

Androlaelaps rotundus FONSECA (ACARI: LAELAPIDAE)
ASSOCIATED WITH AKODONTINE RODENTS IN
PARAGUAY: A MORPHOMETRIC EXAMINATION OF A
PLEIOXENOUS ECTOPARASITE

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ABSTRACT

A multivariate analysis of morphometric data suggests that the nominally pleioxenous ectoparasite, *Androlaelaps rotundus*, includes at least three distinct host-associated populations in Paraguay. Where multiple akodontine hosts occur sympatrically, each host species is accompanied by a morphologically distinct mite population. These host-mite associations were consistent across all localities, implying that *A. rotundus* is a complex of unrecognized species.

Key words: ectoparasites, laelapidae, *Androlaelaps*, *Eubrachylaelaps*, akodontini, *Akodon*, *Bolomys*, Paraguay.

RESUMO

***Androlaelaps rotundus* Fonseca (Acari: Laelapidae) associada com roedores akodontinos no
Paraguay: um exame morfométrico do ectoparasito pleoxeno**

Uma análise multivariada de dados morfométricos sugere que o ectoparasito pleixeno *Androlaelaps rotundus*, composto por distintas populações hospedeiro-associadas, no Paraguai. Quando múltiplos hospedeiros akodontinos ocorrem simpatricamente, cada espécie de mamífero é acompanhada por uma população morfologicamente distinta de ácaro. Estas associações hospedeiro-ácaro repetiram-se nos estudos realizados em diferentes localidades, mostrando que *A. rotundus* é um complexo de espécies críticas indistinguíveis.

Palavras-chave: ectoparasitos, laelapidae, *Androlaelaps*, *Eubrachylaelaps*, akodontini, *Akodon*, *Bolomys*, Paraguai.

INTRODUCTION

The laelapid mite subgenus *Eubrachylaelaps* Ewing occurs throughout the New World, associated with peromyscine rodents in North America and with akodontine rodents in South America. The subgenus is morphologically diverse in North America, with seven species recognized presently. In South America only one nominal species, *Androlaelaps (Eubrachylaelaps) rotundus* Fonseca, is known. This widely distributed mite has been

reported in all ectoparasite surveys where akodontine rodents are present (Botelho & Williams, 1980; Castro *et al.*, 1987; Fonseca, 1958; Furman, 1972; Lareschi, 1996; Linardi *et al.*, 1987; Linardi *et al.*, 1991; Mares *et al.*, 1989; Mauri, 1964; Mauri & Capri, 1970; Whitaker & Dietz, 1987; Whitaker & Abrell, 1987), and displays a pleioxenous association with a number of different, but phylogenetically related, akodontine hosts.

In Paraguay, akodontine rodents compose a prominent component of the small mammal fauna.

Many localities have more than one akodontine species, and populations of *A. rotundus* may occur on different host species at the same locality. We used a comparative approach to examine the hypothesis that populations of *A. rotundus* infesting different host species in the same region are morphologically distinct. The study has three objectives: (1) evaluate the utility of a simple set of characters in describing morphological variation in *A. rotundus*, (2) examine the mite populations infesting different akodontine hosts within and among localities, and (3) evaluate the monotypy of *A. rotundus*.

TAXONOMIC HISTORY AND HOST ASSOCIATIONS

Androlaelaps (Eubrachylaelaps) rotundus is associated strongly with South American rodents of the tribe Akodontini. Although many studies have emphasized the broad host range of these mites, including numerous records from non-akodontines, prevalences and intensities of infestation support the primacy of a biological relationship with akodontine rodents. Problems inherent in the design of surveys, sampling biases, and the instability of both mammal and arthropod systematics, often make it difficult to gain a clear understanding of naturally occurring associations. For example, in Venezuela, Furman (1972) reported *A. rotundus* from seven species of sigmodontine rodents, two murine rodents, a caviomorph rodent, a marsupial, several species of bats, and a bird. However, of a total of 772 mites, 719 (93%) were recorded from 70 individuals of the akodontine, *Akodon urichi* J. A. Allen & Chapman, 1897. The importance of the association between *Androlaelaps rotundus* and *Akodonurichi* is revealed clearly by a prevalence of 60 percent, and mean intensity of 10.27 mites per infested host individual.

