Phylogenetic relationships and biogeographic considerations of four new species of *Cnemalobus* (Coleoptera: Carabidae) from Patagonia

SERGIO ROIG-JUÑENT, RODOLFO CARRARA, EIDER RUIZ-MANZANOS, FEDERICO AGRAIN, PAULA SACKMANN and MARCELO F. TOGNELLI


Four new species of *Cnemalobus* Guérin-Ménéville, 1838 (Carabidae) from the northern steppe of Patagonia and extra-Andean mountains are described in this work. Two of these species, *Cnemalobus nevado* sp. n. and *Cnemalobus diamante* sp. n., are from the Payunia (Argentina), the northernmost region of Patagonia. One species, *C. somuncura* sp. n., is from the vicinity of the Somuncurá Plateau. The other species, *Cnemalobus troll* sp. n., is from the northwestern steppe. Illustrations and keys for these new species are provided. The phylogenetic relationships among the new species were defined using a cladistic analysis for the genus *Cnemalobus*, based on 56 characters of the external morphology and male and female genitalia. The cladogram showed that *C. nevado* sp. n. and *C. diamante* sp. n., comprise a monophyletic group that is the adelphotaxon of an apical clade of species that mainly inhabit mountain habitats in central Chile. *Cnemalobus somuncura* sp. n. and *C. troll* sp. n. are also sister species and comprise the apical group of the Patagonian species. *Cnemalobus nevado* and *C. diamante* occur in the Payunia, and their distribution is restricted to different mountains and are isolated from each other. Given that these two mountains are 200 km apart, it is not likely that dispersal has occurred in these large and flightless species. The ancestral species might have been broadly distributed, and, as a result of habitat changes, they became isolated into restricted habitats in the upper part of each mountain, where speciation might have occurred. The other two new species, *C. somuncura* and *C. troll*, are placed in the group of Patagonian species that inhabit the lowlands or plateaus. Distributional data, together with phylogeny, showed that the sister species of *Cnemalobus* have an allopatric distribution. Strict sympatry (same locality) occurs in the northwestern region of the Patagonian Steppe. Nevertheless, this strict sympathy may be an artifact of geographical scale. For example, within the same area, some species may inhabit grasslands next to forests, while other species inhabit only steppe areas.

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Introduction

The genus *Cnemalobus* Guérin-Ménéville, 1838 (Coleoptera, Carabidae) is the only genus of an endemic tribe from austral South America and consists of 28 described species (Roig-Juñent 1993a, 1994a, 2002; Lagos & Roig-Juñent 1997). These species are characteristic of grassland areas in both mountain and lowland habitats, and in many of these places they are the largest carabid beetles. Recent ecological studies carried out in
different extra-Andean Mountain Systems and habitats of the Patagonian Steppe have revealed a rich fauna of insects, including new species of Coleoptera (Roig-Juñent & Sallenave 2005; Flores & Carrara 2006). Among the collected Coleoptera, four new species of Cnemalobus were found. Two of these species are from montane areas and two are from steppe areas. The objectives of this study were to describe these new species, establish their phylogenetic relationships, describe their habitat, and analyze the pattern of distribution of this group of species of the Patagonian Steppe.

Material and methods

Examined material

Specimens deposited in the following institutions were analyzed: AMNH: American Museum of Natural History, New York (USA) (Lee Herman); FIML: Fundación e Instituto Miguel Lillo (Argentina) (Maria V. Colomo); IADIZA: Instituto Argentino de Investigaciones de las Zonas Áridas (Argentina) (Adriana Marvaldi); MACN: Museo Argentino de Ciencias Naturales “Bernandino Rivadavia” (Argentina) (Arturo Roig Alsina); MLP: Museo de La Plata (Argentina) (Norma Díaz).

The methods and terminology used for dissecting, measuring, and illustrating the specimens were from previous revisions (Roig-Juñent 1993a, 1994a, 2002).

Cladistic Analysis

Characters. – A total of 56 characters were used in the analysis. All characters, with their respective states, are shown in Table 1. Distribution of the states among the terminal taxa are shown in the data matrix (Table 2). The apomorphic states are shown in the obtained cladograms (Figs 46-47). The characters with more than two states are organized with the most similar states adjacent to each other, and the most divergent states on opposite ends (i.e. character 1). We treated as non-additive those states that code structures with patterns of divergence that are too complex to be ordered as transformation series (characters 4, 13, 23, 42 and 43). The polymorphic characters for a certain taxon are represented by letters in the data matrix (Table 2).

Table 1. Characters and character states used in the phylogenetic analysis of Cnemalobus

