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CLADISTIC AND BIOGEOGRAPHIC ANALYSES OF THE WEEVIL GENUS *LISTRODERES* SCHOENHERR (COLEOPTERA: CURCULIONIDAE)

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Abstract—The weevil genus *Listroderes* Schoenherr is a monophyletic group defined by the body vestiture consisting of subcircular to suboval scales, and comprises 35 species endemic to southern South America. A cladistic analysis of the genus was carried out using 44 characters from external morphology, body vestiture, and male and female genitalia. The *curvipes* (three species), *nodifer* (five species) and *robustus* (four species) species groups and the 23 species of the *costirostris* species group were considered terminal taxa. Apomorphic states were identified using the genus *Hyperoides* Marshall as outgroup. The analysis yielded 122 equally parsimonious cladograms, each with 89 steps and a consistency index of 0.42; a successive weighting procedure resulted in nine cladograms (consistency index of 0.69 and retention index of 0.85). In the general consensus cladogram, *nodifer–robustus* and *curvipes-costirostris* are two pairs of sister species groups. The *costirostris* group comprises the subgroups *foveatus, angusticeps, costirostris, delaiguei, bimaculatus* and *elegans*, in phylogenetic order. A distributional analysis of the species of *Listroderes* led to identification of four areas of endemism, namely central Chile, sub-Antarctic, central Argentina and Chaco. A vicariance biogeographic analysis of these areas, based on area cladograms of *Listroderes, Hyperoides, Naupactus taeniatulus* species group (Coleoptera: Curculionidae), and *Lucilia* generic group (Asteraceae) was carried out applying the three-area statements technique. According to the general area cladogram the sequence of area-fragmentation is as follows: (central Chile (sub-Antarctic (central Argentina, Chaco))). This sequence is congruent with the history hypothesized for the region, where the uplift of the Andes (Oligocene–Pliocene) led to a progressive aridification, replacing the ancient subtropical forest by open-country environments.

Introduction

The weevil genus *Listroderes* Schoenherr (Coleoptera: Curculionidae) is widespread throughout Argentina, Chile, Bolivia, Peru, Paraguay, Uruguay and southern Brazil. Within this range, species of *Listroderes* occupy a wide variety of habitats, mainly xerofilous forests, savannas, steppes and grasslands.

Germain (1895a,b,c,d, 1896a,b) partially reviewed the genus when studying the Chilean Rhytirrhinini. Hustache (1926) described the majority of the Argentinian species. More recent papers by Kuschel presented corrections and new combinations (Kuschel, 1946, 1950, 1986) or descriptions of new species (Kuschel, 1949, 1952). Morrone (1993a,b,c,d) restricted *Listroderes* to 35 species and four species groups. He also described two new genera based on species formerly assigned to *Listroderes*, and revalidated its former synonyms *Antarctobius* Fairmaire, *Trachodema* Blanchard and *Hyperoides* Marshall (Morrone, 1992a,b, 1993e,f).

The species *L. costirostris* Schoenherr, *L. apicalis* Waterhouse, *L. foveatus* (Lea) and *L. delaiguei* Germain have parthenogenetic populations. Furthermore, partheno-

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genesis seems to be the main reproduction mode in *L. costirostris*, which comprises several parthenogenetic clones (Morrone, 1993d). This is remarkable, because apparently *Listroderes* is the only representative of the Rhytirrhinini with this kind of reproduction. Other parthenogenetic Curculionidae are well known to evolutionary biologists (Suomalainen et al., 1976, and references therein; Lokki and Saura, 1980). A phylogenetic hypothesis for the species of *Listroderes* could help to understand the evolution of parthenogenesis within the group.

Finally, the geographical distribution of *Listroderes* is of interest. When compared to its related genera, e.g. *Antarctobius* Fairmaire, *Falklandius* Enderlein, *Lanteriella* Morrone, *Falklandiellus* Kuschel, *Trachodema* Blanchard, *Lamiarhinus* Morrone and *Hyperoides* Marshall, it appears that *Listroderes* has been highly successful in occupying the areas of the Chacoan dominion (*sensu* Cabrera and Willink, 1973), while the remaining genera are mainly restricted to the sub-Antarctic dominion or central Chile (Morrone, 1990, 1992a,b,c, 1993f, in press). Recently, Nelson and Ladiges (199 a,b,c) developed the three-area statements technique, which has been applied empirically only once (Ladiges et al., 1992). This technique seemed to me appropriate for formulating a biogeographic hypothesis to explain this distributional pattern.

The objectives of this paper are:

1. to perform a cladistic analysis of the species of *Listroderes*;
2. to provide a cladistically-based classification of the genus;
3. to analyze the geographic distribution patterns exhibited by the species of *Listroderes*;
4. to relate *Listroderes* species distributions to those of other taxa, using a cladistic biogeography approach, in order to postulate hypotheses on the biogeographical relationships among areas where they are distributed.

Material and Methods

TAXA

Listroderes Schoenherr forms a monophyletic group that is distinguished from other related genera by one apomorphy: "body vestiture consisting of subcircular to suboval scales" (character 38 in the data matrix). Three monophyletic species groups [*nodifer* (five species), *robustus* (four species) and *curvipes* (three species)] and the 23 species of the *costirostris* species group (Morrone, 1993a,b,c,d) are considered as terminal taxa. Table 1 lists these species and species groups, their acronyms, and geographical distribution.

