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Multivariate discrimination among cryptic mites of the genus *Androlaelaps* (Acari: Mesostigmata: Laelapidae) parasitic of sympatric akodontine rodents (Cricetidae: Sigmodontinae) in northeastern Argentina: possible evidence of host switch followed by speciation, with the description of two new species

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Abstract Laelapids are among the most common ectoparasites of rodents. Currently, it is under discussion whether there is a single polixenous species that parasites a variety of hosts, or whether there are cryptic species highly host specific. Herein, multivariate morphometric analyses of cryptic sympatric laelapids of the genus *Androlaelaps* allowed us to identify different species. These species are specific of their akodontine hosts, *Akodon montensis* and *Thaptomys nigrita*, in localities situated in northeastern Argentina. In addition, we analyzed similar laelapids associated with the akodontines *Deltamys kempi* and *Akodon cursor*. Using principle component analyses we differentiated four laelapid species, each one host specific, independent of sympatry of the hosts, and without geographical variation. From these four species, we described two new species (*Androlaelaps navonae* n. sp. and *Androlaelaps wingei* n. sp.). We determined the four species based on a range of variations in several characters, mainly size. These four laelapid species belong to the *Androlaelaps rotundus* species group, specific to akodontines. These species are very similar among them but differ from the remainder species of the group by their small size, distance between *j6* setae similar to the distance between the *z5* setae, strong ventral setae, opisthogaster with 13 pairs of strong setae (one close to the distal margin of epigynal shield), and anal shield wider than long. Further studies will elucidate whether they constitute a new laelapid genus. Phylogenetic and ecological factors influencing host-specificity are discussed, and we propose that host colonization could have taken place by host switching of a single laelapid species among rodent species, followed by speciation.

Keywords Mesostigmatic ectoparasites · Mites · Cryptic species · Rodent hosts · Host switch · Speciation

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Introduction

The Mesostigmata constitute a morphologically and ecologically diverse group of mites, many of which are parasitic on small mammals (Dowling 2006). Among the mesostigmatics, Laelapidae is one of the most commonly found families associated with rodents. Laelapidae is also the most speciose group and comprises a gradual transition from predatory to parasitic mites. For most laelapids associated with mammals it is unknown whether they are nidicolous, facultative, or obligate parasites; probably parasitism has arisen multiple times (Dowling 2006). At present, factors structuring host association of laelapids and rodent hosts in the Neotropics are poorly known, and it is under discussion whether a single polixenous species parasitizes a variety of hosts, or whether there are different host-specific cryptic species (Dowling 2006). Laelapid mites have been considered host-generalist parasites for years, as a single species was found parasitizing a high number of host species (Strandtmann and Wharton 1958; Furman 1972; Lareschi and Mauri 1998) but other studies considered laelapids host-specific (Gettinger 1992; Lareschi 2011). Intraspecific morphological variation was recorded for laelapids (Furman 1972). By using morphometric multivariate analyses, variation was recorded for a single nominal species in relation to host-mammal species, indicating that laelapid mites are primarily monoxenous (Gettinger and Owen 2000; Gettinger et al. 2011). In addition, different morphotypes of *Gigantolaelaps* Nesbitt were mentioned not only associated to host species, but also to vary geographically (Martins-Hatano et al. 2012).

Concerning laelapids parasitic on akodontine rodents (Cricetidae, Sigmodontinae), morphometric characters were proposed to identify morphotypes of *Androlaelaps rotundus* Fonseca related with distinct host species (Gettinger and Owen 2000; Lareschi and Barros-Battesti 2010). Thereafter, those specimens preliminarily included in a single complex species, were described as new species host-specific of akodontine rodents from the *Akodon* division (Cricetidae, Sigmodontinae; sensu D'Elía 2003) (Lareschi and Gettinger 2009; Lareschi 2010, 2011; Lareschi and Velazco 2013). *Androlaelaps rotundus* species group was proposed to include the nominal species, as well as *Androlaelaps maurii* Lareschi and Gettinger and *Androlaelaps misionalis* Lareschi (Lareschi 2011). However, there are probably still cryptic species in the group which are necessary to study. In classic morphological analysis, cryptic speciation may lead to an underestimation of the number of species. In addition, in parasitic organisms convergent evolution obliterates morphological differentiation among species (Price 1980).

Multivariate analyses based on morphometric characters have been largely used to identify cryptic species among taxonomic groups (Borsa 2002; Klimov et al. 2004; Cazorla 2009; Gettinger et al. 2011). In this study we validate whether multivariate analyses are useful to discriminate cryptic laelapid mites of the genus *Androlaelaps* Berlese parasitic on the akodontines *Akodon montensis* Thomas and *Thaptomys nigrita* (Lichtenstein), sympatric in northeastern Argentina, i.e. in the Interior Atlantic Forest (IAF), along the southeastern region of Brazil, eastern Paraguay and far north-east of Argentina (Di Bitetti et al. 2003), locally known as Selva Paranaense or Selva Misionera (Cabrera 1976). The IAF, worldwide identified as an area of high species diversity and endemism, has been dramatically modified and reduced to about 7.5 % of its original area of 1,200,000 km^2, due to human activity from the sixteenth century to the present (Di Bitetti et al. 2003; Galindo-Leal and Gusmão Câmara 2003).

We specifically tested whether there is a strong host-related variance in a single mite species, *An. misionalis*, or whether there are cryptic species. Because the geographical ranges of *Ak. montensis* and *T. nigrita* broadly overlap, we also analyzed possible

geographical effects. In addition, we analyzed similar mites associated with the akodontines *Deltamys kempi* Thomas and *Akodon cursor* (Winge). By comparing host and parasite phylogeny, we discussed whether phylogenetic and ecological factors are influencing host-specificity. In addition, we hypothesized probable routes of host colonization.

Materials and methods

Survey localities

The study was carried out in the following localities situated in Misiones Province, Argentina: (1) Reserva Privada de Usos Múltiples Valle del Cuña Pirú, Departamento Cainguás (27°05′17″S, 54°57′09″W, 179 m), samples in May 2005; and (2) Parque Provincial Urugua-í (25°51′10.29″S, 54°10′41.53″W, 287 m) samples in May and August 2013.