Androlaelaps rotundus was first described from an "unidentified wild mouse" in the State of São Paulo, Brazil (Fonseca, 1935). Although the type host was not known, a series of topotypes (specimens from the same locality) of *A. rotundus* were collected from the akodontine *Bolomys lasiurus* (Lund, 1841) (Furman, 1955; Jameson, 1951). Later, when Fonseca (1958) examined a collection of mites from small mammals surveyed by the National Plague Service in northeastern Brazil, he reported *A. rotundus* from a long list of host

species, but most of the mites were taken from two akodontines, identified as *Zygodontomys pixuna* and *Akodon arviculoides*. Fonseca (1957) concluded that *A. rotundus* is a highly variable mite species, capable of infesting multiple host species. However, because *Z. pixuna* and *A. arviculoides* are now synonyms of *Bolomys lasiurus* (Wilson & Reeder, 1993), Fonseca's taxonomic decision to refer these specimens to a single species appears to have been justified biologically. Nevertheless, this conclusion may have influenced other taxonomists when they encountered mites on other akodontines.

The diversity of the primary host group, the Akodontini, increases in both temperate and Andean habitats, and *A. rotundus* has been reported from a large number of different akodontine hosts in the southern cone countries of Chile, Bolivia, Argentina, Uruguay, and Paraguay. In a small collection of ectoparasites from Paraguay, Whitaker and Abrell (1987) reported *A. rotundus* from *Akodon nigrita* (Lichtenstein, 1929) and *Akodon varius* Thomas, 1902. In Argentina, Mauri & Capri (1970) noted the specificity of association between *A. rotundus* and hosts of the genus *Akodon*, including *Akodon azarae* (J. Fischer, 1829), *A. kempi* (Thomas, 1917), *A. obscurus* Waterhouse, 1837 (= *Bolomys obscurus*), *A. varius*, and *Akodon boliviensis tucumanensis* (= *A. spegazzinii* Thomas). Lareschi (1996) reported a strong association between *A. rotundus* and *Akodon azarae* in the province of Buenos Aires, Argentina. In Brazil, *A. rotundus* was reported from *Akodon cursor* (Winge, 1887), from the Federal District (Mares *et al.*, 1989) and the State of Santa Catarina (Linardi *et al.*, 1991). In addition, *Bolomys lasiurus* is a common akodontine in many parts of central Brazil, and *A. rotundus* has been reported from this host in the Brazilian State of Minas Gerais (Botelho & Williams, 1980; Linardi *et al.*, 1987; Whitaker & Dietz, 1987), and the Federal District, near Brasília (Mares *et al.*, 1989).

MATERIAL AND METHODS

In an ongoing survey of small mammals in Paraguay, rodents and small marsupials are captured in live traps, and etherized and brushed for ectoparasites before they are prepared as standard museum specimens. Ectoparasite sampling techniques are described in Gettinger (1992). All

mite specimens used in this study were mounted individually in Hoyer's medium, ringed in glyptal, and measured with a stage-calibrated ocular micrometer.

The adult female mite was used in all morphometric analyses, because it is the most abundant life stage in populations sampled from the host mammal, and it is the stage upon which formal mite species descriptions are based. Thirty-eight continuous characters were chosen, representing different parts of the laelapid body: dorsal shield (two), dorsal chaetotaxy (eight), gnathosoma (four), sternal shield (six), epigynial shield area (five), anal shield (five), peritreme (one), and legs (seven). See Appendix 1 for a list and descriptions of characters. Some characters were chosen because they have been used in the taxonomic literature as discriminators between taxa, and others were added as descriptors of shape. Mite specimens were selected randomly for measurement, but were included only if all 38 characters could be seen clearly and measured. General morphological terminology follows Krantz (1978).

The NT-SYS multivariate statistical package (Rohlf, 1993) was used to perform all numerical systematic analyses and to display results. Each of the 38 characters was standardized to a mean of 0.0 and a standard error of 1.0, to equalize the effect of character size on the relationships among individuals. The first three eigenvectors were extracted from the pair-wise character correlation matrix. The original matrix of standardized measurements was then projected onto these three eigenvectors, and a three dimensional model was constructed based on these projections. This model enables visualization of inter-individual relationships in the three-dimensional space that best represents the complete (38-dimensional) character space. In addition, a minimum spanning tree among the 82 individuals was calculated from inter-individual distances based on the standardized characters, and this tree was mapped onto the three-dimensional model. This enhances visualization of relative inter-individual distances and enables detection of distortions in the relationships as depicted in the 3-D model.

Because the initial principal component analysis indicated the presence of well-delineated subsets of individuals within the data, additional

analyses were conducted on these subsets separately, to detect patterns of host-related or geographic variation within these groups of mites. These analyses followed the same protocol described previously.