<table>
<thead>
<tr>
<th>Character Number</th>
<th>Character State</th>
<th>Description</th>
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<tbody>
<tr>
<td>1</td>
<td>0</td>
<td>Number of posterior supraorbital setae: (0) one; (1) two; (2) three to five</td>
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<tr>
<td>2</td>
<td>0</td>
<td>Eyes shape: (0) subcircular; (1) acuminate, wide; (2) acuminate, thin.</td>
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<tr>
<td>3</td>
<td>0</td>
<td>Antennomere 11: (0) lanceolate; (1) sharpened at apex; (2) lengthened.</td>
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<tr>
<td>4</td>
<td>0</td>
<td>Antennomere 5-10: (0) subrectangular (2 times as long as wide); (1) subcircular (as long as wide); (2) lengthened (more than 3 times as long as wide).</td>
</tr>
<tr>
<td>5</td>
<td>0</td>
<td>Pubescence on antennomeres: (0) surface nearly completely covered; (1) only at apical third; (2) lateroapically only.</td>
</tr>
<tr>
<td>6</td>
<td>0</td>
<td>Lateroapical margin of antennomeres 5-10: (0) without an excavated area; (1) with an elliptic excavated area.</td>
</tr>
<tr>
<td>7</td>
<td>0</td>
<td>Number of setae on penultimate labial palpomere: (0) 7-10; (1) 2-5.</td>
</tr>
<tr>
<td>8</td>
<td>0</td>
<td>Pronotal margin: (0) narrow, not enlarged at apex; (1) narrow, thickened at apex; (2) cylindrical, wide; (3) cylindrical, very wide.</td>
</tr>
<tr>
<td>9</td>
<td>0</td>
<td>Pronotal setae: (0) absent; (1) 3-9; (2) 10-33; (3) more than 40.</td>
</tr>
<tr>
<td>10</td>
<td>0</td>
<td>Setae on pronotal margin: (0) in all its length; (1) on anterior 3/4; (2) on anterior 1/2.</td>
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<tr>
<td>11</td>
<td>0</td>
<td>Posterior pronotal setae: (0) absent; (1) present.</td>
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<tr>
<td>12</td>
<td>0</td>
<td>Posterior pronotal foveae: (0) absent; (1) present.</td>
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<tr>
<td>13</td>
<td>0</td>
<td>Prosternal setae: (0) only on apex; (1) on posterior 1/2; (2) on posterior 2/3.</td>
</tr>
<tr>
<td>14</td>
<td>0</td>
<td>Prosternal apophysis: (0) short, not surpassing the epimeron; (1) long (surpassing epimeron) and ventrally excavated; (2) long (surpassing epimeron) and not excavated.</td>
</tr>
<tr>
<td>15</td>
<td>0</td>
<td>Metepimera: (0) subquadrangular; (1) heart-shaped.</td>
</tr>
<tr>
<td>16</td>
<td>0</td>
<td>Metepimera: (0) glabrous; (1) with setae.</td>
</tr>
<tr>
<td>17</td>
<td>0</td>
<td>Metasternum: (0) with setae; (1) glabrous.</td>
</tr>
</tbody>
</table>
18. Protibial tooth: (0) absent; (1) present.
19. Protibial external margin in male: (0) straight; (1) convex at middle region; (2) very convex at middle region.
20. Lateral setae on protarsal claws: (0) non squamiform; (1) squamiform.
21. Adhesive setae on protarsomere 1: (0) covering apical 2/3; (1) covering apical 1/2; (2) covering apical 1/3.
22. Lateral setae on protarsomere 1 in male: (0) one; (1) two.
23. Length of external lateral setae on protarsomere 2 and 3 in male: (0) 3 times as long as wide; (1) more than 6 times as long as wide.
24. Insertion point of lateral setae on protarsomere 1 in male: (0) small notch; (1) notch longer at base; (2) notch with both edges very extended.
25. Dorsolateral setae on protarsomere 2 and 3 in male: (0) one; (1) 2-3.
26. Ventrolateral setae at protarsomere 2 and 3 in male: (0) on a row (1) disordered.
27. Number of squamiform ventrolateral setae on protarsomere 2 and 3 in female: (0) one; (1) two; (2) three.
28. Protarsomere 1 in male: (0) little expanded at apex; (1) apex 1.5 times as wide as base; (2) apex at least 2 times as wide as base.
29. Metatarsi: (0) as long as wide; (1) 2 times as long as wide; (1) 3 times as long as wide.
30. Metatarsis: (0) with apical region crenulate; (1) with apical region non crenulate.
31. Metatibial setae: (0) 3 times as long as wide; (1) more than 6 times as long as wide.
32. Elytral plica: (1) present; (0) absent.
33. Lateral series: (0) absent; (1) forming a row; (2) forming 2 rows.
34. Basal setae at elytra: (0) absent; (1) forming a row; (2) forming 2 rows.
35. Elytral punctuation of the umbilicate setae: (0) smaller or subequal to previous protuberance; (1) more than 2 times as big as previous protuberance.
36. Elytral humerus: (0) absent; (1) present.
37. Elytral epipleura: (0) without sulcus; (1) with a longitudinal sulcus near humerus.
38. Humeral groove: (0) flat; (1) concave.
39. Striae 8: (0) straight, parallel to lateral series; (1) curved at anterior third, posterior 2/3 subparallel to lateral series; (2) curved at anterior third and very separate and curved at posterior third.
40. Striae 8: (0) weakly impressed; (1) forming a groove at posterior 1/3.
41. Groove on last sternite: (0) absent; (1) present.
42. Last sternite in female with setae on internal margin: (0) absent; (1) covering apical 1/2; (2) covering apical 2/3.
43. Last sternite at apical margin: (0) thin, 0.5 times as wide as posterior groove; (1) nearly as wide as posterior groove; (2) much wider than posterior groove; (3) very thin, with posterior groove weakly marked.
44. Median lobe: (0) wide, medially enlarged; (1) thin, cylindrical; (2) very wide, medially enlarged.
45. Median lobe at apex: (0) curved towards left; (1) straight; (2) curved towards right.
46. Median lobe at apex: (0) without fold; (1) with fold.
47. Median lobe at apex: (0) sharpened; (1) wide.
48. Copulatrix piece: (0) cylindrical; (1) spatulate, not curved; (2) spatulate, curved; (3) spiral-shaped; (4) absent.
49. Internal sac at apical lobe: (0) shorter than copulatrix piece; (1) longer than copulatrix piece.
50. Internal sac at apical lobe: (0) without basal constriction; (1) with basal constriction.
51. Internal sac at apical lobe: (0) widest at medial region; (1) cylindrical, medial region not enlarged.
52. Internal sac at apical lobe: (0) biggest at longitudinal axis; (1) biggest axis transverse to internal sac.
53. Internal sac at basal lobe (1): (0) absent; (1) small; (2) wide and divided; (3) wide and not divided.
54. Internal sac at basal lobe (2): (0) absent; (1) small; (2) wide.
55. Right parameres: (0) rounded at apex; (1) sharpened at apex.
56. Spermathecal bursa: (0) absent; (1) short (2 times as long as wide); (2) long (3 times as long as wide); (3) very long (more than 4 times as long as wide).
Taxa. – All the species of the tribe Cnemalobini were considered as terminal taxa. Therefore, the study includes the 28 known species of *Cnemalobus*, the four new species (*Cnemalobus diamante* sp. n., *C. nevado* sp. n., *C. troll* sp. n., and *C. somuncura* sp. n.), the genus *Zabrus* Clairville, 1806, and the species *Morion cordatus* Chaudoir. The cladograms were rooted following the Parsimony outgroup analysis method proposed by Farris (1982) and suggested by Nixon & Carpenter (1993), which consists of adding an outgroup in the matrix and analyzing it without forcing any type of relationship and then rooting between the internal group and the outgroup. The genus *Zabrus* and the genus *Morion* Latreille, 1810 were chosen as outgroups. Representative species of the genus *Zabrus* were *Zabrus blapoides* Creutz, *Z. tenebriformis* Goeze and *Z. asiaticus* Castelnau. This genus is included in the sister group of the tribe Cnemalobini (Roig-Juñent 1993b). The genus *Morion* Latreille belonging to the tribe Morionini, was proposed as a tribe related to Cnemalobini (Maddison et al. 1999).

Data Analysis. – To obtain the shortest cladograms, the data matrix was analyzed (Table 2).

### Table 2. Data matrix used in the phylogenetic analysis of *Cnemalobus*, with *Zabrus* and *Morion* as outgroup.

Characters and character states are explained in Table 1. When a species has more than one character state it is represented by the following letters: A= 0,1; B= 1,2; C= 2,3.