Sampling and sample preparation

The study was carried out on mites collected from four rodent species identified as *Ak. montensis*, *T. nigrita*, *Ak. cursor* and *D. kempi* (Cricetidae, Sigmodontinae, Akodontini). Mite samples from *Ak. montensis* and *T. nigrita* were obtained from captured animals (in locality 2), or provided by colleagues (locality 1). Additional mites from these two hosts were obtained from additional sites, from other field sessions, or provided by colleagues. Mites from *Ak. cursor* and *D. kempi* were provided by colleagues. Mites were cleared in lactophenol, mounted in Hoyer's medium, and studied by light microscopy equipped with a drawing tube. Some mites were also photographed. Measures were taken by using a stage-calibrated ocular micrometer. Taxonomic characters are presented in micrometers (μm). Evans and Till (1979) were followed for setal nomenclature, and Musser and Carleton (2005) for host taxonomy. At the moment, some rodents still maintain a field number of collection, which is a temporary code still they are deposited in a Biological Collection (e.g. LTU); some mites also hold a field number, which consist of the same field number as the hosts; for each individual mite of a single host it was added a number, separated by a hyphen (e.g. LTU594-1). Voucher specimens of mites are housed at the collection of División de Entomología, Museo de La Plata (MLP), La Plata, Argentina, and Anexos de la Colección de Mamíferos del Centro Nacional Patagónico (CNP), Puerto Madryn, Chubut, Argentina. Specimens of *T. nigrita*, as well as those of *Ak. montensis* captured in Argentinean localities are housed at the Colección de Mamíferos del Centro Nacional Patagónico (CNP). Individuals of *D. kempi* are housed at the Laboratorio de Ecología de Roedores (LER), Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina. Rodents from Brazil are housed at Museu de Zoologia, Universidade Federal de Viçosa, Minas Gerais, Brazil (MZUFV), whereas those from Paraguay are at the Natural Science Research Laboratory of the Museum of Texas Tech University (TTU), Lubbock, TX, USA.

Morphometric and statistical analyses

Multivariate morphometric analyses were conducted on 40 features of the dorsum, venter, gnatosoma and legs of the mites. Characters are listed in Appendix 1; the main ones are

shown in Fig. 1. When comparing mites of the four rodent species, only 39 characters were considered since measurement of the length of *j6* setae (*Lj6*) was not available for *D. kempi*, and this character is not significantly different among mites associated with distinct host species (Table 2). The analysis was carried out on mites identified preliminary as *An. misionalis* and *An. misionalis*-like species from the hosts and localities mentioned above. For each mite included in the analysis, acronyms, host species and locality are provided in Appendix 2.

The analyses were carried out using the software STATISTICA and PAST (Hammer et al. 2001). Variables were *ln*-transformed in order to standardize data. Because some variables did not show homoscedasticity in their variances, we prefer to use Kruskal–Wallis test and post hoc probabilities with Bonferroni adjustment for testing differences in the medians between groups of mites. Using only the significant variables, Principal Components Analysis (PCA) was carried out on the covariance matrix, including all specimens. Then, we analyzed the two groups of mites more similar (collected from *Ak. montensis* and *T. nigrita*, respectively), by using the same methodology.

Results

Akodon montensis and *T. nigrita* were found sympatrically in both localities, and parasitized with female mites. All these mites were identified belonging to the *An. rotundus* species group. Multivariate morphometric analyses carried out on the most diagnostic characters (see Appendix 1 and Fig. 1) allowed separation of four groups of mites, each associated with a different host species.

Multivariate analyses

From a matrix of 1950 original data, a total of 42 (2.1 %) missing values were found. Out of all the variables considered, 27 (69.2 %) had no missing values, whereas those that had omissions were between 2.5 and 12.8 % of the specimens (1–5). Missing data were replaced by intra-group means.

Higher coefficients of variation (CV) correspond to mites collected from *Ak. montensis*, especially in the variables *>Wes*, *LscIV* and *Lgn*. The other variables had similar values of CV between groups, or displayed an inconsistent pattern (Table 1). Concerning differences between groups, K–W test was significant for 36 of the 39 variables studied (Table 2).

The first three Principal Components meet 60.6 % of the variance. The first PC, related to size, distinguishes mites identified as *An. maurii* (from *D. kempi* rodents), a smaller species (*<LDS*; *<WDS*), from the other mites (Fig. 2a). The loadings of this first component are almost all positive, confirming its correlation with size, except in three variables (*Lst4*, *Lst5* and *Lpaa*) which are negative, indicating that these variables are proportionately lower in *An. maurii* (Table 3). The second PC separates mites collected from *Ak. cursor* from the other mites (Fig. 2b). The largest positive loadings of this component correspond to *Lad1*, *LSS* and *LpscII*, all variables proportionately higher in mites from *Ak. cursor*. Other variables with high and positive loadings are: *Lz5*, *gn-h3*, *Lst4*, *LpscIII* and *Lad3*, whereas *Lpaa* and *Lpoa* have high loadings and are negative (Table 3). The third PC separates mites from *Ak. montensis* from those collected from *T. nigrita* (Fig. 2b). Highest positive loads in this component correspond to *Lst1*, *>Wes* and *Lpaa*; high negative loadings correspond to *Lj5* and *Lz5*. Mites from *Ak. montensis* present proportionally lower values in *Lst1*, *>Wes* and *Lpaa*, and higher ones in *Lj5* and *Lz5*.

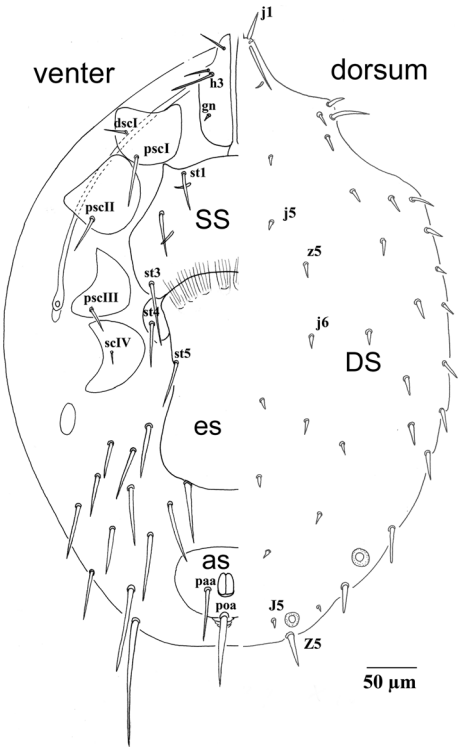

Fig. 1 *Androlaelaps misionalis*, illustrating the main characters used in morphometric analysis: dorsal shield (*DS*), gnathosomal seta (gn), hypostomal seta (h3), sternal shield (SS), first sternal seta (st1), third sternal seta (st3), epigynal shield (es), epigynal seta (st5), metasternal seta (st4), paranal setae (paa), postanal seta (poa), anal shield (as), proximal seta of coxa I (pscI), distal seta of coxa I (dscI), posterior seta of coxa II (pscII), posterior seta of coxa III (pscIII), seta of coxa IV (scIV)