The 82 specimens of *Androlaelaps rotundus* that were used in this study were collected from four species of akodontine at 17 localities in nine Paraguayan departments (Fig. 1). In the following listing of host specimens, the number preceded by "TK" is the field catalog number. One female mite was selected randomly from each host individual. Host voucher specimens will be deposited in the Museo Nacional de Historia Natural del Paraguay, and the Museum of Texas Tech University.

Locality numbers, names and descriptions are those that are being used uniformly in publications pertaining to the "Mammals of Paraguay and their Ectoparasites" project (Fig. 1). Each TK number is a unique field catalog number that is associated with a single primary specimen and with all materials collected from that specimen. **(1) Estancia La Victoria** (23° 39.03'S, 58° 34.79'W), Depto. Presidente Hayes: TK60032, TK60033, TK60055, *Akodon azarae*; TK60072, *A. toba*, TK60108, TK60109, TK60110, TK60128, TK60175, TK60176, TK60198, TK60202, *Bolomys lasiurus*. **(2) Estancia El 43** (21° 56.20'S, 60° 14.56'W) and **Cañada Elisa** (22° 02.11'S, 60° 19.92'W), Depto. Boquerón: TK60207, TK60212, TK60213, TK60222, *A. toba*; TK60278, *B. lasiurus*. **(3) Cerro León** (20° 26.25'S, 60° 19.19'W), Depto. Alto Paraguay: TK60437, *B. lasiurus*. **(5) Lago Ypoá** (26° 01.35'S, 57° 28.73'W), Depto. Paraguari: TK60581, TK60582, TK60595, *A. azarae*; TK60579, *B. lasiurus*. **(8) Isla Yacyretá** (27° 24.49'S, 56° 45.79'W), Depto. Misiones: TK60828, *B. lasiurus*. **(9) Parque San Rafael** (26° 45.32'S, 55° 51.83'W), Depto. Itapúa: TK60892, TK60929, TK60948, *A. cursor*; TK60894, TK60902, TK60958, *B. lasiurus*. **(12) Cerro Corá** (22° 37.20'S, 56° 02.62'W), Depto. Amambay: TK61305, *A. cursor*. **(14) Estancia Yacaré** (26° 39.49'S, 58° 04.07'W), Depto. Ñeembucú: TK61705, TK61706, TK61726, TK61764, *A. azarae*; TK61729, TK61732, *A. cursor*. **(15) Reserva Natural del Bosque Mbaracayú** (24° 08.75'S, 55° 19.14'W), Depto. Canindeyú: TK61791, TK61794, TK61816, *A. cursor*; TK61813, TK61849, TK61855, TK61924, *B. lasiurus*. **(16) Estancia Loma Porá** (23° 33.15'S, 57° 34.30'W), Depto. Presidente Hayes; TK61936, TK61937, TK62051, TK62074,

TK62100, *A. azarae*; TK62087, TK62088, TK62205, TK62207, *A. toba*; TK61983, TK61984, TK61985, TK62036, TK62125, TK62126, TK62127, TK62129, TK62130, *B. lasiurus*. **(17) Laguna Placenta** (21° 08.62'S, 59° 24.86'W) and **Estancia Tres Marias** (21° 18.09'S, 59° 33.73'W), Depto. Alto Paraguay: TK62223, *A. toba*; TK62224, TK62228, TK62431, TK62433, *B. lasiurus*. **(18) Estancia Samaklay** (23° 28.81'S, 59° 48.43'W), Depto. Presidente Hayes:

TK62654, TK62655, TK62662, TK62712, *A. toba*; TK62525, TK62578, TK62673, TK62684, TK62685, *B. lasiurus*. **(20) Dest. Gabino Mendoza** (20° 03.30'S, 61° 47.22'W), Depto. Alto Paraguay and **Parque Cué** (20° 07.65'S, 61° 45.40'W), Depto. Boquerón: TK63277, TK63297, TK63300, TK63309, TK63319, *A. toba*. **(21) Reserva Itabó** (24° 27.68'S, 54° 38.33'W), Depto. Canindeyú: TK63515, TK63549, *B. lasiurus*.