<table>
<thead>
<tr>
<th>Species</th>
<th>Characters:</th>
<th>States:</th>
</tr>
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<tbody>
<tr>
<td><em>Zabrus</em></td>
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<td><em>Morion cordatus</em></td>
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<td><em>C. araucanus</em></td>
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<td><em>C. bruchi</em></td>
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<td><em>C. convexus</em></td>
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<td><em>C. coquimbanus</em></td>
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<td><em>C. curtisii</em></td>
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<td><em>C. cyaneus</em></td>
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<td><em>C. cylindricus</em></td>
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<td><em>C. deplanatus</em></td>
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<td><em>C. desmareserti</em></td>
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<td><em>C. gentilii</em></td>
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<td><em>C. germaini</em></td>
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<td><em>C. hirsutus</em></td>
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<td><em>C. litoralis</em></td>
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<td><em>C. mapuche</em></td>
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<td><em>C. mendozaensis</em></td>
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<td><em>C. montanus</em></td>
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<td><em>C. nequensis</em></td>
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<td><em>C. nuria</em></td>
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<td><em>C. obscurus</em></td>
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<td><em>C. pegnai</em></td>
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<td><em>C. piceus</em></td>
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<td><em>C. pulchellus</em></td>
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<td><em>C. reichardti</em></td>
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<td><em>C. striatipenis</em></td>
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<td><em>C. striatus</em></td>
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<td><em>C. substriatus</em></td>
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<td><em>C. sulciferus</em></td>
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<td><em>C. tupungatensis</em></td>
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<td><em>C. nevado</em></td>
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<td><em>C. diamante</em></td>
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<tr>
<td><em>C. somuncura</em></td>
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<td></td>
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<tr>
<td><em>C. troll</em></td>
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using parsimony software (TNT: Tree Analysis Using New Technology, vers. 1.0 by Goloboff et al. 2003). The data set was studied using the implied weighting method (Goloboff 1993) applying $K = 3$ (constant concavity). This concavity value was chosen because it was the most conservative one for the taxonomy of this group. The analysis was performed using a heuristic search that generated 100 Wagner trees with a random addition sequence. The topology of the trees was rearranged using tree-bisection reconnection (TBR) (mult* 100), and 100 cladograms were kept in memory for each tree (Hold/100). TBR (Max*) was used again to apply a new heuristic search on the resulting shorter cladograms. It was determined that 10,000 was the maximum number of trees that could be held in the memory (Hold 10,000). The jacknifing technique was applied to measure the sustainability of the clades obtained. Five hundred replicates were carried out, starting with two trees and generating 50 trees for each replicate (mult* 50).

Optimization of bioclimatic variables. – In this analysis, climatic data from the localities where the specimens have been collected were obtained. Then, the maximum and minimum values for each bioclimatic variable were extracted using a Geographic Information Systems software. This is equivalent to obtaining the bioclimatic envelope for each species (BIOCLIM, Nix 1986). Finally, the ranges of the climatic variables (maximum and minimum) for each species were optimized on the cladogram. Nineteen bioclimatic variables (Fig. 48), plus altitude, were optimized on the morphological data cladogram. Bioclimatic variables were obtained from the WorldClim database (Hijmans et al., 2005). All variables were optimized with TNT parsimony software (Version 1.1 Goloboff et al. 2003), using the cladogram obtained with morphological data. The TNT software uses Farris optimization (Farris 1970), and treats continuous characters as such. Common synapomorphies were listed and used to detect changes in each node. Because TNT only accepts data in the range of 0-65 for continuous analysis, all bioclimatic values were transformed using the following formula:

$$\log_{10}(\text{Data} + 10)$$

After optimization, all bioclimatic variables were back-transformed to their normal values (Fig. 48) to detect the direction of the climatic change on each node.

Results and discussion

Systematics

Cnemalobus nevado sp. n.
Roig-Juñent & Carrara

Species epithet. – The name refers to the “Cordón del Nevado” in Mendoza (Argentina), where the species was found.

Diagnosis. – Two supraorbital setae are located behind the posterior edge of the eye; antennomeres 3-10 short, subquadrangular; pronotal lateral margin very narrow, with 11-16 setae; eighth elytral stria not parallel to the lateral series, very curved at apical third; metatrochanter and metafemur distinctly wide; spermathecal bursa twice as long as wide.

Description. – Habitus as in Figure 23, body shorter and thicker than other species of this genus. Length 19.2-21.1 mm. Coloration black. Glossa with two setae and with the apical margin notched; mentum without or with two setae, with a long tooth. Antennomeres subquadrangular, as long as wide, with lateroapical setae. Spherical eye, acuminate at base with the anterior margin oblique and the posterior straight. Pronotum (Fig. 23) transverse (length/width = 0.64); dorsal surface convex; posterior margin notched; epipleura wide, not narrowed in middle; anterior and middle regions of dorsum with narrow margins, slightly enlarged at base, with 11-16 setae all over the margin; posterior fovea with two setae; posterior angles rounded. Prosternum with numerous setae between middle and apex, prosternal apophysis short. Elytron three times as long as wide (length/width = 2.94), convex, with subparallel margins, striae weakly impressed; interval 3 with one or two apical setae; eighth elytral stria not parallel to the lateral series of setae, with 22-40 setae, curved and engraved at apical region (Fig. 11); interval 9 not convex and enlarged at apical third (Fig. 11); lateral series of setae with 25-37 setae. Protibia medially enlarged; tibial tooth wide and long, surpassing the apical margin of protarsomere 1, very curved outwards in males (Fig. 23); tooth in female wider and longer than in male, reaching the base of protarsomere 3, but not curved; male protarsomeres expanded externally at apex, protarsomere 1 wider than long, with one lateral apical seta, as Cnemalobus striatus (Waterhouse) (Fig. 1)
Figs 1-8. Male protarsomeres and protibiae of *Cnemalobus*. Fig. 1, lateral view of protarsomere 1 of *C. striatus* (Waterhouse) (sl= lateral seta); Fig. 2, lateral view of protarsomere 1 of *C. convexus* Germain; Fig. 3, ventral view of protarsomere 1 of *C. striatus*; Fig. 4, ventral view of protarsomere 1 of *C. pulchellus* Roig-Juñent (svl= ventrolateral setae); Fig. 5, dorsal view of protarsomeres of *C. striatus*; Fig. 6, dorsal view of protarsomeres 2 and 3 of *C. mendozensis* Roig-Juñent; Fig. 7, dorsal view of protibia of *C. mendozensis*; Fig. 8, dorsal view of protibia of *C. araucanus* Germain.
and an unordered group of ventrolateral setae as *Cnemalobus pulchellus* Roig-Juñent (Fig. 4); protarsomeres 2 and 3 two times as wide as long, with one dorsolateral seta (as *C. striatus* Fig. 5). Metafemur very wide, subequal in width from base to apex. Metatrochanter more than 1/2 as long as metafemur.

**Male genitalia** (Figs 27-28) with median lobe arched, not enlarged in middle; with apex short and narrow; right ligula wide and short, narrowed at apex; internal sac as wide and 2/3 as long as medial lobe; basal lobe (1) of internal sac wide and divided, basal lobe (2) of internal sac thin and conical (Fig. 27, lb2); apical lobe long, wide and C-shaped (Fig. 27 and 28, la), subequal in width from base to apex; copulatrix piece spatulate, not curved at apex (Fig. 27-28, pc, 42).

**Female genital tract** (Fig. 29) with long spermatheca (Fig. 29, e); bursa of the spermatheca long (more than twice as long as wide), with apical region straight (Fig. 29, bu); spermatheca with accessorial gland; common oviduct long and wide; bursa copulatrix as a long tube; stylomeres long and curved, with acute apex; two nematiform setae (Fig. 29, n).

**Comparative remarks.** – One of the most notable characters of *Cnemalobus nevado* sp. n. is the relative size of the metatrochanter, which is longer than half the length of the metafemur. Also, the metafemur is very wide. Within the genus *Cnemalobus*, few species, such as the Chilean species *C. pegnai* Nègre and *C. hirsutus* Lagos & Roig-Juñent, have wide metatrochanter and metafemur. Another remarkable character of this species is that all of the supraorbital setae are in the same fovea.