Mites associated with *Ak. montensis* vs. *T. nigrita* differed significantly in medians of 12 variables (Table 4). Three of these measures are concurrent with the results of the first PCA: *Lst1*, *Lpaa* and *Lad3*; these measures are higher in mites from *T. nigrita*. A new PCA between both groups of mites and including the 12 variables confirm these findings, placing individuals of both species along the first axis (Fig. 3). The highest positive charges (loads), that separate mites of *T. nigrita* towards the positive part of the first PC1, are *Lst1*, *Lpaa* and *Lad3*. We found no patterns of geographic variation between the mites obtained from different localities of *Ak. montensis*.

The PCA indicates that mites from *Ak. montensis* and *T. nigrita*, collected in sympatry and during the same sampling, sort differentially in multivariate space, maintaining their morphometrical identity (Fig. 4). These results support that mites of *T. nigrita* grouped together regardless of the geographic origin and differ from those parasitic on *Ak. montensis.*

Systematics

Androlaelaps rotundus *species group*

Mites of this species complex are characterized by the presence of dorsal shield with 37 pairs of setae simple (*j*/*J* and *z*/*Z* series complete), central setae very short (12–19 µm), setae *j5* about 1/3–1/4 as long as distance from base of *j5* to *z5*, and an enlarged *ad1* seta in femur I, with length subequal to width of femur at level of seta. This complex includes seven species:

Table 1 Coefficient of variation (CV) of the variables measured from *Androlaelaps* mites collected from the different host species

Variables	Hosts			
	Akodon montensis	*Thaptomys nigrita*	*Deltamys kempi*	*Akodon cursor*
LDS	0.35004	0.211314	0.216160	0.270851
WDS	0.67809	0.383082	1.416260	0.710070
j5–j5	0.93154	1.328608	1.202166	1.074175
z5–z5	0.63243	0.706526	0.941113	0.423632
Lj5	4.63005	4.589032	3.477037	3.739918
Lz5	2.95263	2.488445	3.739918	3.321085
J5–J5	1.11405	0.691215	0.768672	0.819865
Z5–Z5	1.18532	0.672016	0.757305	0.512709
LJ5	3.88694	3.991448	2.484260	3.963372
LZ5	1.27294	0.834507	0.835831	0.681123
gn-gn	3.03524	1.052858	0.619686	0.887472
Lgn	6.93801	6.224957	4.490455	3.088506
Lh3	4.09766	3.476412	2.123429	1.729538
Lgn-Lh3	1.77267	1.714084	1.292880	1.428899
LSS	1.34201	0.660168	0.951293	0.612192
WSS	1.01871	0.886189	1.042835	0.391675
st1–st1	1.04212	0.547063	0.618163	0.923914
st3–st3	0.57991	0.188326	0.343172	0.483724
Lst1	1.35542	1.218383	1.703893	1.350121
Lst3	1.15812	0.859546	1.524176	1.030081
Les	1.00949	0.472020	0.519940	0.514731
st5–st5	0.74204	0.610861	0.753515	0.879567
>Wes	11.14050	0.941465	0.247020	0.616287
Lst4	1.57886	1.846069	0.323853	0.981500
Lst5	2.87862	1.784664	1.591075	1.783446
Lpaa	1.74346	1.499418	1.455901	1.263799
Lpoa	1.29612	0.789093	0.664437	0.945736
Pst-edge	0.83891	0.889920	0.427448	0.881071
Paa-paa	0.72225	0.812987	1.946002	1.080485
>Was	1.37729	0.651519	0.658660	0.682111
LpscI	0.87500	1.068456	0.853972	0.507768
LdscI	3.06341	2.939092	2.877299	2.575369
LpscII	2.49975	1.801098	1.336043	1.583000
LpscIII	2.67540	2.829482	2.013517	1.222542
LscIV	7.15214	4.062614	6.020545	2.999701
Lad1	2.11488	1.780366	0.229556	0.810530
Lad3	2.04885	3.092639	1.472511	1.145236
j6–j6	0.91600	0.483010	0.389565	0.605563
Lid	0.47442	0.404458	0.968074	0.570055

Table 2 Mean ± SD; in parentheses the sample sizes of *Androlaelaps* mites sampled from different host species