CHARACTERS

Data from 44 characters (Table 2) were derived from external morphology (24), male and female genitalia (13) and body vestiture (7). For more details about these characters see Morrone (1993a,b,c,d). Within each character, apomorphic character states were identified by the outgroup comparison method (Watrous and Wheeler, 1981) with the genus *Hyperoides* Marshall, hypothesized to be the sister genus of *Listroderes* (Morrone, 1993e).

Table 1
Species groups and species of *Listroderes*, their acronyms and geographical distribution.

Taxa	Acronym	Geographical distribution
curvipes species group	CUR	Central and southern Chile
nodifer species group	NOD	Central and southern Chile
robustus species group	ROB	Central Chile
L. affinis Hustache	AFF	Southern Chile and southern Argentina
L. angusticeps Blanchard	ANG	Central Chile
L. annulipes Blanchard	ANN	Central and northern Chile
L. apicalis Waterhouse	API	Central and northern Argentina, Uruguay and southern Brazil
L. bimaculatus Boheman	BIM	Central Chile
L. brevisetis Hustache	BRE	Central Argentina
L. bruchi Hustache	BRU	Central Argentina
L. charybdis Morrone	CHA	Northeastern Argentina
L. confusus Hustache	CON	Central Argentina, Uruguay and southern Brazil
L. costirostris Schoenherr	COS	Central Chile, Central and northern Argentina, Uruguay and southern Brazil
L. delaiguei Germain	DEL	Central and southern Chile, central Argentina, Uruguay and southern Brazil
L. elegans Hustache	ELE	Eastern Argentina and Uruguay
L. foveatus (Lea)	FOV	Central Argentina, Uruguay and southern Brazil
L. howdenae Morrone	HOW	Central Chile
L. leviculus Kuschel	LEV	Southern Chile
L. obrieni Morrone	OBR	Southern Chile
L. punicola Kuschel	PUN	Bolivia, Peru and northern Chile
L. pusillus Hustache	PUS	Central Argentina
L. robustior Sch. & Mshl.	ROS	Central and southern Chile
L. scylla Morrone	SCY	Northern Argentina
L. uruguayensis Kuschel	URU	Uruguay and southern Brazil
L. wagneri Hustache	WAG	Central Argentina
L. wittei Hustache	WIT	?

CODING AND ANALYSIS

Multistate characters were treated in two different manners: (a) characters 18, 24 and 25 were ordered (= additive); and (b) characters 9, 15 and 19 were unordered (= non-additive). 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. Consistency (Kluge and Farris, 1969) and retention (Farris, 1989) indices were calculated excluding autapomorphies and synapomorphy of the group. I used the successive weighting procedure in Hennig86, which 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 on successively produced cladograms until they no longer change (Farris, 1989). When the analyses yielded more than one cladogram, a strict consensus tree was calculated with the nelsen option of Hennig86. The program CLADOS Version 1.1 (Nixon, 1992) was used for examination of character distributions.

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

Plesiomorphic states	Apomorphic states
1. Frons with fovea (0)	With impression (1)
2. Eyes medium-sized (0)	Large (1)
3. Rostrum shorter than prothorax (0)	Slightly longer than prothorax (1)
4. Ventral carina of scrobe lacking tooth (0)	With tooth (1)
5. Epistome slightly convex (0)	Flat (1)
6. Scape extending beyond hind margin of eye (0)	Not extending beyond hind margin of eye (1)
7. Prothorax flanks straight (0)	Bisinuate (1)
8. Prothorax flanks slightly divergent toward apex (0)	Subparallel (1)
9. Prothorax dorsum slightly convex (0)	Flat (a); convex (b)
10. Prothorax lacking subcircular impressions (0)	With two subcircular impressions (1)
11. Postocular lobes poorly developed (0)	Well developed (1)
12. Prothorax lacking median sulcus (0)	With median sulcus (1)
13. Prothorax lacking median keel (0)	With median keel (1)
14. Prothorax surface not sculptured (0)	Sculptured (1)
15. Prothoracic anterior impressions poorly developed (0)	Well developed (a); absent (b)
16. Humeri rounded (0)	Prominent (1)
17. Elytral surface lacking tubercles (0)	With little tubercles (1)
18. Intervals flat (0)	Slightly convex (1); costiform (2)
19. Anteapical tubercle absent (0)	Conical (a); subquadrate, small (b); subquadrate, large (c)
20. Females without elytral apical tubercles (0)	With elytral apical tubercles (1)
21. Oblique series of declivital tubercles absent (0)	Present (1)
22. Mesotibiae with one spur (0)	With two spurs (1)
23. Metatibiae with two spurs (0)	With one spur (1)
24. Aedeagus symmetrical (0)	Slightly asymmetrical (1); strongly asymmetrical (2)
25. Aedeagus very slender in lateral view (0)	Slender (1); robust (2)
26. Apex of aedeagus rounded (0)	Acute (1)
27. Apex of aedeagus lacking darker lines (0)	With darker lines (1)
28. Hemisternites long (0)	Short (1)
29. Hemisternites base simple (0)	Bilobed (1)
30. Hemisternites lacking papillae (0)	With papillae (1)
31. Hemisternites lacking teeth (0)	With teeth (1)
32. Styli present (0)	Absent (1)
33. Sternum 8 subcircular (0)	Subrectangular (1)
34. Sternum 8 small (0)	Large (1)
35. Apodeme long (0)	Short (1)
36. Sternum 8 setae long (0)	Short (1)
37. Body sparsely squamose (0)	Densely squamose (1)
38. Body vestiture consisting of lanceolate scales (0)	Subcircular to suboval scales (1)
39. Scales finely striate (0)	Strongly striate (1)
40. Rostrum lacking scales (0)	With scales (1)
41. Elytra lacking patches (0)	With little yellowish patches (1)
42. Legs lacking scales (0)	With scales (1)
43. Ventrites lacking scales (0)	With scales (1)
44. Small to medium-sized (<9 mm) (0)	Large (>9.1 mm) (1)

Table 3

Data marix used in the cladistic analysis of *Listroderes*, with *Hyperoides* (HYP) as outgroup. Refer to Table 1 for acronyms and Table 2 for characters.