**Distribution and habitat.** – *Cnemalobus nevado* sp. n. was collected in grasslands on the western slope of the “Cordón del Nevado”, between 1995 and 2850 m altitude (Figs 31-32, 34). This mountain is an independent orogenic system, located 200 km away from the Andean Mountains. The El Nevado Mountain System extends from north to south, from 35° S to 36° S latitude, reaching its maximum altitude at the El Nevado Volcano (3833 m). The annual mean temperature is 15 °C, and mean annual precipitation is 200 mm (Páez et al. 2004). Vegetation at the base (1995 m) is composed of shrubby steppes on sandy soils with *Neo- sparton aphyllum* (Verbenaceae), alternating with dune vegetation, such as *Sporobolus rigens* (Poaceae) and saxicolous vegetation on basalts. *Adesmia pinifolia* (Fabaceae), *Anarthrophyllum rigidi- lum* (Fabaceae) becomes the dominant plant species at higher altitudes on the high volcanic plateaus (2850 m) (Roig et al. 1998).

**Type material.** – Holotype: male, Argentina, Mendoza: Intersección Ruta al Nevado y Ruta Mina Ethel, 35°36’08.45” S, 68°40’40.15” W, 1995 m, II/06, S. Roig col. (IADIZA). Paratypes: 6 males and 11 females, labeled as paratype, Argentina, Mendoza, Nevado, 1995 m, II/06, S. Roig col. (IADIZA): 4 males, 3 females: 35°37’46.56”S, 68°32’38.76”W; 2 males, 2 females: 35°36’35.40”S, 68°31’40.3”W; 4 females: 35°36’ 47.60”S, 68°31’39.60”W; 2 females: 35°37’40.50”S, 68°32’37.50”W.
Species epithet. – The name refers to the Diamante Volcano in Mendoza, Argentina. This species was found at the top of this volcano.

Diagnosis. – Three or four supraorbital setae, each one in a different fovea; antennomeres 3-10 short, subquadrangular; pronotal margin straight, with 31-35 setae on each side; eighth elytral stria not parallel to the lateral series of setae, curved at apical third; metacoxa longer than half the length of metafemur; metafemur very wide, nearly as wide as long.

Description. – Habitus as in Figure 24. Length 21.0-24.6 mm. Coloration black. Glossa with two apical setae, anterior margin concave; mentum with two setae, with tooth short and wide. Antennomeres subcuadrangular, with lateroapical setae. Eyes globular, ovate, acuminate; anterior edge rounded, posterior oblique. Pronotum transverse (length/width = 0.61); dorsal surface convex; posterior margin straight; epipleura very wide, not narrowed in middle; lateral margins narrow, slightly enlarged at apex, with 31 to 35 setae on each side along all the margin; posterior fovea with one or two setae; posterior angles rounded. Prosternum with numerous setae between middle and apex; prosternal apophysis short. Elytra convex, parallel (length/width = 2.99); epipleura smooth, without carina; interval 3 with one apical seta; eighth elytral stria not parallel to the lateral series of setae, strongly curved at apical third as in C. nevado (Fig. 11), with 35-44 setae; interval 9 flat and very wide at apical third; lateral series with 39-44 setae. Protibia very wide in middle, with external margin very curved; tibial tooth wide, reaching the base of protarsomere 3.

Female genital track (Fig. 30) with long spermatheca, curved (Fig. 30, e); bursa of spermatheca

Fig. 12. Ventral sulcus at elytral epipleura of Cnemalobus mendozensis.
Figs 13-16. Median lobe apex of, Fig. 13, *Cnemalobus convexus* Germain; Fig. 14, *C. piceus* Roig-Juñent; Fig. 15, *C. araucanus* Germain; Fig. 16, *C. curtisii* (Waterhouse). Figs 17-22. Copulatrix pieces of: Figs 17-18, *Cnemalobus convexus*; Figs 19-20, *C. piceus*; Figs 21-22, *C. curtisii*. 
long (two times as long as wide), with apical region strongly curved (Fig. 30); spermathecal gland ovate (Fig. 30, gl), stylomeres long and curved, with acute apex; one nematiform seta (Fig. 30).

**Comparative remarks.** – *Cnemalobus diamante* sp. n. has numerous characters in common with *C. nevado* sp. n., such as eighth elytral stria not parallel to the lateral series of setae and strongly curved at apical third, and metafemur and metatrochanter wider. However, this species has more setae on the pronotum and in the lateral series and more elongated elytra than *C. nevado*.

**Distribution and habitat.** – *Cnemalobus diamante* sp. n. was found in the Diamante Volcano (34°38’S and 69°05’W) in the province of Mendoza, Argentina (Fig. 34). The habitat is a high altitude grassland (2200 m), comprised mainly of *Poa ligularis* (Poaceae) and *Stipa speciosa* (Poaceae) (Roig et al. 1998). This volcano is in the middle of the Patagonia biogeographical province (Fig. 33), on shrubland steppes on sandy floors, with *Neosparton aphyllum* alternating with dune vegetation dominated by *Sporobolus rigens*. The mean annual temperature is 10 ºC, and mean annual precipitation is 300 mm (Páez et al. 2004).


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**Cnemalobus troll** sp. n.
**Roig-Juñent & Sackmann**

(Figs 25, 35-37, 42-43)

**Species epithet.** – The name refers to the creature of Scandinavian mythology, the troll, because of its large size.

**Diagnosis.** – Two or three supraorbital setae; antennomeres 3-10 long, two times as long as wide; pronotal margin very wide, with 15-30 lateral setae on each margin, two or three setae on the apical fovea; eighth elytral stria parallel to the lateral series of setae, not curved at apical third; aedeagus with copulatrix piece of internal sac spatulate, long and curved.

**Description.** – Habitus as in Figure 25. Length: 19.0-27.7 mm. Coloration black to dark brown. Two or three supraorbital setae; glossa with two lateroapical setae, anterior margin notched, anterior angles straight; mentum with two setae; tooth shorter than the epilobes. Antennomeres lengthened, more than twice as long as wide, only with lateroapical setae. Eyes protruding, rounded, anterior edge rounded posterior oblique. Pronotum (Fig. 25) transverse (length/width = 0.61); dorsal surface slightly convex; posterior margin notched; pronotal epipleura very wide, enlarged at base; lateral margin of pronotum wide, enlarged at apex, with 15-30 setae covering 2/3 of pronotal apex; posterior fovea with 2-3 setae; posterior angles rounded, surpassing posterior margin. Prosternum with few setae, most at apex of prosternal apophysis; prosternal apophysis short. Elytron long, about three times as long as wide (length/width = 2.83), with margins subparallel, without visible enlargement; seventh elytral stria with 6 to 13 setae, sometimes constituting a complete series of setae from base to apex; eighth elytral stria parallel to the lateral series, with 41-48 setae; ninth interval flat, weakly enlarged at apex, such as in other Patagonian species (Fig. 10); lateral series with 17-26 setae; elytral epipleura with ventral sulcus (such as *C. mendozensis* Roig-Juñent, Fig. 12). Male protibia slightly enlarged in middle; tibial tooth short and wide, reaching the base of protarsomere 2; protarsomeres expanded lateroapically; protarsomere 1 longer than wide, with one lateral seta (as in Fig. 1) and with an unordered group of ventrolateral setae (as in Fig. 4); male protarsomere 2 1.5 times as wide as long, with two dorsolateral setae (as Fig. 6); protarsomere 3 with one dorsolateral seta. Protibia not enlarged in middle; tibial tooth wide and long, surpassing apical margin of protarsomere 1, straight (Fig. 25).