Variables	Hosts			
	Akodon montensis	*Akodon cursor*	*Thaptomys nigrita*	*Deltamys kempi*
LDS***	534.42 ± 11.81a (19)	566.0 ± 9.66b (10)	525.64 ± 6.98c (11)	484.2 ± 6.48d (10)
WDS***	436.42 ± 18.20 (19)	472.8 ± 20.62 (10)	426.00 ± 9.85 (11)	403.6 ± 35.19 (10)
j5–j5***	58.58 ± 2.22a (19)	57.3 ± 2.50a (10)	56.82 ± 3.06a (11)	52.8 ± 2.53b (10)
z5–z5***	121.63 ± 3.71a (19)	121.6 ± 2.50a (10)	123.27 ± 4.15a (11)	111.3 ± 4.97b (10)
Lj5 ns	16.58 ± 2.19 (19)	15.5 ± 1.58 (10)	15.45 ± 1.86 (11)	14.9 ± 1.45 (10)
Lz5***	17.50 ± 1.42 (18)	15.7 ± 1.42 (10)	16.91 ± 1.14 (11)	15.5 ± 1.58 (10)
J5–J5***	83.47 ± 4.10 (19)	87.9 ± 3.25 (10)	84.36 ± 2.62 (11)	65.9 ± 2.13 (10)
Z5–Z5***	122.74 ± 7.03 (19)	129.4 ± 3.20 (10)	122.45 ± 3.88 (11)	105.0 ± 3.77 (10)
LJ5 ns	10.84 ± 1.01 (19)	10.8 ± 1.03 (10)	10.91 ± 1.04 (11)	10.2 ± 0.63 (10)
LZ5***	86.00 ± 4.84 (19)	93.2 ± 3.03 (9)	92.89 ± 3.86 (9)	79.6 ± 2.88 (10)
gn–gn***	51.16 ± 5.61a (19)	51.50 ± 1.78a (10)	51.27 ± 2.10a (11)	44.20 ± 1.03b (10)
Lgn**	12.84 ± 2.29a (17)	13.2 ± 1.03a (10)	11.20 ± 1.69b (10)	12.8 ± 1.4a (10)
Lh3*	25.67 ± 4.48 (15)	24.3 ± 1.34 (10)	24.70 ± 2.87 (10)	27.3 ± 1.89 (10)
gn-h3***	36.20 ± 2.60 (15)	39.9 ± 2.08 (10)	33.55 ± 2.02 (11)	32.7 ± 1.49 (10)
LSS***	109.42 ± 6.93a (19)	122.4 ± 3.66b (10)	109.36 ± 3.35a (11)	105.9 ± 4.72a (10)
WSS***	168.00 ± 9.17a (19)	163.9 ± 3.28a (10)	161.64 ± 7.09a (11)	145.1 ± 7.14b (10)
St1–st1***	84.05 ± 3.89a (19)	82.9 ± 3.35a (10)	84.27 ± 2.00a (11)	71.1 ± 1.91b (10)
St3–st3***	164.05 ± 4.84b (19)	161.3 ± 3.95b (10)	167.27 ± 1.62a (11)	145.2 ± 2.86c (10)
Lst1***	43.26 ± 2.21a (19)	45.1 ± 2.33a (10)	47.36 ± 2.20b (11)	44.7 ± 2.95a (10)
Lst3***	63.11 ± 3.05b (19)	66.7 ± 2.87a (10)	62.82 ± 2.23b (11)	60.0 ± 3.71c (10)
Les***	120.95 ± 5.93a (19)	122.9 ± 3.07a (10)	121.82 ± 2.75a (11)	105.3 ± 2.54b (10)
St5–st5***	99.58 ± 3.40a (19)	102.8 ± 4.13a (10)	102.00 ± 2.90a (11)	84.7 ± 2.83b (10)
>Wes***	123.63 ± 27.04 (19)	134.7 ± 4.11 (10)	136.73 ± 6.34 (11)	118.2 ± 1.40 (10)
Lst4***	59.89 ± 3.91a (19)	60.8 ± 2.49a (10)	54.64 ± 4.03b (11)	62.4 ± 0.84a (10)
Lst5***	44.68 ± 5.53a (19)	42.0 ± 2.79a (10)	41.10 ± 2.92a (10)	55.8 ± 3.50b (10)
Lpaa***	39.84 ± 2.59a (19)	38.4 ± 1.78a (10)	43.00 ± 2.45b (11)	40.9 ± 2.18a (10)
Lpoa***	69.39 ± 3.96a (18)	65.0 ± 2.58b (10)	70.11 ± 2.62a (9)	58.5 ± 1.58c (10)
pst-edge***	65.42 ± 2.27a (19)	65.5 ± 2.41a (10)	66.55 ± 2.46a (11)	60.6 ± 1.13b (9)
paa–paa ns	34.63 ± 0.90 (19)	35.1 ± 1.37 (10)	34.73 ± 1.01 (11)	33.8 ± 2.25 (10)
>Was***	96.53 ± 6.54a (19)	97.3 ± 3.06a (10)	92.55 ± 2.73b (11)	85.1 ± 2.51c (10)
LpscI***	48.37 ± 1.64a (19)	48.6 ± 0.97a (10)	48.82 ± 2.04a (11)	43.8 ± 1.40b (10)
LdscI***	21.22 ± 1.99a (18)	21.8 ± 1.79a (9)	22.55 ± 1.97a (11)	18.6 ± 1.58b (10)
LpscII***	36.37 ± 3.11a (19)	40.5 ± 2.37b (10)	36.45 ± 2.25a (11)	35.8 ± 1.69a (10)
LpscIII**	27.53 ± 2.39 (19)	30.4 ± 1.26 (10)	28.36 ± 2.58 (11)	28.5 ± 1.90 (10)
LscIV***	14.33 ± 2.66 (18)	12.9 ± 1.05 (9)	14.70 ± 1.70 (10)	11.8 ± 1.75 (10)
Lad1***	46.80 ± 4.23a (15)	56.0 ± 1.83b (10)	47.63 ± 3.70a (8)	47.8 ± 0.42a (10)
Lad3***	29.67 ± 2.26a (15)	37.5 ± 1.58c (10)	34.13 ± 4.42b (8)	31.4 ± 1.58a (10)
j6–j6***	127.06 ± 6.06a (17)	128.7 ± 3.80a (10)	129.91 ± 3.05a (11)	105.8 ± 1.93b (10)
Lid***	597.32 ± 18.29a (19)	663.0 ± 24.52b (10)	585.36 ± 14.87a (11)	583.1 ± 36.07a (10)
Lj6 ns	16.32 ± 1.63 (19)	16.4 ± 2.27 (10)	15.64 ± 2.11 (11)	–

Kruskal–Wallis test with Bonferroni adjustment of medians

The asterisks indicate the level of significance of treatment effects (Kruskal–Wallis test: * $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$; ns, $P > 0.05$). Means within a row followed by different letters are significantly different (Bonferroni post hoc analysis: $P < 0.05$)

An. rotundus sensu stricto, *Androlaelaps ulysespardinasi* Lareschi (from *Akodon philipmyersi* Pardiñas, D'Elía, Cirignoli and Suárez), *Androlaelaps aerosus* Lareschi and Velazco (from *Akodon aerosus* Thomas), *An. misionalis*, *An. maurii*, and the two new species described below: *Androlaelaps navonae* n. sp. and *Androlaelaps wingei* n. sp.

Androlaelaps navonae n. sp.

(Only females were collected; see Table 2 for measurements; Figs. 5, 6).