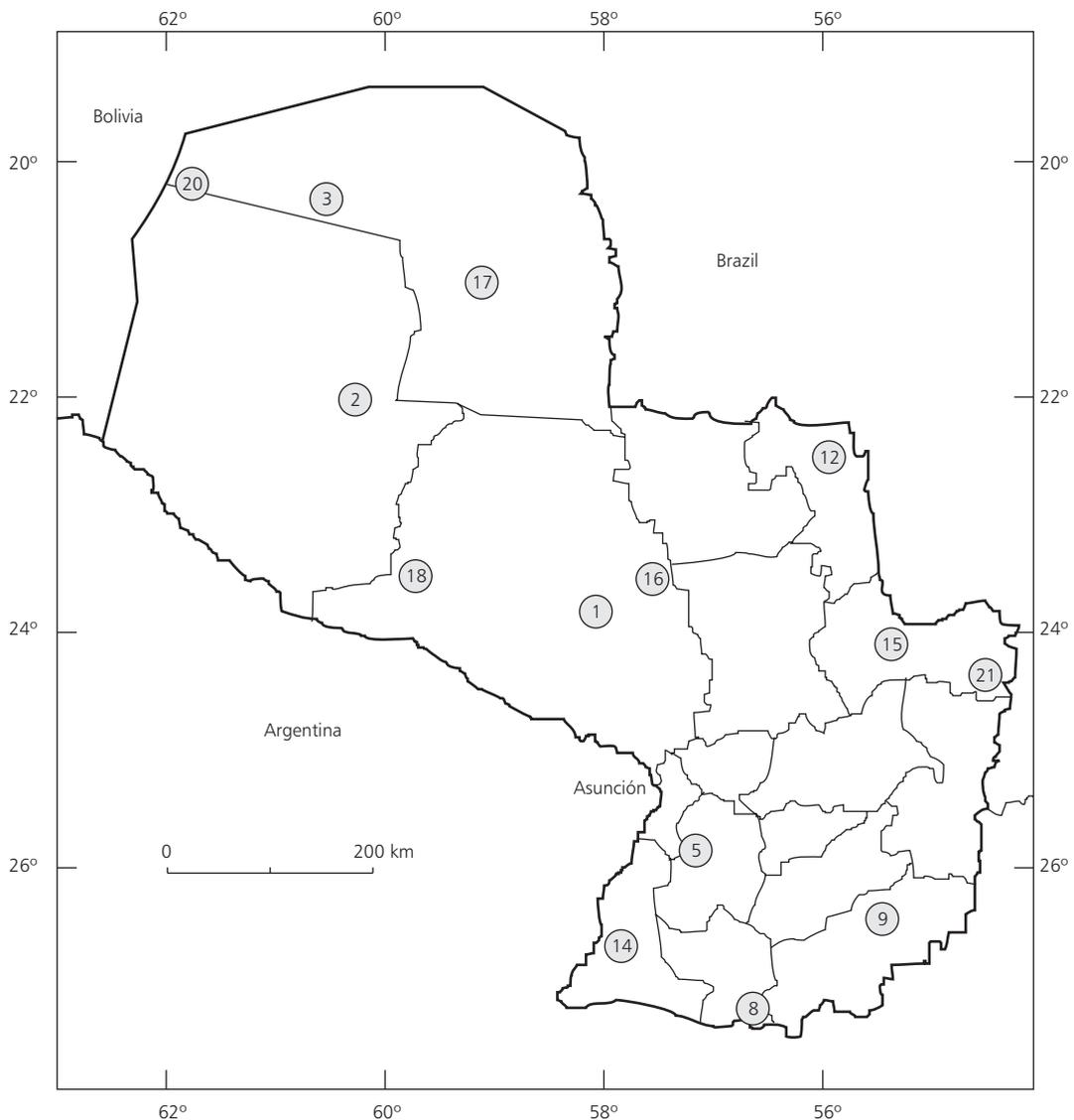


Fig. 1 — Map of Paraguay indicating localities from which mites were examined. See text for locality descriptions and lists of mites and akodontine hosts examined from each locality.

RESULTS

A projection of the individual mites onto the first three principal components (Fig. 2), resulted in three distinct morphological groupings: (1) mites collected from *Akodon cursor* (“c” in the Fig. 2); (2) mites collected from *Bolomys lasiurus* (“B”); and (3) mites collected from *Akodon azarae* (“a”) and from *A. toba* (“t”). The first three components account for 66.4, 13.0, and 3.6 percent of the observed variance, respectively (Table 1). An evaluation of the minimum-spanning tree indicates that there is no noteworthy distortion of the relationships among mite individuals (i.e., specimens which are placed close together in the model also are closely connected by the tree).