**Male genitalia** (Figs 35-36, 43) Median lobe thin and curved, with apex narrowed and short; right ligula wide and long; internal sac as long as median lobe; basal lobe (1) of internal sac long, not divided (Fig. 35, lb1), basal lobe (2) wide, rounded, with tubercles (Fig. 35, lb2); apical lobe of internal sac wide and curved, C-shaped (Figs 35-36, la), subequal in width from base to apex; copulatrix piece spatulate and very arched at apical region (Figs 35-36, pc, 43).

**Female genital track** (Fig. 37) spermatheca long and curved (Fig. 37, e); spermathecal bursa very short (less than two times as long as wide), with apical region straight (Fig. 37, bu); spermathecal gland elongated (Fig. 37, gl), stylomeres long and straight, with acute apex; with two nematiform setae (Fig. 37, n).
Figs 23-26. Habitus of: Fig. 23, male of *Cnemalobus nevado* sp. n.; Fig. 24, female of *C. diamante* sp. n.; Fig. 25, male of *C. troll* sp. n.; Fig. 26, male of *C. somuncura* sp. n. (Scale = 5 mm).
Comparative remarks. – Cnemalobus troll sp. n. shares several characters with other Patagonian species, such as *C. neuquensis* Roig-Juñent and *C. mendozensis* Roig-Juñent. However, it differs from this group of species by having: lateral series of elytral setae at the apical 1/3; pronotum not strongly expanded at apex; coloration of legs and antennae completely black; abdominal sternum with the fovea of the setae different. The copulatrix piece is strongly curved, and the spermathecal bursa is very short.

**Distribution and habitat.** – *Cnemalobus troll sp. n.* occurs in the Argentinean provinces of Río Negro and Neuquén (Fig. 38), in the northwestern region of the Patagonian Steppe. *Cnemalobus troll sp. n.* typically occurs in steppe habitats that are dominated by both shrubs (e.g. *Mulinum spinosum*, *Coliguaya* sp.) and herbaceous plants (e.g. *Stipa* sp., *Festuca* sp., *Senecio* sp.), on sandy to gravel soils (smooth cobbles of diameter > 10 cm). Furthermore, this species may occur in both well preserved and grazed habitats. On one occasion, we found this species on the tree species *Maipén boaria* (Celastraceae) and *Schinopsis patagonicus* (Anacardiaceae) in the vicinity of Bariloche (Río Negro) (Sackmann personal observation).

**Type material.** – Holotype: male Argentina, Neuquén, Pasando Sañico, XI/04, 40º09’09”S, 70º21’59.76”W, 896 m, P. Sackmann coll. (IADIZA). Paratypes: male, Argentina, Neuquén, Corral de Piedra, Ruta 237, XI/04, 40º21’59.04”S, 70º27’27”W, 989 m, P. Sackmann coll. (IADIZA); male, Argentina, Neuquén, Bajada Collón Curá, XI/04, 40º24’50.76”S, 70º35’30.48” W, 895 m, P. Sackmann coll. (IADIZA); male, Argentina, Neuquén, Camino Catán Lil, I/05, 39º52’01.20”S, 70º41’18.96” W, 1059 m, P. Sackmann coll. (IADIZA); male and female Argentina, Neuquén, Cruce Camino L. Angostura, I/05, 41º01’57.36”S, 71º09’19.44”W, 814 m, P. Sackmann coll. (IADIZA); female Argentina, Río Negro, Cruce Ruta Aeropuerto, I/05/, 41º07’15.60”S, 71º13’12”W, 837 m, P. Sackmann coll. (IADIZA); male, Argentina, Neuquén, 19 km sitio 4, I/05, 40º05’02.04”S, 70º42’45.96”W, 710 m, P. Sackmann coll. (IADIZA); female, Argentina, Neuquén, Ea. Quemtreu, XI/04, 40º09’09.48”S, 70º46’24.45”W, 640 m, P. Sackmann coll. (IADIZA); 6 males Argentina, Río Negro, Cruce Ruta Aeropuerto, I/04, 41º07’15.60”S, 71º13’12”W, 837 m, P. Sackmann coll. (IADIZA, MLP, MACN); male, Argentina, Ruta a Comallo, Km 256, XI/04, 41º02’22.20”S, 70º29’15.72”W, 1076 m, P. Sackmann coll. (IADIZA); female, Argentina, Neuquén, 15.80 km sitio 5, XI/04, 40º05’39.48”S 70º53’27.60”W, 727 m, P. Sackmann coll. (IADIZA); five males and one female, Argentina, Neuquén, Camino a Piedra del Águila, I/05, 40º32’54.60”S, 70º44’21.12”W, 813 m, P. Sackmann coll. (IADIZA, FIML).

**Cnemalobus somuncura** sp. n.
Roig-Juñent & Agrain
(Figs 26, 39-41, 44-45)

**Specific epithet.** – The name refers to the plateau of Somuncurá (Río Negro and Chubut provinces, in Argentina) where several of the specimens were collected.

**Diagnosis.** – Two supraorbital setae; antennomeres 3-10 long, two times as long as wide; pronotal margin very wide, with 6-9 lateral setae on each side; eighth elytral stria parallel to the lateral series of setae, slightly curved at apex; aedeagus with copulatrix piece of internal sac spatulate, long and curved.

**Description.** – Habitus as in Fig. 26. Length 21.0-28.0 mm. Coloration black to dark brown. Glossa with two lateroapical setae, anterior margin notched, anterior angles straight; mentum with two setae; tooth as long as epilobes. Antennomeres lengthened more than two times as long as wide, with lateroapical setae. Eyes flattened, slightly protruding (Fig. 26); anterior margin rounded and posterior oblique. Pronotum transverse (length/width = 0.71); disc slightly convex; posterior margin weakly notched; epipleura very wide, enlarged towards back; wide margins, enlarged at apex, with 6-9 setae covering 2/3 of margin length; posterior fovea with one setae; two longitudinal posterior foveae; posterior angles rounded surpassing posterior margin. Prosternum with few setae, at margins and apex of prosternal apophysis; prosternal apophysis short. Elytron long (length/width = 3.01), three times as long as wide, with subparallel margins, without visible enlargement; flat; seventh elytral stria with 7-10 setae forming a complete series in some cases; eighth elytral stria parallel to lateral, with 34-44 setae; ninth interval flat, weakly enlarged at apex; lateral series of setae with 7-12 setae. Male protibia not enlarged in middle; tibial tooth short and wide, reaching the base of protarsomere 2; protarsomeres expanded laterally, protarsomere 1 longer than wide, with one lateral seta and one disordered group of ventrolateral setae; protarsomere 2 1.5 times as wide as long, with two dorsolateral setae; 3 with one dorsolateral seta.