Dorsum (Fig. 5a). Dorsal shield reticulate about 18–20 % longer than wide, covering about 85–90 % of total idiosoma (Fig. 6). Distance between *j6* setae (125–134 μm) similar or greater than *z5*–*z5* distance (115–128 μm), and more than twice the distance between *j5* setae (53–67 μm). Gland pores as illustrated. Idiosoma ovoid, about 1.4 as long as wide; posterior margin rounded (Figs. 5a, 6). *Gnathosoma* (Fig. 5b). Hypognathal groove with six rows of teeth; strong tritosternum with unornamented base and thick laciniae. Gnathosomal (*gn*) and three pairs of hypostomal setae present; minute with exception of hypostomal seta *h3*, more than twice as long as the others (25 vs. <11 μm). Chelicerae (Fig. 5c) chelate-dentate; movable digit (*md*) with hooked tip and one tooth in distal third, fixed digit (*fd*) with no teeth and long setiform pilus dentilis (*pd*); arthrodial corona of shortened processes. *Venter* (Figs. 5b, 6). Sternal shield about 1.4/1.5 times broader than long with a reticulate presternal region. Anterior margin slightly convex and broadest at lateral angles between coxae II and III; anterior margin slightly expanded at level of first sternal seta *st1*. Posterior margin strongly concave; with three pairs of sternal setae: *st1* and *st2*, tips reaching or overpassing the base of the following setal bases; *st3* extending beyond the base of metasternal seta *st4*. Sternal seta *st1* short, about 25 % shorter than *st3*. With two pairs of elongate/lyriform pores on shield. Metasternal seta *st4* (56 μm) longer than *st1* (48 μm), but shorter than *st3* (63 μm). Epigynal shield broad, with lateral expansion posterior to seta and convex sided (Fig. 6); anterior margin strongly convex, with very short anterior flap of radiating lines, and rounded posteriorly; bearing single pair of setae (*st5*), shorter than sternal seta *st1*, *st3*, and metasternal *st4*. Peritrematic shield well sclerotized, extending 20 μm posterior to stigma. Metapodal shields weakly sclerotized, ovoid, longer (32 μm) than wide (15 μm). Opisthogaster reticulate with 13 pairs of strong setae, two pairs close to border of epigynal shield. Anal shield (Figs. 5b, 6) almost as long as broad; greatest width posterior level of the anus. Paranal (*paa*) setae setiform about 60 % of the length of postanal (*poa*), inserted immediately posterior level of mid-anus, reaching to insertion of longer, stronger postanal seta. Cribrum well developed, composed of three rows of teeth. Anal opening about half its length from anterior margin of anal shield.

Diagnosis

Androlaelaps navonae n. sp. is similar to *An. maurii* and *An. misionalis* in general appearance, but differs from these species (as well as from *A. wingei* n. sp.) by a group of means of some measurements (see Table 2). *Androlaelaps navonae* n. sp. is similar to *An. misionalis* but differs from *An. maurii* because of its short epigynal seta *st5* (length <35 % of total epigynal shield length vs. 50 % in *An. maurii*). Moreover, *An. navonae* n. sp. differs from both, *An. misionalis* and *An. maurii*, in having *Z5* seta >8 × longer than *J5*, whereas in the remainder species *Z5* seta ≤8 × longer than *J5*; in having the distance

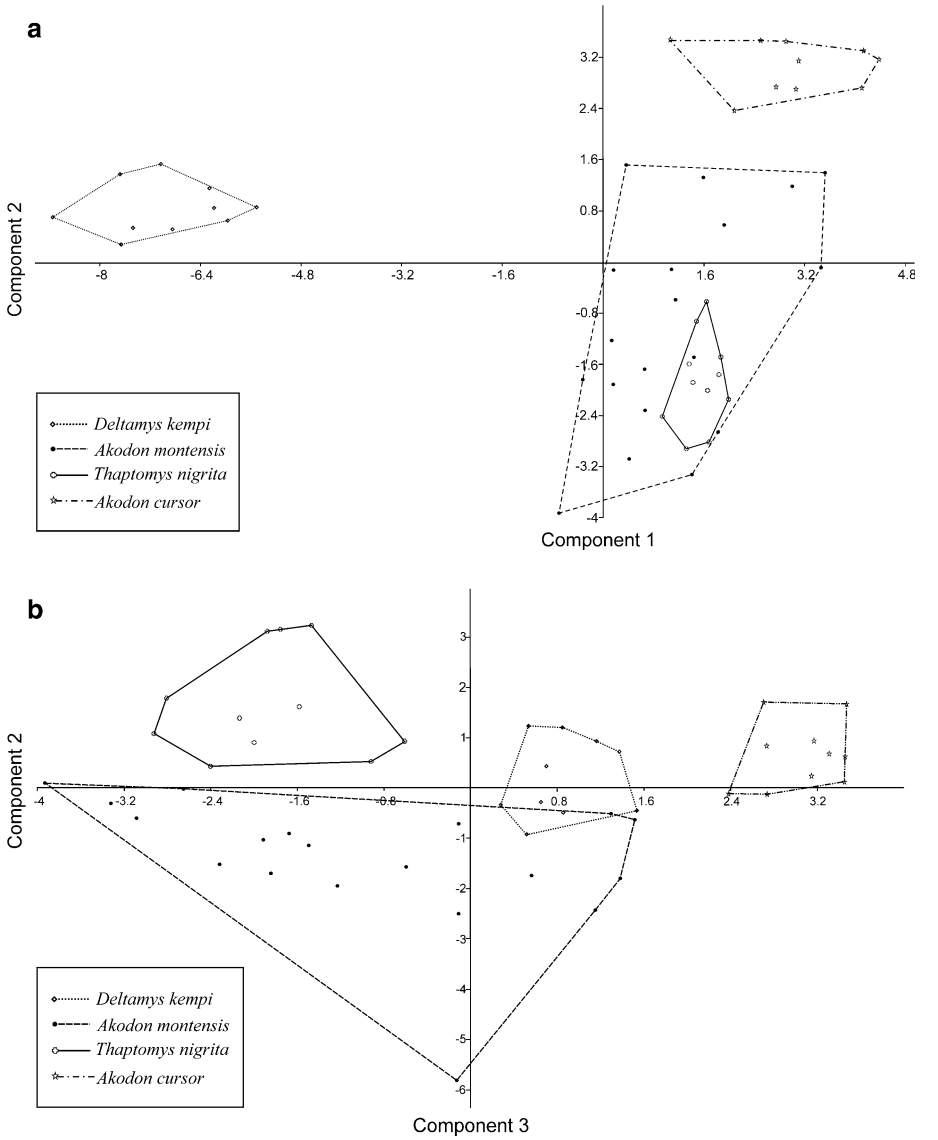

Fig. 2 Principal component analyses, considering mites parasitic of the four rodent species, *D. kempi*, *A. montensis*, *T. nigrita*, and *A. cursor*. **a** First and second components; **b** second and third components

between *j6* setae in the dorsal shield >2 × the distance between *j5* setae, whereas similar in *An. misionalis* and *An. maurii*; in having setae *st5* shorter than sternal seta *st1*, whereas subequal in *An. misionalis* and longer in *An. maurii*; and in having the epigynal shield with lateral expansion posterior to seta and convex sided.