	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	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
HYP	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	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CUR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	c	1	0	0	1	1	1	1	0	1	0	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0
NOD	0	0	0	0	0	0	0	0	0	0	0	0	0	0	a	0	0	1	a	0	1	1	1	0	2	0	1	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0
ROB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	a	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
AFF	0	0	1	1	0	1	0	1	a	0	1	0	0	0	a	0	0	1	b	0	0	0	0	0	2	0	0	0	1	0	1	1	1	0	0	0	1	1	0	0	0	0	0	1
ANG	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	1	a	0	0	0	0	1	1	1	0	0	1	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0
ANN	0	1	0	0	0	1	0	1	0	0	1	0	0	0	a	0	0	1	a	0	0	0	0	2	1	0	0	0	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	1
API	0	0	0	1	0	1	0	1	0	0	1	0	0	0	a	0	0	1	b	0	0	0	0	1	1	0	0	0	1	0	1	1	1	0	0	0	1	1	0	1	0	1	0	0
BIM	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	a	0	0	0	0	2	1	1	0	0	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	1
BRE	1	0	0	1	0	1	1	1	a	0	1	1	0	0	a	0	0	2	b	0	0	0	0	0	2	0	0	0	1	0	1	1	1	0	0	1	1	1	0	1	0	1	1	0
BRU	0	0	1	1	0	1	0	1	a	0	1	0	1	0	a	0	0	1	a	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	1
CHA	0	1	0	0	1	1	0	1	0	0	1	1	0	1	a	0	0	1	b	0	0	0	0	0	1	0	0	?	?	?	?	?	?	?	?	?	0	1	1	0	0	0	0	0
CON	0	0	0	1	0	1	0	1	a	0	1	0	0	0	a	0	1	1	b	0	0	0	0	1	2	0	0	0	1	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0
COS	0	0	0	1	0	1	0	1	0	0	1	0	0	0	a	0	0	1	a	0	0	0	0	2	2	0	0	0	1	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0
DEL	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	1	b	0	0	0	0	1	1	1	0	0	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0
ELE	0	0	0	0	1	1	0	1	0	1	1	1	0	0	0	0	0	1	a	0	0	0	0	0	2	0	0	0	1	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0
FOV	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	a	0	0	0	0	1	2	0	0	0	1	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0
HOW	0	0	0	1	0	1	0	1	0	0	1	0	1	0	a	1	0	2	b	0	0	0	0	0	2	0	0	0	1	0	1	1	1	0	0	0	1	1	0	1	0	1	1	0
LEV	0	0	0	0	0	1	0	1	b	0	1	0	0	0	b	0	0	1	a	0	0	0	0	0	2	0	0	?	?	?	?	?	?	?	?	?	0	1	1	0	0	0	1	0
OBR	0	1	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1	a	0	0	0	0	0	2	1	0	0	1	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0
PUN	0	0	0	1	0	1	0	1	0	0	1	0	0	0	a	0	0	1	a	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0
PUS	0	0	0	1	0	1	0	1	0	0	1	0	0	0	a	0	0	1	b	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0
ROS	0	0	0	1	0	1	0	1	a	0	1	0	0	0	a	0	0	1	a	0	0	0	0	1	1	1	0	0	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	1
SCY	0	0	0	1	0	1	0	1	0	0	1	0	0	0	a	0	0	1	b	0	0	0	0	1	2	0	1	?	?	?	?	?	?	?	?	?	1	1	0	1	0	1	0	0
URU	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	1	a	0	0	0	0	0	2	0	0	0	1	0	1	1	1	0	0	0	0	1	1	0	1	0	0	0
WAG	0	1	0	0	1	1	0	1	0	1	1	1	0	0	a	0	0	1	a	0	0	0	0	1	2	0	0	?	?	?	?	?	?	?	?	?	0	1	1	0	0	1	1	0
WIT	0	0	0	0	0	1	0	0	0	1	1	0	0	0	b	0	0	1	a	0	0	0	0	0	1	0	0	?	?	?	?	?	?	?	?	?	0	1	1	0	0	1	1	0

BIOGEOGRAPHY

Cladistic biogeographic methods are detailed in Nelson and Platnick (1981), Humphries and Parenti (1986), Page (1990) and Crisci et al. (1991). Areas of endemism were defined by the congruent distributional limits of two or more species of *Listroderes* [Figs 4(a)–(d), 5(a), (b)].

In order to analyze the generality of geographical patterns of *Listroderes*, the cladograms of three other taxa of the area were considered:

1. *Hyperoides* Marshall (Coleoptera: Curculionidae) (Morrone, 1993e);
2. *Naupactus taeniatulus* species group (Coleoptera: Curculionidae) (Lanteri, pers. comm.);
3. *Lucilia* generic group (Asteraceae) (Anderberg and Freire, 1991).