**Male genitalia** (Figs 39-40, 44) with medial lobe thin and arched, with apex narrow and short; right ligula wide and long; internal sac as wide as and shorter than medial lobe; basal lobe (1) of...
Figs 27-28. Male genitalia of *Cnemalobus nevado sp. n.* Fig. 27, right lateral view of median lobe with the internal sac everted; Fig. 28, idem, left lateral view; Scale = 1 mm. La = apical lobe of internal sac; Lb2 = basal lobe 2 of internal sac; pc = copulatrix piece. Figs 29-30. Female genital track of: Fig. 29, *Cnemalobus nevado sp. n.*, ventral view; Fig. 30, *C. diamante sp. n.*, ventral view. Scale = 1 mm. e = spermatheca; bu = bursa of spermatheca; gl = accessory gland of spermatheca; n = nematiform setae.
internal sac wide, depressed, not divided, basal lobe (2) of internal sac wide, rounded (Figs 39-40); apical lobe long, wide, and C-shaped, with base as wide as medial and apical region; copulatrix piece spatulate and very curved at apical region (Fig. 44).

Female genital track (Fig. 41) with very long and curved spermatheca (Fig. 41, e); bursa of spermatheca very short (nearly more than twice longer than wide), with apical region straight and sharpened (Fig. 41, bu); stylomeres long and curved at apex, subapical organ with two nemantiform setae.

Comparative remarks. – Cnemalobus somuncura sp. n. shares numerous characters with C. troll n. sp.. However, Cnemalobus somuncura sp. n. has fewer pronotal setae and a shorter and less curved apical lobe of the internal sac than that of C. troll.

Distribution and habitat. – Cnemalobus somuncura sp. n. is distributed in the Argentinean province of Chubut (Fig. 45), in the surroundings of the Somuncurá Plateau, and on the coast of Chubut. Somuncurá is a basaltic plateau with altitudes ranging from 890 to 1664 m, located in the Patagonian biogeographic province; however, it is surrounded by halophytic elements of the Monte biogeographic province (Perotti et al. 2005). The climate is cold and dry, with temperatures ranging from -10ºC to -30ºC in winter, with constant freezing and scarce precipitation. Characteristic of the Patagonian region, the predominant winds are strong and from the west. These winds blow mainly in the summer, contributing to the desertification of the landscape. Plant species are highly adapted to water deficit, stony or sandy soils, and constant winds. Because of these characteristics, this area supports a great diversity of endemic plant species such as Grindelia coronensis Bartola & Tortosa, Grindelia pygmaea Goatherd, Senecio chipauquilensis Troiani & Steibel, Senecio ganganensis Goatherd and Senecio megaoereus Zardini (Asteraceae), Adesmia serrana Belt (Fabaceae), Sixyrinchium somuncurense Ravenna (Iridaceae) and Lecanophora ruiz-leali Krapovickas (Malvaceae) (Bartoli et al. unpublished data).

The coastal areas of Chubut Province are located in the biogeographical province of Patagonia, at San Jorge Gulf (Hueck & Seibert 1981). This area has a mean annual temperature of 10ºC, and is dominated by mosaics of Chuquiraga avellanedeae (Asteraceae) and Stipa chrysophylla (Poaceae). Towards the northeast, the coastal steppes form a
Monte-like xeromorphic ecotone, which is attributed to the poor annual precipitation (less than 200 mm), soil salinity, and the existence of Monte elements that encroach on the steppe (Andors & Vuilleumier 1996).


Key to the Cnemalobus species of Argentina

1 Penultimate segment of labial palpi with 7-10 setae; pronotal posterior fovea without setae ... ......................................................................................... C. striatus (Waterhouse)
   – Penultimate segment of labial palpi with 1-5 setae; pronotal posterior fovea with setae .......... 2

2 Eighth elytral stria strongly curved at apical third, interstriae 9 very wide apically (more than three times wider than the width of the basal third, Fig. 11); antennae short, antennomeres 4-10 more than two times as long as wide) ................................................. 3
   – Eighth elytral stria not curved at apical third (Fig. 9), or very slightly (less than two times wider than the width of the basal third Fig. 10); antennae short (antennomeres 4-10 as long as wide) or long (antennomeres 4-10 more than two times as long as wide) ................................................. 5

3 Pronotum as long as wide; metatibia enlarged in middle, much longer than wide; metatrochanter 0.5 times or less than the length of metatibia; copulatrix piece of internal sac cylindrical (as Figs 17-18) .... C. bruchi Roig-Juñent
   – Pronotum transverse, wider than long; metatibia very wide, subequal in width from apex to base, as long as wide; metatrochanter more than 0.5 times as long as metatibia; copulatrix piece of internal sac spatulate (Fig. 41) ........ 4

4 Two supraorbital setae in one fovea, after the posterior edge of eye; elytra short, two times as long as wide, with rounded apex (Fig. 23); pronotum with 11-16 lateral setae on each side .................................................. Cnemalobus nevado sp. n.
   – Three or four supraorbital setae, each seta in one fovea from the middle line to the posterior edge of eye; elytra 2.7 times as long as wide, with acuminate apex (Fig. 24); pronotum with 31-35 lateral setae on each side .................................................. Cnemalobus diamante sp. n.

5 Eighth elytral stria subparallel to lateral series of setae, proximal, apical third slightly curved, therefore interval 9 subequal in width from base to apex (Fig. 9); antennomeres as long as wide or at most 1.5 times as long as .... 6
   – Eighth elytral stria subparallel and close to lateral series at the basal portion of the basal third, separated on the apical region of the basal third (Fig. 10), and continues subparallel again to the apex; interval 9 two times wider at apex than the width of the base (Fig. 10); antennomeres 4-10 more than 2 times as long as wide) ........................................................................ 8

6 Pronotum with setae covering at most anterior 2/3 of lateral border; elytra base without disordered group of setae ..... C. deplanatus Roig-Juñent
   – Pronotum with setae along the entire lateral border length; elytra base with one disordered group of setae ........................................................................ 7

7 Pronotal lateral margin narrow; antennomeres slightly longer than wide ..... C. australis Germain
   – Pronotal lateral margin very wide; antennomeres almost as long as wide C. mapache Roig-Juñent

8 Protarsomeres 2 and 3 of male with one dorso-lateral seta; pronotal lateral margin narrow anteriorly; meso and metatibial setae short and thick ................................................................. 9
   – Protarsomeres 2 and 3 of male with 2-3 dorso-lateral setae; pronotal lateral margin wide all along its length; meso and metatibial setae long and thin ................................................................. 10

9 Elytra usually with setae on intervals 1, 2 and 3; prosternum with few setae, mainly at apophysis C. desmarestii (Germain-Ménéville)
   – Elytra glabrous at intervals 1, 2 and 3; prosternum with numerous setae from the middle of apophysis .............................................. C. tupungatensis Roig-Juñent

10 One supraorbital seta; pronotal lateral margin not expanded ......................................... 11
   – Two or three supraorbital setae; pronotal lateral margin very wide and expanded.......................... 12
Figs 35-37. *Cnemalobus troll* sp. n. Fig. 35, left lateral view of median lobe with internal sac everted; Fig. 36, idem, right lateral view; Fig. 37, female genital tract, ventral view. Scale = 1 mm. e = spermatheca; bu = bursa of spermatheca; gl = accessory gland of spermatheca; n = nematiform setae; La= apical lobe of internal sac; Lb1= basal lobe 1 of internal sac; Lb2= basal lobe 2 of internal sac; pc = copulatrix piece.
11 Pronotal lateral margin narrow at base; elytral humerus rounded; apical lobe of internal sac long, longer than copulatrix piece, curved and sharpened towards apex. *C. litoralis* Roig-Juñent.