Table 3 PCA loadings of the first three axes

	Axis 1	Axis 2	Axis 3
LDS	0.2405	0.1475	-0.05195
WDS	0.1797	0.2022	−0.07515
j5–j5	0.1628	−0.132	−0.04772
z5–z5	0.2135	−0.1061	0.05396
Lj5	0.05926	−0.05967	−0.286
Lz5	0.07973	−0.2375	−0.2122
J5–J5	0.2583	0.005708	−0.02551
Z5–Z5	0.242	0.03909	0.001675
LZ5	0.2029	0.005701	0.2128
gn–gn	0.1612	−0.07865	−0.04473
Lgn	0.0005157	0.2402	−0.1596
gn-h3	0.1622	0.2507	−0.1653
LSS	0.1496	0.3036	0.04256
WSS	0.2111	−0.007312	−0.1898
st1–st1	0.2356	−0.09452	−0.06868
st3–st3	0.2366	−0.1448	0.02149
Lst1	0.02033	−0.07752	0.4215
Lst3	0.1534	0.1534	0.03642
Les	0.2423	−0.06196	−0.009724
st5–st5	0.2478	−0.04207	0.08684
>Wes	0.03762	−0.000906	0.3599
Lst4	−0.07311	0.2214	−0.1883
Lst5	−0.1989	0.0559	−0.07789
Lpaa	−0.03239	−0.2226	0.3048
Lpoa	0.1862	−0.2482	−0.04285
>Was	0.2103	0.06982	−0.1368
LpscI	0.2103	−0.08637	0.04179
LdscI	0.1526	−0.1114	0.1735
LpscII	0.08773	0.3001	0.001992
LpscIII	0.04061	0.2654	0.0791
LscIV	0.1067	−0.1115	−0.1351
Lad1	0.07688	0.3728	0.1082
Lad3	0.07575	0.2441	0.42
j6–j6	0.2459	−0.06021	0.01694

Taxonomic summary

Type host

Thaptomys nigrita (Lichtenstein) (Sigmodontinae: Akodontini), CNP4262. This voucher specimen is housed at the Colección de Mamíferos del Centro Nacional Patagónico (CNP), Puerto Madryn, Chubut, Argentina.

Table 4 Kruskal-Wallis (H) test and post hoc probabilities with Bonferroni adjustment (P), between mites associated with *Akodon montensis* and *Thaptomys nigrita*

	H	P
LDS	5.036	0.024
WDS	2.365	0.12
j5–j5	2.47	0.11
z5–z5	1.78	0.18
Lj5	1.727	0.19
Lz5	2.177	0.14
J5–J5	0.471	0.49
Z5–Z5	0.023	0.88
LJ5	0.03	0.86
LZ5	11.444	0.0007
gn–gn	0.8	0.37
Lgn	4.004	0.045
Lh3	0.038	0.84
gn-h3	9.67	0.0019
LSS	0.0047	0.96
WSS	3.39	0.066
st1–st1	0.86	0.35
st3–st3	3.36	0.067
Lst1	13.32	0.0003
Lst3	0.032	0.86
Les	1.01	0.32
st5–st5	2.92	0.087
>Wes	6.76	0.009
Lst4	8.2	0.004
Lst5	5.93	0.01
Lpaa	7.77	0.005
Lpoa	0.38	0.54
pst-edge	2.06	0.15
paa–paa	0.03	0.86
>Was	5.24	0.02
LpscI	0.22	0.64
LdscI	3.65	0.056
LpscII	0.002	0.96
LpscIII	1.23	0.27
LscIV	0.089	0.76
Lad1	0.11	0.74
Lad3	9.64	0.0019
j6–j6	4.24	0.04
Lid	1.47	0.22

Type locality

Parque Provincial Urugua-í, Misiones Province, Argentina (25°51′10.29″S, 54°10′41.53″W).