33 of 38 standardized characters load highly on PC1 (all positively), indicating that this component is primarily an expression of size (Table 1). The mites from *Akodon cursor* are smallest, those from *A. azarae* and *A. toba* the largest, and those from *Bolomys lasiurus* are of intermediate size (Fig. 2). Four characters load heavily on PC2; S3S3, S5S5, and GWGS correlate positively, and LPARA negatively. This component serves to discriminate between mites from *B. lasiurus* and those from *A. cursor*, with the mites from *A. azarae* and *A. toba* intermediate on this component. Although mites from *A. azarae* and mites from *A. toba* are separated by factors pertaining to PC3, no characters load heavily on this component, and the component is not significant by the broken-stick model (Rohlf, 1993).

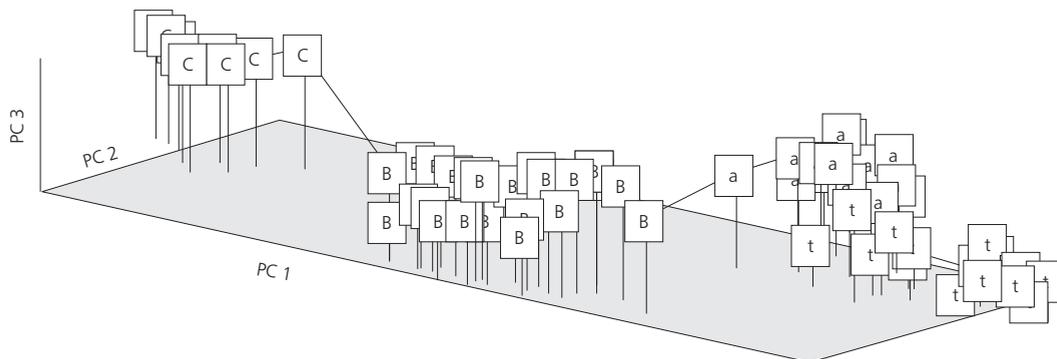


Fig. 2 — Three-dimensional diagram, with minimum-spanning tree, resulting from principal component analysis of all mite specimens. Mites labeled according to host species, as follows: a, *A. azarae*; c, *Akodon cursor*; t, *A. toba*; B, *Bolomys lasiurus*.

An analysis including only mites from *Akodon azarae* and *A. toba* suggests that these two groups of mites are distinct morphologically (Fig. 3). Although some overlap exists between these two groups along PC1, the minimum-spanning tree includes only one connection between them, reinforcing the distinctness of the groups. Although the first three principal components are all significant by the two groups, and it is only this component on which characters load heavily. 17 of the 38 characters (44.7 percent) load heavily on PC1, all positively, indicating that a subset of about half of the characters examined contributes to a size component that distinguishes the mites associated with these two host species.

To compare host species variation with geographic variation, mites collected from *Bolomys lasiurus* were assigned to three groups based on collection locality: C, Chaco localities (western region); R, localities along the Paraguay River; and E, localities in the eastern region of Paraguay. Based on these groupings, principal component analysis indicates no discernible pattern of geographic variation among these mite populations (Fig. 4). Although the first three components are significant by the broken-stick model, only five characters load heavily on any component (four on PC1, one on PC2). Evidently, no characters exhibit discernable geographic patterning in mites from this host species.

TABLE 1

Loadings of characters on components 1, 2, and 3, and scaled eigenvalues (percentage of matrix variance explained) for those components, from principal component analysis of: (1) all mite specimens, (2) mites from *Akodon azarae* and *A. toba*, and (3) mites from *Bolomys lasiurus*. Underlining indicates high (i.e., 0.7 or greater) loading of a character on a component. *, indicated that the component is "significant", i.e., explains a larger percentage of the matrix variance than would be expected randomly, by the broken-stick model (Rohlf, 1993). Characters and their acronyms are listed in Appendix 1.

