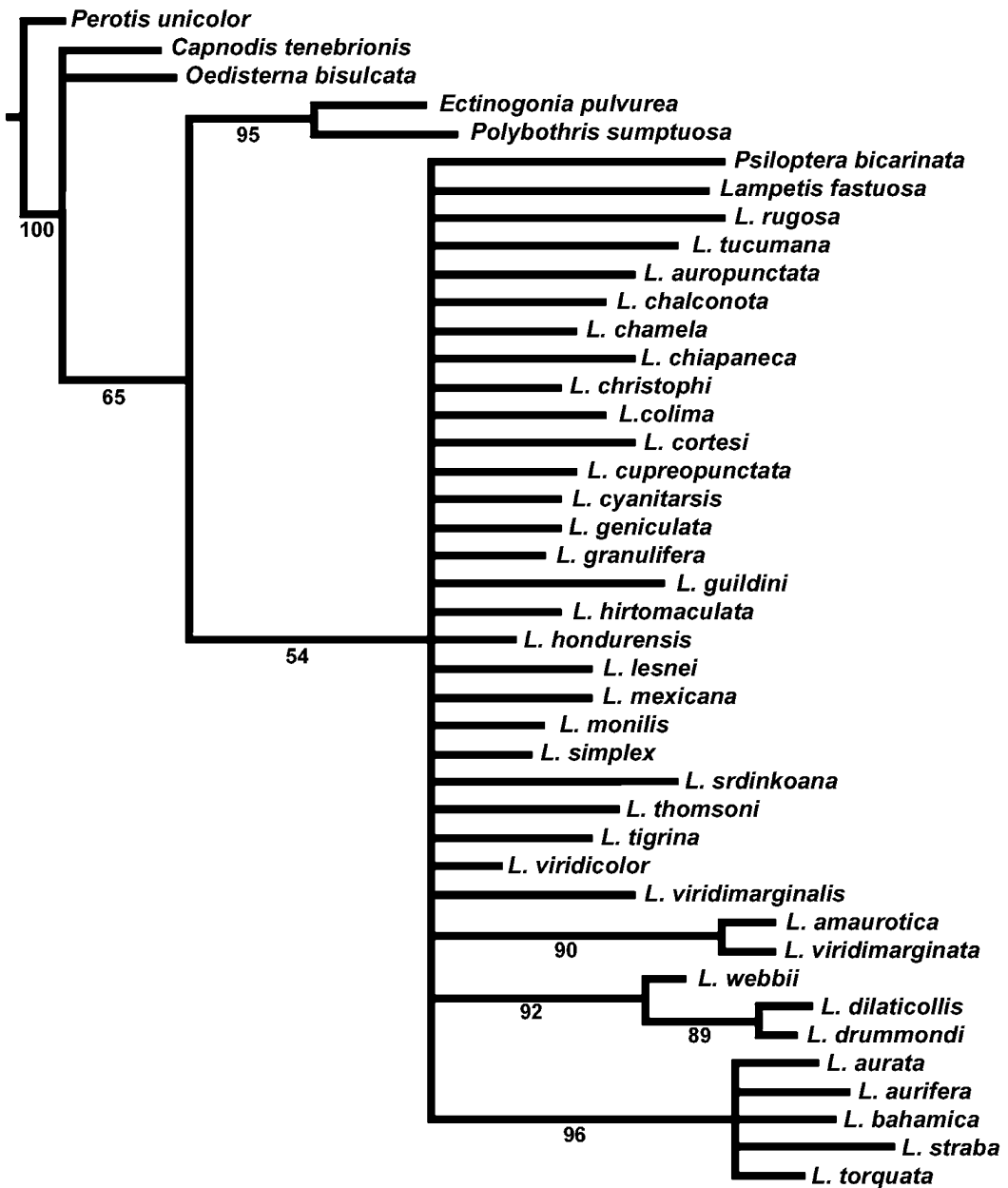


Figure 10. Cladogram resulting from the bootstrap analysis of *Lampetis* (*Spinthoptera*) of North and Central America and the West Indies, and 11 species of different generic groups of the subtribe Dicercina (outgroups). Numbers are the percentages obtained.

cladogram (Figure 9). The Nearctic generalized track 2 includes *Lampetis* (*Spinthoptera*) *dilaticollis* and *L. webbii*, assigned to clade A. Two generalized tracks from the Mexican transition zone (4 and 5) include *L. chalconota* and *L. cortesi*, and *L. chalconota*, *L. cortesi*, and *L. obscura*, respectively (clade C). Generalized track 6, from the Mexican transition zone and the Mesoamerican dominion, includes *L. cortesi*, *L. cupreopunctata*, *L. granulifera*,

L. monilis, *L. simplex*, and *L. obscura* (clade C). The Antillean generalized tracks 9 and 10 include *L. straba* and *L. torquata*, and *L. aurata* and *L. aurifera*, respectively (clade B). The Mesoamerican generalized tracks 12, 14, and 15 include *L. chalconota*, *L. granulifera*, *L. monilis*, and *L. obscura*; *L. monilis* and *L. simplex*; and *L. cortesi* and *L. granulifera*, respectively (clade C). The remaining six generalized tracks appear twice in the cladogram (clades A and C, and B and C), suggesting an ancient radiation of this taxon in the area.

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