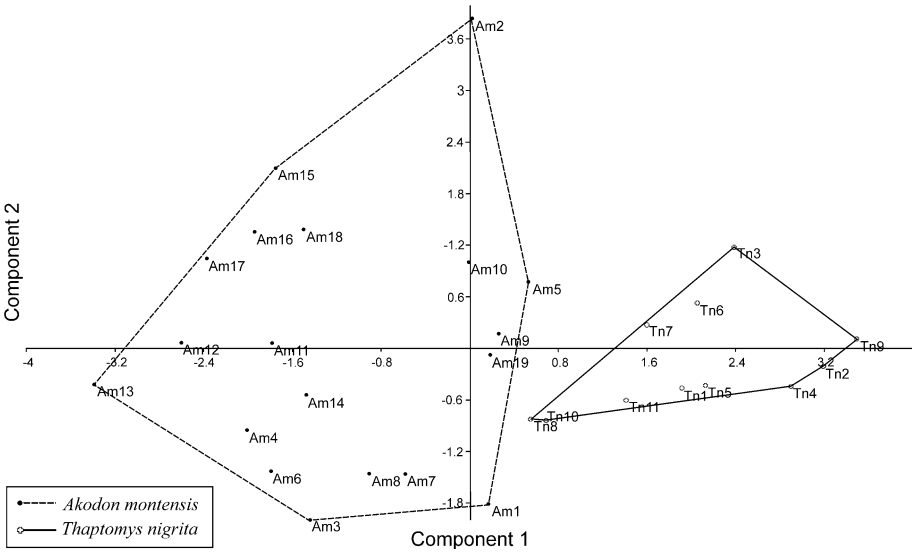

Fig. 3 Principal component analyses based on significantly different variables in their medians considering mites from *A. montensis* (Am) and *T. nigrita* (Tn). Am1 (LTU391-1), Am2 (LTU391-2), Am3 (LTU391-3), Am4 (LTU391-4), Am5 (LTU391-5), Am6 (LTU391-6), Am7 (LTU391-7), Am8 (LTU391-8), Am9 (LTU391-9), Am10 (LTU391-10), Am11 (TK129542-1), Am12 (TK129542-2), Am13 (JN509-1), Am14 (JN509-2), Am15 (CG38-1), Am16 (CG38-2), Am17 (LTU594-1), Am18 (LTU594-2), Am19 (CNP1835), Tn1 (CNP1926-1), Tn2 (CNP1926-2), Tn3 (CNP1791-1), Tn4 (CNP1791-2), Tn5 (CNP1791-3), Tn6 (CNP1791-4), Tn7 (CNP1791-5), Tn8 (CNP1791-6), Tn9 (CNP1926-3)

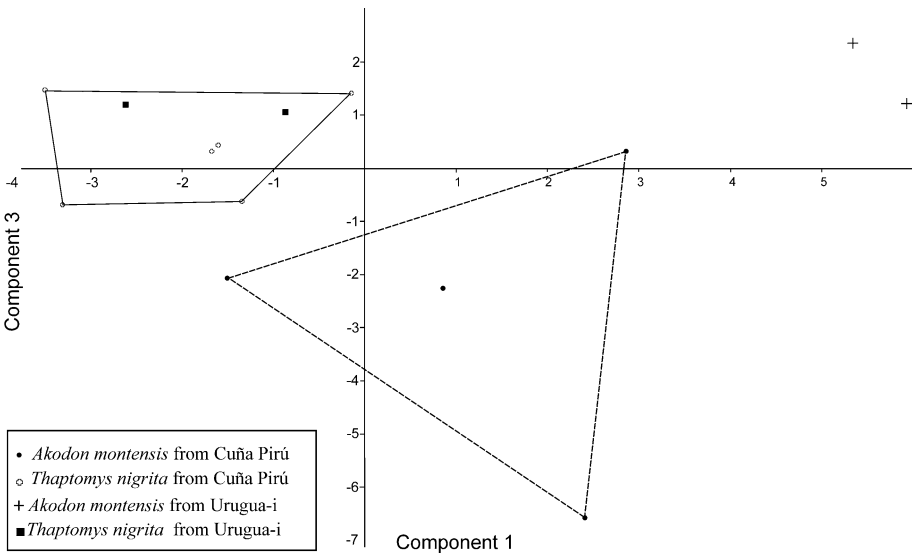

Fig. 4 Principal component analyses considering only mites collected from *A. montensis* and *T. nigrita* in localities where they were captured in sympatry

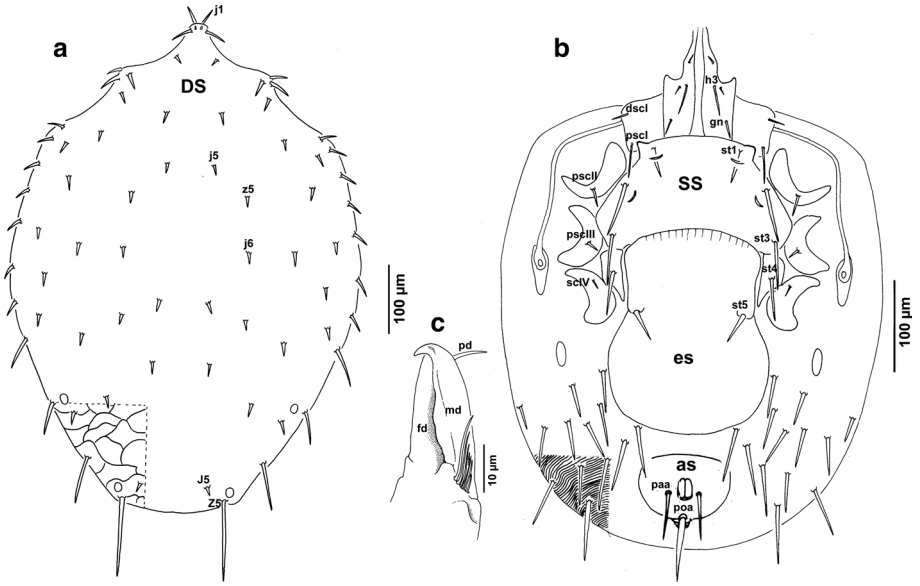

Fig. 5 *Androlaelaps navonae* n. sp. **a** Dorsum. **b** Venter. **c** Gnathosoma. Dorsal shield (DS); gnathosomal seta (gn); hypostomal seta (h3); sternal shield (SS); first sternal seta (st1); third sternal seta (st3); epigynal shield (es); epigynal seta (st5); metasternal seta (st4); paranal setae (paa); postanal seta (poa); anal shield (as); proximal seta of coxa I (pscI); distal seta of coxa I (dscI); posterior seta of coxa II (pscII); posterior seta of coxa III (pscIII); seta of coxa IV (scIV); fixed digit (fd); movable digit (md); pilus dentilis (pd)

Fig. 6 *Androlaelaps navonae* n. sp.

Type material

The type series was deposited in: Collection of División de Entomología, Museo de La Plata (MLP), La Plata, Argentina (holotype MLP-CNP4262-1, and seven paratypes; Annexes of Colección de Mamíferos del Centro Nacional Patagónico (CNP), Puerto Madryn, Chubut, Argentina (two paratypes).

Etymology

In homage to Graciela Navone, an Argentinean parasitologist from the CEPAVE, in recognition of her contribution not only to the knowledge of helminthes, but her enthusiasm in promoting interdisciplinary parasitological studies, considering parasites of various taxa (arthropods included) as well as their mammal hosts.

Biology

Only females were collected. Neither eggs, nor immature stages were observed inside the females. Male, nymph and larva unknown

Androlaelaps wingei n. sp.

(Only females were collected; see Table 2 for measurements; Fig. 7).

Very similar to *A. navonae* n. sp. (see Fig. 5a–c) with the exception of some measurements (see Table 2) and the shape of the epigynal shield (Fig. 7).