- Pronotal lateral margin wide at base; elytral humerus flat; apical lobe of internal sac as long as copulatrix piece, wide and slightly narrowed. *C. curtisi* (Waterhouse)

12 Legs reddish in color; body color with some metallic reflections; elytral lateral series of setae since humeral margin; two supraorbital setae on posterior edge of eye; abdominal sterna with setae in weakly impressed foveae ....... 13

- Legs black in color; body color without metallic reflections; elytral lateral series of setae on apical 2/3; one supraorbital seta on anterior edge of eye and another on posterior edge; setae of abdominal sternae in coarsely impressed foveae. .................. 14

13 Pronotal posterior angles surpassing posterior margin of pronotum .... *C. mendozensis* Roig-Juñent

- Pronotal posterior angles not surpassing posterior margin of pronotum ...... *C. gentilii* Roig-Juñent

14 Eyes not protruded (Fig. 26); six to nine setae on each pronotal lateral margin ........................................... 15

- Eyes protruded (Fig. 25), with 13-30 setae on each pronotal lateral margin ........................................... 15

15 15-30 setae on each pronotal margin; elytral humerus with disordered group of setae; posterior angles rounded, surpassing posterior margin ........................................... 15

- 13-21 setae on each pronotal margin; elytral humerus with setae not in a disordered group, only on lateral series; posterior angles not surpassing posterior margin ........................................... 14

Phylogenetic Relationships

The cladistic analysis using equal weights of the character state data produced 24 cladograms of 182 steps, a consistency index of 0.48, and a retention index of 0.79 (Fig. 15). The strict consensus obtained from these cladograms (Fig. 46) is congruent with those obtained in previous studies (Roig-Juñent & Flores 1995; Roig-Juñent 2002). However, they differ in that: i) *C. bruchi* is the sister species of all the species of the genus, and ii) the basal group of species of the Norte Chico region of Chile (i.e. Coquimbo desert) is not supported in this analysis. Although only the basal node has a jacknifing value of 100, other nodes have values higher than 90. Two of the four new species described *C. somuncura* and *C. troll*, belong to the steppe species group. The other two new species, *C. nevado* and *C. diamante*, are sister species, and constitute a well supported group. Nevertheless, the relationship of *C. nevado* and *C. diamante* with the species of the apical clades is not resolved.

The implicit weighting analysis produced only 1 cladogram, (fit = 392.4). The main difference between the analysis with implicit weighting and using equal weights is that in the cladogram of the former technique *C. reichardti* and *C. cylindricus* constitute the basal group of the genus. The other groups obtained in the analysis applying equal weights are recovered and the two new species, *C. diamante* and *C. nevado*, constitute the basal group of a clade of mainly Chilean species, that inhabit highlands from central Chile.

Biogeographic Considerations

Main historical effects that may have affected the distribution of Chemalobus species. — *Chemalobus* is a very old genus linked to Australian groups (Reichardt, 1979). These genera originated in Gondwana, probably in the Cretaceous or earlier (Roig-Juñent et al., in press). Species within this genus have a low dispersion capacity because of their large size and lack of wings. Because *Chemalobus* is distributed on both sides of the Andean Mountains, Roig-Juñent and Flores (1995) postulated that the genus may have origin-
Figs 39-41. *Cnemalobus somuncura* sp. n., Fig. 39, right lateral view of median lobe with internal sac everted; Fig. 40, idem, left lateral view; Fig. 41, female genital track, ventral view. Scale = 1 mm. Figs 42-44. Copulatrix piece of: Fig. 42, *Cnemalobus nevado* sp. n.; Fig. 43, *C. troll* sp. n.; Fig. 44, *C. somuncura* sp. n.
nated before the rising of this mountain range. It is possible that the ancestor of *Cnemalobus* spp. inhabited the warm and extensive lowland plains that existed before the rising of the Andean Mountains during the Miocene ("Age of the Southern Plains", Ortiz-Jaureguizar & Cladera 2006). Donato (2006) explains that the plains were formed by different advances and retractions of the "Paranean Sea", and paleontological evidence indicates that the entire area had very consistent climatic conditions and vegetation.

During the Andean Mountains uplift, the distribution of the biota may have been affected in two ways: (a) by geographically separating the monophyletic groups, and (b) by changes in the environmental conditions that led to the division of groups. For the first hypothesis, it has been suggested that geographical division of these groups resulted from the uplift of the Andean Mountains (Roig-Juñent & Flores, 1995; Flores & Roig-Juñent 2001). With respect to the second hypothesis, as a result of the successive uplifts of the Andean Mountains (14 to 10 m.y.), a physical barrier was formed that hampered the flow of wet winds from the Pacific as they moved inland (Riccardi & Rolleri 1980). This change caused a marked decrease in environmental temperature and an increase in environmental seasonality on the eastern side of the Andean Mountains, and generated a strong division of environments between the western and eastern sides (Pascual et al. 1996). By nine million years ago, progressive desertification had led to the formation of xeric environments in the eastern part of South America (e.g. Patagonian Steppes, Monte Desert; Pascual et al. 1996). The first biogeographic hypothesis is consistent with our findings regarding the distribution patterns and phylogenetic relationships of the new species of *Cnemalobus*. However, our finding of the Patagonian species that inhabit mountain habitats, and are closely related to Chilean species, suggests that the separation of species may be a product of environmental changes rather than of geographical isolation resulting from the uplift of the Andean Mountains.

We found that apical and basal clades (montane and steppe clades) inhabit environments with different characteristics. The montane clade (Fig. 47), includes *C. nevado*, *C. diamante*, and all Chilean species that inhabit not only Andean Mountain areas from 2000 to 2850 m (Roig-Juñent 2002) but also other extra-Andean Systems located to the east (Argentina) and to the west (Chile) of this formation. In Argentina, there are two extra-Andean Systems (i.e. Sierra del Nevada massif and Precordillera, both located in Mendoza Province) and one volcano (i.e. Cerro Diamante located in Mendoza Province). The Argentinean extra-Andean Systems were formed by the same orogeny uplift of the Andean Mountains. In Chile, the extra-Andean and Andean Systems include Coastal Cordillera, Central Cordillera, and mountain regions of southern Chile.

The steppe clade (Fig. 47) consists of species that inhabit the lowlands east of the Andean Mountains. All of these species are distributed in steppe areas (except one species distributed in the Chacoan lowlands) and occur from sea level (Atlantic coast) to 1800 m altitude (Payunia Plateau). We hypothesize that, if all species of the steppe clade inhabit these lowlands, it is likely that the ancestor species occurred there as well (the same could be postulated for the montane clade). Mountain habitats are more humid environments than those of the lowland steppe because precipitation and air density generate higher atmospheric humidity (Roig-Juñent and collaborators, personal observations). Apparently, the common ancestor had the plasticity to inhabit areas with different environmental conditions, both humid and dry.