Area cladograms were constructed by replacing the name of each terminal taxon with the name of the area(s) in which it occurs. In Fig. 6(a)–(d) the original area cladograms of *Listroderes*, *N. taeniatulus* species group, *Hyperoides* and *Lucilia* generic group are presented. The general area cladogram was obtained by the three-area statements technique (TAS) (Nelson and Ladiges, 1991a,b), implemented for assumptions 0 and 1 (implementation of assumption 2 is limited to hand resolu-

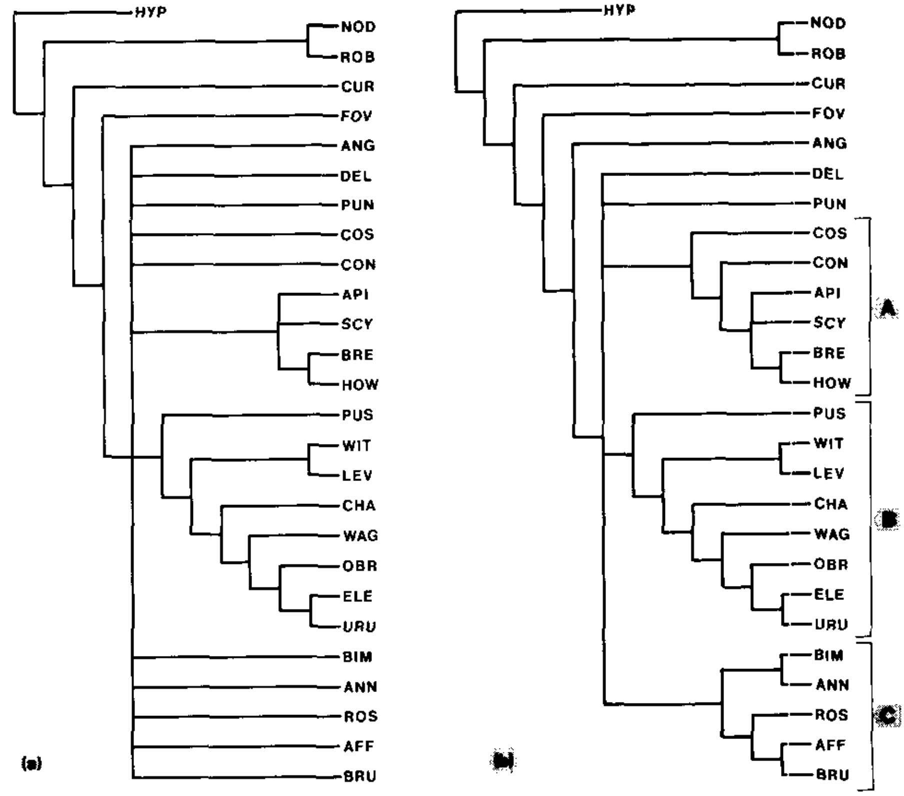

Fig. 1. Strict consensus cladograms of species of *Listroderes* using *Hyperoides* as outgroup. (a) Consensus of the 122 most parsimonious cladograms (length = 89; consistency index = 0.42). (b) Consensus of nine minimum-length trees resulting after successive weighting procedure (length = 219; consistency index = 0.69). For acronyms refer to Table 1.

tion; Ladiges et al., 1992). This technique codes distributional data for area cladograms as a suite of three-area statements. Output of the area data is a matrix for parsimony analysis. The matrix (Table 5) was produced with the program TAS (Nelson and Ladiges, 1991c), and analyzed with Hennig86, applying the ie* option. The resulting general area cladogram is presented in Fig. 6(e).

Results

CLADISTIC ANALYSIS

The analysis using equal weights yielded 122 equally parsimonious cladograms, each with 89 steps, a consistency index of 0.42, and a retention index of 0.65 [in Fig. 1(a) their strict consensus cladogram]. When successive weighting was applied, nine minimum-length cladograms resulted after the second round of weighting, with length 219, a consistency index of 0.69 and a retention index of 0.85. The strict consensus tree for these cladograms is shown in Fig. 1(b). Values for the range and number of steps, consistency index (CI), retention index (RI) and weight (RI × CI × 100) in the weighted trees are listed in Table 4. The nine result-

Table 4

Character consistencies and retention indices as the best fits of the 122 most parsimonious cladograms obtained applying mhenning* and bb*. Final weights were obtained after the second round of the successive weighting procedure. Uninformative characters were excluded.

Character	Range of steps	Number of steps	Consistency index(CI)	Retention index (RI)	Weight (RI×CI×100)	Final weight
2	1	3	0.33	0.33	1	1
3	1	1	1	1	10	10
4	1	4	0.25	0.75	2	1
5	1	1	1	1	10	10
6	1	2	0.50	0.75	3	3
7	1	1	1	1	10	10
8	1	3	0.33	0.71	2	2
9	2	4	0.50	0.50	2	2
10	1	3	0.33	0.33	1	1
11	1	1	1	1	10	1
12	1	4	0.25	0.25	1	1
13	1	2	0.50	0	0	0
15	2	6	0.33	0.60	4	2
18	2	3	0.66	0.50	3	3
19	2	7	0.42	0.50	3	2
23	1	2	0.50	0.50	2	2
24	2	8	0.25	0.53	2	1
25	2	8	0.25	0.50	1	1
26	1	6	0.16	0	0	0
27	1	2	0.50	0	0	0
29	1	1	1	1	10	10
31	1	1	1	1	10	10
32	1	1	1	1	10	10
33	1	1	1	1	10	10
36	1	1	1	1	10	10
37	1	4	0.25	0.75	4	2
39	1	2	0.50	0.87	4	4
40	1	1	1	1	10	10
42	1	3	0.33	0.60	2	2
43	1	3	0.33	0.50	1	1
44	1	1	1	1	10	10