Character	All Mite Specimens			<i>A. azarae</i> and <i>A. toba</i>			<i>Bolomys lasiurus</i>		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
LDS	<u>0.957</u>	0.229	0.037	<u>0.891</u>	0.166	0.072	<u>0.783</u>	0.020	0.127
WDS	<u>0.921</u>	0.326	-0.012	<u>0.817</u>	0.168	0.138	<u>0.801</u>	0.085	0.138
AJ5AJ5	<u>0.884</u>	0.131	-0.032	0.585	0.276	-0.208	0.459	-0.339	0.039
AZ5AZ5	<u>0.875</u>	-0.291	-0.063	<u>0.728</u>	0.188	0.050	0.542	-0.050	0.280
LAJ5	<u>0.738</u>	-0.045	0.566	-0.588	-0.360	-0.120	0.082	0.287	0.244
LAZ5	<u>0.722</u>	-0.084	0.580	-0.600	0.507	-0.106	-0.016	0.195	0.373
BJ5BJ5	<u>0.836</u>	0.367	-0.196	<u>0.747</u>	0.066	-0.086	0.380	-0.176	0.399
BZ5BZ5	<u>0.867</u>	0.317	-0.040	0.582	0.134	-0.177	0.386	-0.265	0.455
LBJ5	<u>0.696</u>	-0.201	0.402	-0.260	0.139	0.679	0.167	0.422	-0.365
LBZ5	<u>0.870</u>	0.267	0.009	0.587	0.242	0.204	0.106	<u>0.752</u>	0.011
CAPCAP	<u>0.908</u>	0.234	-0.085	<u>0.784</u>	0.063	-0.066	0.016	-0.324	0.649
LCAP	0.870	<u>-0.165</u>	0.013	0.539	0.106	0.082	0.431	0.088	-0.388
LINN	<u>0.717</u>	-0.644	0.107	0.349	0.109	-0.183	0.357	0.252	-0.049
CAPINN	<u>0.960</u>	0.107	-0.009	<u>0.771</u>	-0.017	-0.137	0.414	-0.286	0.343
LSS	<u>0.846</u>	-0.032	-0.207	<u>0.736</u>	0.151	-0.265	0.212	-0.545	0.493
WSS	0.844	0.271	0.059	0.441	0.551	0.408	0.667	-0.037	-0.067
S1S1	0.915	0.053	0.076	0.369	0.568	0.177	0.552	0.164	0.005
S3S3	0.442	<u>0.774</u>	0.049	0.218	0.632	0.178	<u>0.779</u>	-0.167	-0.129
LS1	<u>0.745</u>	-0.561	-0.151	<u>0.732</u>	-0.515	0.009	-0.245	0.492	-0.044
LS3	<u>0.861</u>	-0.283	-0.089	<u>0.707</u>	-0.369	0.181	0.258	0.649	0.301
LGS	<u>0.810</u>	-0.040	0.123	0.239	0.641	-0.362	0.629	-0.168	-0.076
S5S5	0.303	<u>0.875</u>	-0.011	0.426	0.433	0.566	<u>0.784</u>	-0.174	-0.387
GWGS	0.127	<u>0.764</u>	-0.047	0.337	0.454	0.461	0.675	-0.106	-0.233
LS4	0.813	-0.162	-0.375	<u>0.885</u>	-0.239	0.034	-0.189	0.540	0.506
LS5	<u>0.886</u>	-0.346	-0.216	<u>0.920</u>	-0.190	-0.009	0.050	0.379	0.587
LPER	<u>0.963</u>	-0.034	-0.020	<u>0.706</u>	0.249	-0.131	0.295	-0.427	0.004
LPARA	0.587	<u>-0.724</u>	-0.101	<u>0.732</u>	-0.185	-0.346	0.335	0.265	0.165
LPOST	<u>0.809</u>	-0.214	-0.269	<u>0.782</u>	-0.128	-0.069	0.268	0.057	0.119
EDGE	<u>0.757</u>	0.578	-0.055	<u>0.785</u>	-0.235	-0.054	0.502	0.010	0.044
PARPAR	<u>0.724</u>	-0.155	-0.074	0.386	0.182	0.115	0.606	-0.076	-0.129
GWAS	0.570	-0.239	-0.027	0.336	0.336	-0.207	0.642	-0.295	0.040
PROX1	<u>0.935</u>	-0.018	-0.160	<u>0.846</u>	-0.253	-0.012	0.670	0.400	0.047
DIST1	<u>0.943</u>	0.091	0.070	0.524	0.020	-0.386	0.462	0.364	-0.336
POST2	<u>0.960</u>	0.001	-0.025	<u>0.717</u>	-0.229	0.060	0.400	0.148	-0.298

TABLE 1 (continuação)