Results from the analysis to determine the change in environmental conditions of the habitat of the common ancestor of the montane and steppe clades indicate that on the phylogeny of the montane clade species the ancestral environmental
Fig. 46. Strict consensus tree of the 24 cladograms obtained using equal weight and showing the relationships of the species of *Cnemalobus*. Numbers represent characters and character states. Black circles are synapomorphic states and white homoplastic ones.
Fig. 47. Cladogram obtained using implied weights and showing the relationships of the species of *Cnemalobus*. Numbers represent characters and character states. Black circles are synapomorphic states and white are homoplastic states.
conditions were conserved. Node 38 on Fig. 48, corresponding to the hypothetical ancestor of the montane/steppe clade, shows that precipitation seasonality decreases, mainly due to an increase on the precipitation of the driest months. Node 47, belonging to the montane species group, shows...
that the direction of climatic conditions was maintained with an increasing humidity pattern. This situation was contrasted with the steppe species clade, where the optimization on node 37 shows a decrease in temperature. Therefore, we suggest that the montane clade (Fig. 47) continued occupying the humid montane habitats and it is likely that the steppe species had adapted to the new xeric conditions. Consequently, it seems that the uplift of the Andean Mountains may have not acted as a vicariant event isolating the Chilean and Argentinean groups of species, but creating new environmental conditions.

Regional patterns of steppe and montane species of the genus Cnemalobus. – The genus Cnemalobus is very rich in species at the Patagonian Steppe. The diversity of this area is comparable to the Chilean central region, which is considered one of the world’s hotspots of biodiversity (Myers et al. 2000). However, we do not regard the uplift of the Andean Mountains and the intensification of xeric conditions to the east as the only cause of the current diversity in the montane and steppe clades. Roig-Juñent (2002) suggests that the high richness of Cnemalobus species in the central region of Chile is probably a result of the retraction and expansion of the different environments during the Miocene, as well as of fragmentation of the habitat because of the large number of mountain systems in this region. Posadas and Morrone (2001) postulate that, for the entomofauna of this Chilean region, dispersal events were more important (60%) than vicariance events (this finding is consistent with the successive advances and retractions of the southern biota, e.g. Nothofagus forests (Fagaceae) see, Villagrán & Armesto 1980). It is probable that a similar situation in northwestern Patagonia promoted the radiation of steppe species. Environmental changes or isolation of areas, such as extra-andean mountain systems, could have resulted in speciation processes by fragmenting the species geographical distributions. Perhaps this explains why the Patagonian northwestern region has seven of the 10 steppe species. The current distribution of C. nevado and C. diamante is restricted to isolated mountains. Because these species are wingless and of large body size, dispersal from one mountain to another is highly unlikely (200 km away from each other). It is more likely that the ancestral species of C. nevado and C. diamante was broadly distributed, and, as a result of changes in the habitat conditions, the species became restricted to the high altitude areas of each mountain. The origin of this group of species most likely coincides with the uplift of the Andean Mountains, given that the El Nevado Mountain also originated during this time. If this type of habitat fragmentation also occurred in northern Patagonia, there should also be a higher richness of this mountain group in the Payunia area (where these species inhabit), because of the large number of volcanoes in this area (ca. 800, many of them between 2000 m and 4000 m). These groups of volcanoes formed isolated areas, like islands within the continent, where it is likely that Cnemalobus species are diversifying, regardless of its low dispersal ability.

Patterns of species distribution of Cnemalobus: Sympatry and allopatry. – All species of Cnemalobus that inhabit mountain systems have an allopatric distribution pattern. In contrast, some species that inhabit the Patagonian steppe have a sympatric distribution pattern. All sister species have allopatric distribution patterns (see Table 3). Five

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species of the Patagonian Steppe that are not sister species have a strict sympatric distribution pattern (i.e., two species are found in the same place) (Fig. 38 and Table 3). These five species inhabit the northwestern region, one of the richest areas of endemism of the Patagonian Steppe, (Domínguez et al. 2006).

Four species from the locality of Bariloche, in the Argentinean province of Rio Negro, (C. troll, C. neuquensis, C. araucanus, C. deplanatus and C. gentili) appear to have a sympatric distribution pattern. However, closer inspection revealed that this may not be the case. A two year ecological study in the study region, carried out by researchers of the Ecotono Laboratory (CRUB, UNC) (Sackmann et al. 2006; Sackmann & Farji-Brener in press), showed that, although two species of Cnemalobus were collected in the same place, the habitat types (e.g. scrub and steppe) or collection periods (e.g. different months) were different for the two species, C. araucanus and C. deplanatus may have a sympatric distribution pattern, because individuals of each species were collected in the same place, sometimes during the same month, and sometimes during different months. It is also possible that the earlier records did not take into account the environmental characteristics of the site where each specimen was collected, and labeled the locations, generically, as “Bariloche” because of its vicinity to the sample site. For example, C. araucanus occurs in grasslands near Nothofagus forests, whereas C. neuquensis and C. deplanatus occur in steppe areas. One explanation for this pattern is that the area of Bariloche is environmentally heterogeneous (Sackmann et al. 2006). First, there is a marked longitudinal temperature and precipitation gradient (i.e. within 80 km, precipitation changes from 500 mm to 3000 mm), not only at a landscape scale but also at smaller scales of hundreds of meters (Prémoli et al. 2005). Second, the area was affected by diverse historical events, in particular by the Pleistocene glaciations, which modified the selection pressures and the distribution ranges, and produced diverse local extinctions (Donoso et al. 2004). In addition, genetic studies have confirmed the existence of glacial refuges for different woody species that were distributed west and east of the Andean Mountains (Donoso et al. 2004).

Ongoing studies by our lab in the Payunia region show that the three species inhabiting the region do not have a sympatric distribution pattern. Cnemalobus mendozae has a wide distribution, (Fig. 34) with C. nevado and C. diamante occurring inside this distribution area. However, these last two species are restricted to mountain systems (Figs 31-33) whereas C. mendozae occupies the lowlands surrounding these mountains (lowland in Fig. 33).

Our results indicate that the current distribution of the representatives of the genus Cnemalobus is mainly a result of environmental variability. Our conjecture that dispersal processes were more important than vicariant events is supported by the current distribution of the species and their speciation processes. The retraction and subsequent expansion of habitats may have been the main cause for the high speciation rate found in highly variable environments (i.e. Bariloche surroundings and mountain systems). Furthermore, sympatric species are rare, which supports the hypothesis that species initially had an allopatric distribution and later the distribution ranges overlapped as a result of changes in the environment. The radiation observed in the montane and steppe clades (as opposed to the radiation in the basal clades) suggests that environmental changes were one of the main factors in the speciation of the genus. Sympathy could be the result of secondary dispersal, which may occur when a change in climatic conditions produces an expansion or retraction on the distribution range of species (i.e. available area increase and results in a larger distribution range without needing to cross any physical barrier). Additional collecting efforts and ecological studies in Patagonia could provide new information about this group of carabid beetles as well as other insects to reveal the processes that led to the high species richness of northern Patagonia. In this area, mountains are like islands, with their own unique fauna, and isolated from each other by lowland habitats.

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