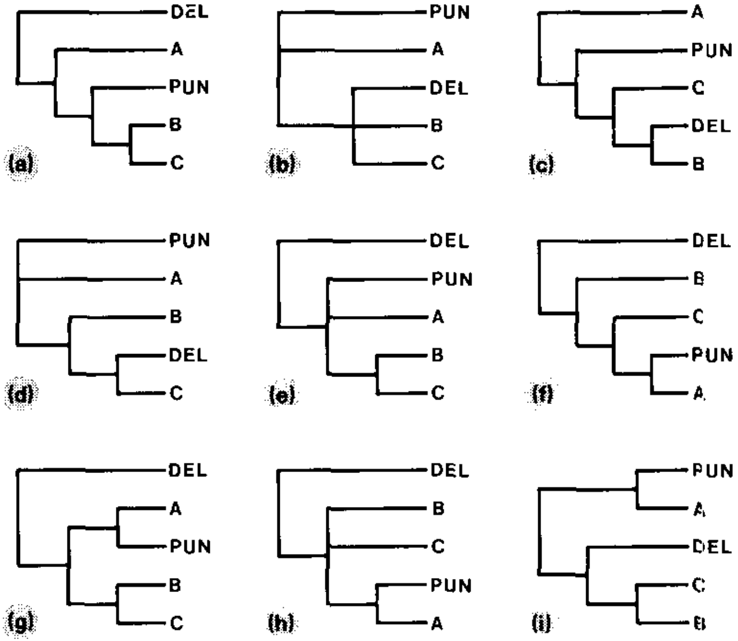

Fig. 2. Simplified topologies of the nine minimum-length cladograms resulting after successive weighting. A, B, C as in Fig. 1(b); DEL = *L. delaiguei*; PUN = *L. punicola*.

ing cladograms after successive weighting can be simplified to show that they differ in the relationships among three clades [labelled A, B and C in Fig. 1(b)] and the species *L. delaiguei* and *L. punicola* [Fig. 2(a)–(i)].

The general consensus cladogram (Nelson consensus cladogram *sensu* Page, 1989) of the nine cladograms, identical to one of the original cladograms [Fig. 2(i)], was chosen to show the characters distribution (Fig. 3). The *nodifer* species group is the sister group to the *robustus* species group, and the *curvipes* species group is the sister group to the *costirostris* species group. Within the *costirostris* species group, there is a phylogenetic sequence of six subgroups: *foveatus*, *angusticeps*, *costirostris*, *delaiguei*, *bimaculatus* and *elegans*.

Based on this cladogram, a phylogenetic classification for the species of *Listroderes* is proposed, combining subordination with phylogenetic sequencing (sequences of species in the *nodifer*, *robustus* and *curvipes* groups from Morrone, 1993a,b,c). The following list orders groups, subgroups and species of *Listroderes* phylogenetically:

Listroderes Schoenherr
—*nodifer–robustus* clade
  nodifer species group: *L. desertorum*, *L. hoffmanni*, *L. erinaceus*, *L. brevirostris* and *L. nodifer*.
  robustus species group: *L. trivialis*, *L. cinerarius*, *L. montanus* and *L. robustus*.
—*curvipes–costirostris* clade
  curvipes species group: *L. curvipes*, *L. fallax* and *L. tuberculifer*.
  costirostris species group
  foveatus subgroup: *L. foveatus*.
  angusticeps subgroup: *L. angusticeps*.