Character	All Mite Specimens			<i>A. azarae</i> and <i>A. toba</i>			<i>Bolomys lasiurus</i>		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
POST3	0.851	0.174	-0.069	0.490	-0.325	0.252	0.337	0.477	0.308
POST4	0.850	-0.417	0.150	0.279	0.558	-0.054	0.227	0.436	0.140
FEM1	0.916	0.178	0.064	0.350	-0.501	0.523	0.469	0.175	-0.039
GEN1	0.921	-0.083	0.161	-0.065	-0.313	0.467	0.142	0.268	-0.258
% VARIANCE	66.4*	13.0*	3.6	37.5*	11.1*	6.9*	21.4*	10.7*	8.2*

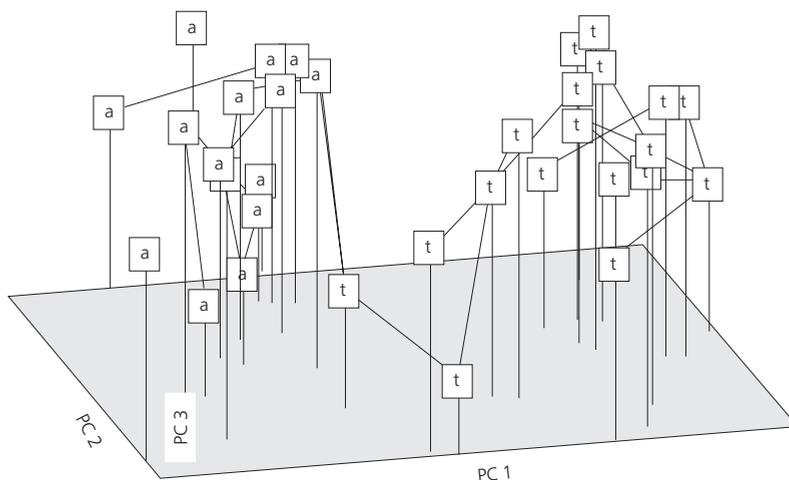


Fig. 3 — Three-dimensional diagram, with minimum-spanning tree, resulting from principal component analysis of mites collected from *Akodon azarae* and *A. toba*. Specimen labels as in Fig. 1.

DISCUSSION

The ectoparasite, *Androlaelaps rotundus*, comprises at least three, and quite possibly four, morphologically distinct species in Paraguay. The initial principal component analysis of the entire data-set produced three non-overlapping groups of mites. Subsequent ordinations of mite from *Akodon azarae* and *A. toba* confirmed the presence of distinctive mite populations on each host species. Observed patterns are consistent with host species variation, and imply that mite groups have differentiated through evolutionary time on their respective hosts.

An ectoparasitic arthropod species that preferentially infests a number of different, but phylogenetically related hosts must have adapta-

tions for dispersing both within and among host species. Although the etymology of the name Laelapidae implies swiftness, the locomotor abilities of these mites are inadequate for the task of actively dispersing. If these acarines are dependent on the host for dispersal (phoresy), transmission between hosts would tend to be vertical, between conspecifics, with little opportunity for transfer to other host species. This is especially true for closely related host species, which in vertebrates tend to be ecologically divergent (especially in sympatry).

The mites associated with *Akodon azarae* and *A. toba* are distinguished easily from those associated with *A. cursor* and with *Bolomys lasiurus*. Besides being much larger, with dorsal shield length greater than 700 micrometers, they also have a distinctive anal shield (longer than wide).