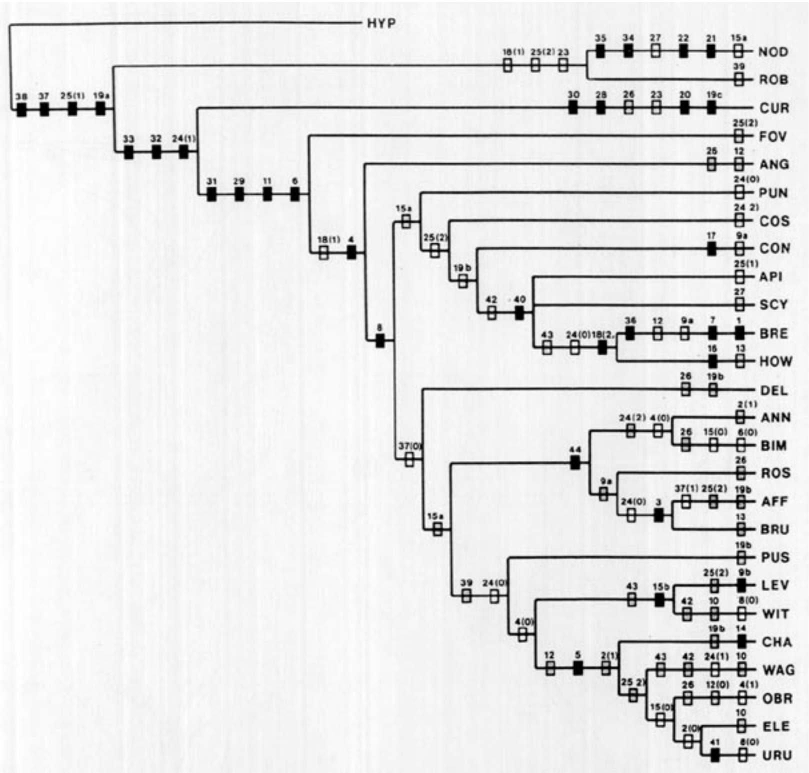

Fig. 3. One of the nine cladograms of *Listroderes* resulting after successive weighting procedure. Character state changes are superimposed: solid black squares = synapomorphies; dotted squares = parallelisms; open squares = reversals. For acronyms refer to Table 1.

costirostris subgroup: *L. punicola*, *L. costirostris*, *L. confusus*, *L. apicalis*, *L. scylla*, *L. brevisetis* and *L. howdenae*.
delaiguei subgroup: *L. delaiguei*.
bimaculatus subgroup: *L. annulipes*, *L. bimaculatus*, *L. robustior*, *L. affinis* and *L. bruchi*.
elegans subgroup: *L. pusillus*, *L. leviculus*, *L. wittei*, *L. charybdis*, *L. wagneri*, *L. obrieni*, *L. elegans* and *L. uruguayensis*.

BIOGEOGRAPHIC ANALYSIS

From the analysis of the mapped distributions of the species groups and species of *Listroderes* [Figs 4(a)–(d), 5(a)], four areas of endemism [Fig. 5(b)] are relevant for formulating biogeographic hypotheses. These areas also correspond broadly to recognized biogeographic regions (approximate correspondence to the scheme of Cabrera and Willink, 1973, in brackets):

1. Central Chile ("central Chilean province, Andean–patagonian dominion");
2. Sub-Antarctic ("sub-Antarctic province, sub-Antarctic dominion");
3. Central Argentina ("Monte province, Chacoan dominion");
4. Chaco ("Chacoan province, Chacoan dominion").

The area cladograms of *Listroderes*, *Hyperoides*, *Naupactus taeniatulus* species group, and *Lucilia* generic group are presented in Fig. 6(a)–(d). Under assumption 1 the nodes of these area cladograms generated 888 characters as three-area statements.

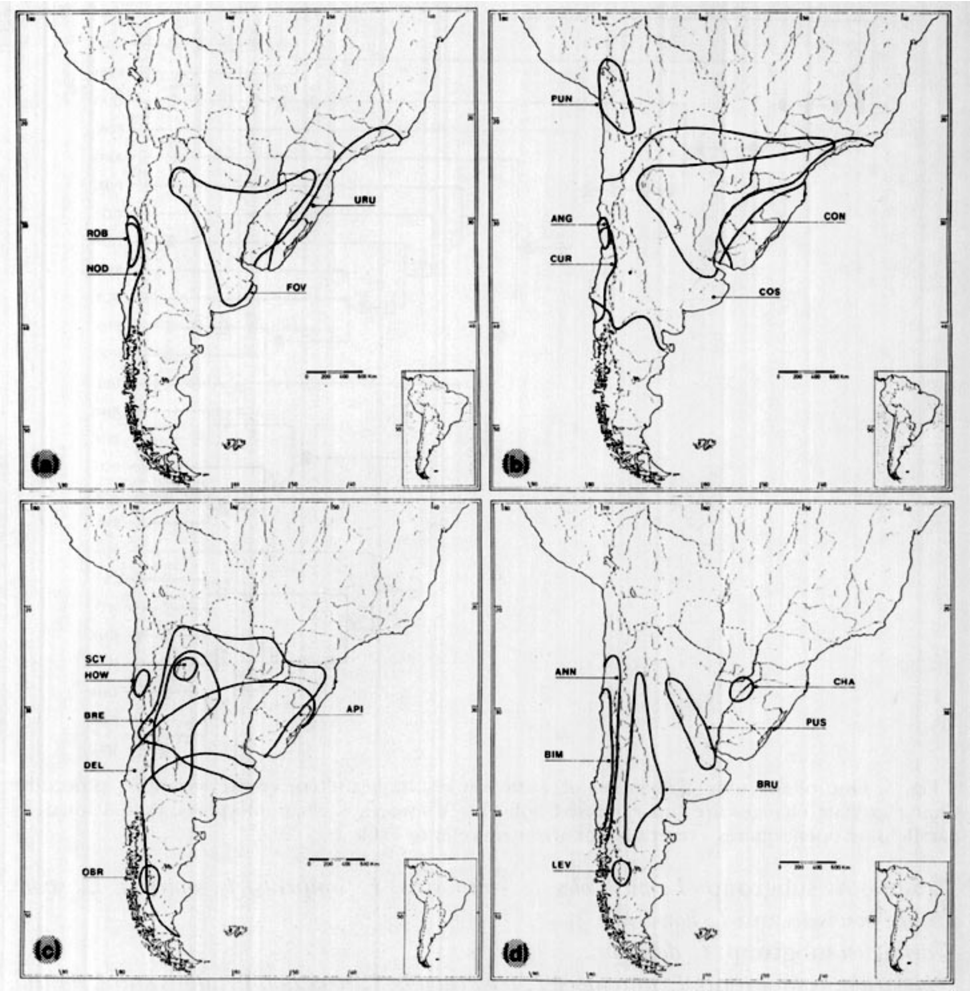

Fig. 4(a)–(d). Geographic distribution of the species of *Listroderes*. For acronyms refer to Table 1.

When data for widespread taxa were taken as informative (assumption 0) they generated a further 170 characters, making a total of 1058 (Table 5).

The analysis of the three-area statements matrix with Hennig86 led to one general area cladogram [Fig. 6(e)]. This general area cladogram shows a south-western–north-eastern progression in the areas involved in the analysis. Assuming an initial widespread distribution, the first event is postulated to have partitioned central Chile from the rest. The next vicariant event isolated the sub-Antarctic, and the last event separated central Argentina from Chaco (Fig. 7).

Discussion

The cladistic analysis supports the current infrageneric classification of *Listroderes* (Morrone, 1993a,b,c,d). In addition, six subgroups may be recognized within the *L. costirostris* species group. The species *L. charybdis*, *L. leviculus*, *L. scylla*, *L. wagneri* and *L. wittei* were assigned tentatively to the *costirostris* species group (Morrone, 1993d); this cladistic analysis supports their inclusion in the group.

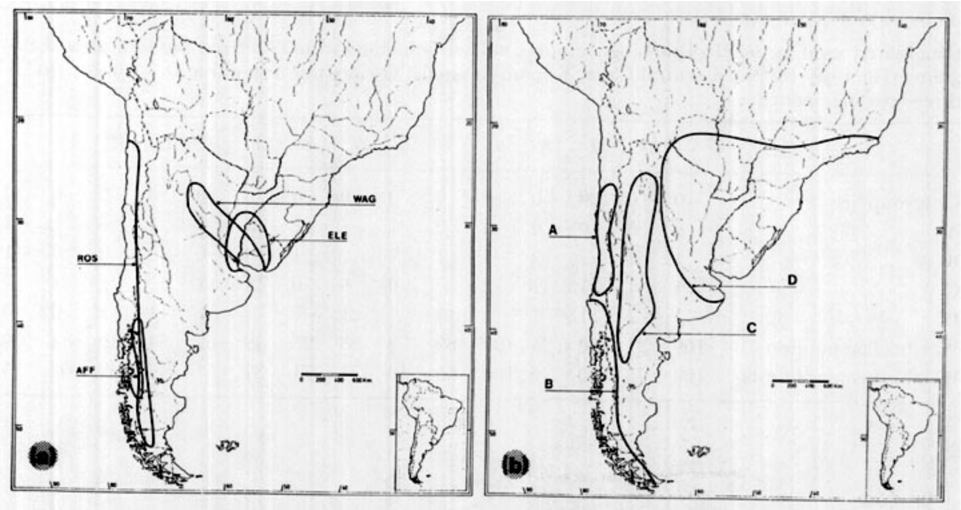

Fig. 5. (a) Geographic distribution of species of *Listroderes*. For acronyms refer to Table 1. (b) Areas of endemism. A = central Chile; B = sub-Antarctic; C = central Argentina; D = Chaco.

Each parthenogenetic species of *Listroderes* results always included in a group of bisexual species. This contrast with the weevil genus *Naupactus* Dejean, where several fairly large species groups are exclusively or almost exclusively parthenogenetic (Lanteri, pers. comm.). It is interesting to note that parthenogenetic species of *Listroderes* show widespread distributions, none of them being endemic to any of the areas involved in the biogeographic analysis.

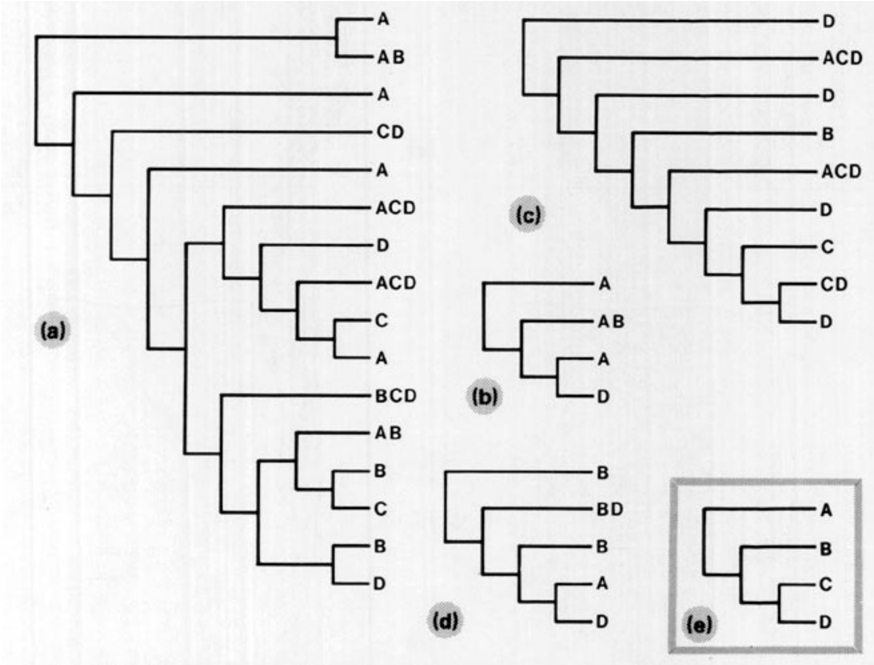

Fig. 6. Area cladograms used in the biogeographic analysis. (a) *Listroderes*; (b) *Hyperoides*; (c) *N. taeniatulus* species group; (d) *Lucilia* group; (e) general area cladogram.