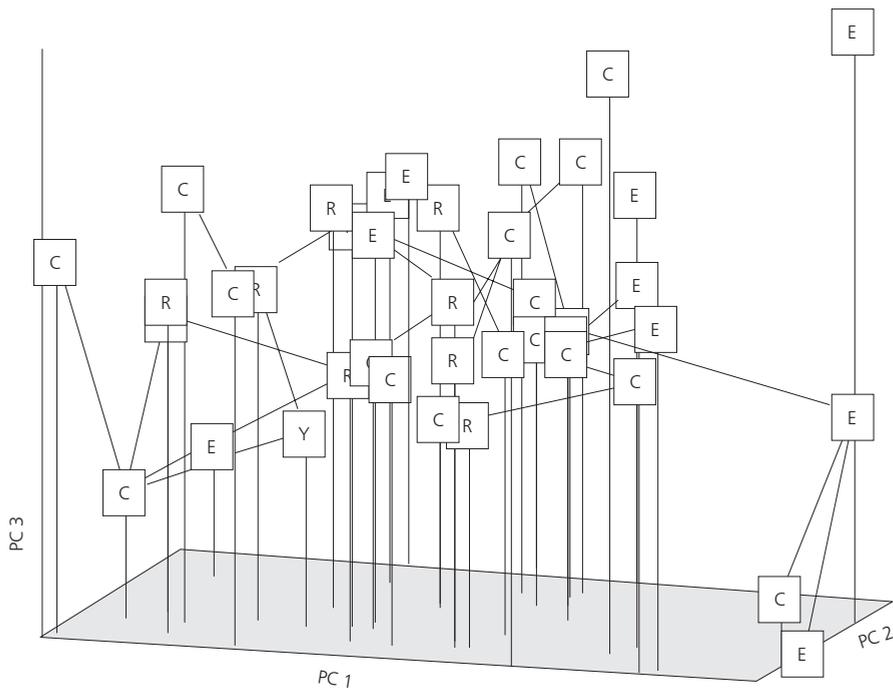


Fig. 4 — Three-dimensional diagram, with minimum-spanning tree, resulting from principal component analysis of mites collected from *Bolomys lasiurus*. Mites labeled according to geographic origin, as follows: E, eastern region; R, Rio Paraguay; C, Chaco (western region).

These mites are clearly distinctive from the types described by Fonseca (1935), but species boundaries between mites associated with *A. azarae* and *A. toba* are still unclear.

Preliminary analysis has revealed considerable morphological variation between mite populations infesting *A. azarae* and *A. toba*. Mites from *A. azarae* are somewhat smaller, with longer dorsal setae and shorter ventral setae, than mites from *A. toba* (Table 2). Specimens of *A. azarae* were collected in central Paraguay on both sides of the Paraguay River, whereas specimens of *A. toba* were collected only west of the Paraguay River, and the two species occurred in sympatry (together with *B. lasiurus*) at two localities (1 and 16) in the Department of Presidente Hayes.

The mites from *A. cursor* are much smaller than the original species described by Fonseca (1935). This host was collected only from localities east of the Paraguay River, but was encountered sympatrically with *A. azarae* at locality 14, and with *Bolomys lasiurus* at localities 9 and 15. In each case, the mites from each host species are easily

distinguishable from those of the other host. Principal component analysis showed clear distinctions among some host-defined groups for *Androlaelaps rotundus* in Paraguay. Many of the characters are important in describing the morphological variation among samples collected from different host species. At least three, and probably four morphological groups of mites have been distinguished by these 38 characters.

Each group is associated consistently with a specific akodontine host. Furthermore, the mites from *Bolomys lasiurus* (which has a broad geographic and ecological distribution and occurs in sympatry with all three *Akodon* species in Paraguay) do not exhibit any pattern of morphological variation associated with geographic factors or sympatry status. To the extent that our samples permit, we observe the same morphological uniformity within host-defined groups, for mites from the three *Akodon* species. For these reasons, we suspect that in Paraguay *Androlaelaps rotundus* comprises three or more biological species, at least two of which remain undescribed.

APPENDIX 1

Characters and their acronyms used in this study. All characters are direct linear measurements, taken from mounted specimens as described in the text. Dorsal shield length (DSL); dorsal shield width at midlevel (DSW); distance between j5 setae (j5–j5); distance between z5 setae (z5–z5); length of j5 (j5L); length of z5 (z5L); distance between J5 setae (J5–J5); distance between Z5 setae (Z5–Z5); length of J5 (J5L); length of Z5 (Z5L); distance between subcapitular setae (CAP–CAP); length of subcapitular setae (CAPL); length of inner hypostomal setae (INN1); distance between subcapitular and inner hypostomal setae (CAP–INN); length of sternal shield (SSL); width of sternal shield at level at second sternal setae (SSW); distance between first sternal setae (S1–S1); distance between third sternal setae (S3–S3); length of anterior sternal setae (S1L); length of posterior sternal setae (S3L); length of epigynial shield (ESL); distance between epigynial setae (E5–E5); greatest width of epigynial shield (ESW); length of poststernal setae (S4L); length of epigynial setae (E5L); length of peritreme (PERI); length of paranal setae (PARAL); length of postanal seta (POSTL); distance from postanal seta to anterior midline of anal shield (POST–EDGE); distance between paranal setae (PARA–PARA); greatest width of anal shield (ASW); length of proximal seta, coxa I, (PROXCOX); length of distal seta, coxa I (DISTCOX); length of posterior seta, coxa II (POSTCOX2); length of posterior seta, coxa III (POSTCOX3); length of posterior seta, coxa IV (POSTCOX4); length of anterior dorsal seta, femur I (DFEM1L); length of posterior dorsal seta, genu I (DGEN1L).

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