Table 5

Data matrix used in the cladistic biogeographic analysis, obtained with TAS from the four area cladograms [Fig. 6(a)–(d)]. A = central Chile; B = sub-Antarctic; C = central Argentina; D = Chaco; 1–14 = three-area statements.

	0	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A	0	0	0	0	0	0	1	1	?	1	?	1	?	1	1
B	1	1	?	?	1	1	1	?	1	0	0	0	0	?	1
C	1	1	1	1	?	?	0	0	0	1	1	?	1	1	?
D	?	?	1	1	1	1	?	1	1	?	1	1	1	0	0
Weights (assumption 0)	100	21	100	25	100	89	78	83	93	49	67	54	55	84	60
Weights (assumption 1)	100	13	100	16	100	55	66	71	71	37	51	49	42	62	55

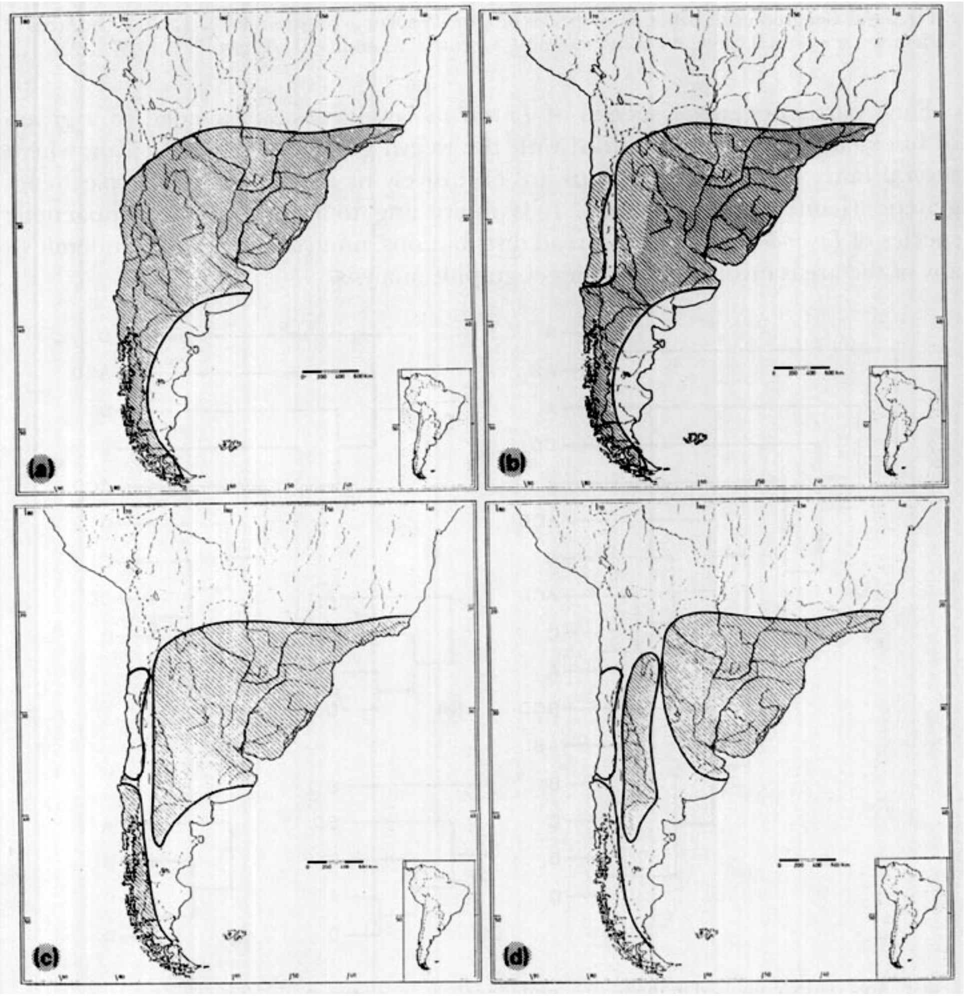

Fig. 7. Progression in the isolation of the areas of endemism of the analysis.

Vicariant events inferred from the general area cladogram are congruent with the history hypothesized for the region. Fossil evidence suggests that, before Eocene, southern South America had a subtropical climate (Patterson and Pascual, 1972), with an ancient forest across all the area (Smith, 1962). In the Paleocene–Oligocene these humid and tropical forested environments had a wider range, stretching to the northern part of the Antarctic peninsula (Pascual and Ortiz Jaureguizar, 1990). The major tectonic event that shaped southern South America was the gradual uplift of the Andes (Kuschel, 1969), which began in the late Oligocene and underwent its major uplift until the Pliocene. By cutting off the Pacific wind drift, this uplift induced the aridity of vast areas of southern South America. With some regional range fluctuations, until early Miocene tropical to subtropical environments were well represented as far as the southern tip of the continent. In the middle Miocene these environments were shifted to the North; extensive open-country environments ranging from wetter subtropical savannas to cold temperate steppes developed at that time (Pascual and Ortiz Jaureguizar, 1990). This south-western–north-eastern progression is reflected in the general area cladogram, where central Chile is the first area separated from the rest, and central Argentina and Chaco are the last areas partitioned.

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