Dorsum. Dorsal shield reticulate about 15 % longer than wide, covering about 85–90 % of total idiosoma. Distance between *j6* setae (125–135 μm) similar or greater than *z5*–*z5* distance (120–127 μm), and more than twice the distance between *j5* setae (55–60 μm). Gland pores as illustrated. Idiosoma ovoid, about 1.4 × as long as wide; posterior margin rounded. *Gnathosoma*. Hypognathal groove with six rows of teeth; strong tritosternum with unornamented base and thick laciniae. Gnathosomal (*gn*) and three pairs of hypostomal setae present; minute with exception of hypostomal seta *h3*, almost twice as long as the others (24 vs. <13 μm). Chelicerae chelate-dentate; movable digit (*md*) with hooked tip and one tooth in distal third, fixed digit (*fd*) with no teeth and long setiform pilus dentilis (*pd*); arthrodial corona of shortened processes. *Ventral*. Sternal shield about 1.3 × broader than long with a reticulate presternal region. Anterior margin slightly convex and broadest at lateral angles between coxae II and III; anterior margin slightly expanded at level of first sternal seta *st1*. Posterior margin strongly concave; with three pairs of sternal setae: *st1* and *st2*, tips reaching the base of the following setal bases; *st3* extending beyond the base of metasternal seta *st4*. Sternal seta *st1* short, about 30 % shorter than *st3*. With two pairs of elongate/lyriform pores on shield. Metasternal seta *st4* (61 μm) longer than *st1* (45 μm), but shorter than *st3* (67 μm). Epigynal shield broad, slightly convex sided; anterior margin strongly convex, with very short anterior flap of radiating lines, and rounded posteriorly; bearing single pair of setae (*st5*), shorter than sternal seta *st1*, *st3*, and metasternal *st4*. Peritrematic shield well sclerotized, extending 24 μm posterior to stigma. Metapodal shields weakly sclerotized, ovoid, longer (30 μm) than wide (14 μm). Opisthogaster reticulate with 13 pairs of strong setae, two pairs close to border of epigynal shield. Anal shield almost as long as broad; greatest width at level of the anus. Paranal (*paa*) setae setiform about 60 % of the length of postanal (*poa*), inserted immediately posterior level of mid-anus, reaching to insertion of longer, stronger postanal seta. Cribrum well developed,

Fig. 7 *Androlaelaps wingei* n. sp.

composed of three rows of teeth. Anal opening about half its length from anterior margin of anal shield.

Diagnosis

Androlaelaps wingei n. sp. is very similar to *An. navonae* n. sp., but differs from this species because of its larger size (566 µm long, 473 µm wide; vs. 527 and 423 µm in *An. navonae*), and the presence of epigynal shield slightly sided convex. Moreover, *An. wingei* n. sp. differs from the remainder species by a group of means of some measurements (see Table 2).

Taxonomic summary

Type host

Akodon cursor (Winge) (Sigmodontinae: Akodontini), MZUFV3949. This voucher specimen is housed at the Museu de Zoologia, Universidade Federal de Viçosa, Minas Gerais, Brazil.

Type locality

Mata do Paraíso Research Station, Viçosa, Minas Gerais, Brazil (20°46′S, 42°51′W).

Type material

The type series was deposited in the Collection of División de Entomología, Museo de La Plata (MLP), La Plata, Argentina (holotype MLP- MZUFV3949-1) and nine paratypes.

Etymology

In tribute to Herluf Winge (1857–1923), vice-curator of the Zoological Museum, University of Copenhagen, for his contribution to the knowledge of the remarkable biodiversity of southeastern Brazil. Winge described and illustrated numerous species of sigmodontine rodents, *Ak. cursor* among them, based on the incredible collections of current and fossil animals performed by P.W. Lund in Lagoa Santa.

Biology

Only females were collected. Immature stages were observed inside two of the females. Male, nymph and larva unknown.

Discussion

A species of parasite known to exploit several host species in a given area can in fact prove to be a complex of several species of superficially identical, highly host-specific parasites (Poulin et al. 2006). Among parasites, morphology presents a problem to phylogenetic reconstruction because of the amount of convergence due to multiple independent evolutions of a parasitic lifestyle (Price 1980). In the present study, although the mites are very similar morphologically, component analyses allowed to distinguish four groups of mites, each one host specific, whether or not hosts lived in sympatry, and without geographical variation. Thus, we postulate that there are four species: *An. maurii* specific for *D. kempi*, *An. misionalis* for *Ak. montensis*, *An. navonae* n. sp. of *T. nigrita*; and *An. wingei* n. sp. of *Ak. cursor.* The four species differ among them by group means of particular measurements, and each species is unique in at least one measurement, differentiating this species from the remainder three. The best discriminators are length and width of dorsal shield: *An. maurii* is the smallest species, whereas *An. wingei* is the biggest. *A. misionalis* and *An. navonae* n. sp. not only are morphologically very similar, but they are easily misclassified because they were collected in sympatry. Multivariate morphometric analyses, based on 40 diagnostic characters, allowed us to recognise these two species specific of their respective host species. *A. navonae* n. sp. and *An. wingei* n. sp. are also very similar, differentiated only in the shape of the epigynal shield and on the basis of their ranges of variation in some characters. Differences among the four mite groups are consistent, independent of locality and despite the fact that they occur in sympatry. Thus, we postulate that we have four species.

The results obtained support that *An. misionalis*, *An. maurii* and the two new species, belong to the *An. rotundus* species group. However, these four species are very similar among them but differ from the remainder species of the *rotundus* group (*An. rotundus* sensu stricto, *An. ulysespardinasi* and *An. aerosus*), based on the presence of the combination of the following characters: small size ($\leq$580 μm long, $\leq$500 μm wide); distance between *j6* setae similar to the distance between the *z5* setae; strong ventral setae; opisthogaster with 13 pairs of strong setae, one close to the distal margin of epigynal shield; and anal shield wider than longer. We postulate that these mites probably constitute a new genus, but further studies, including the revision of mites parasitic of more akodontine species, will be necessary to test this hypothesis.

Inferring the history of host and parasite association is not straightforward. There are different types of events that commonly arise in models of host-parasite evolution. Parasite

species may distribute in parallel with the phylogenetic relationships of their hosts (coevolution), or parasites may infest a wide taxonomic range of rodents that share ecological time and space but are not phylogenetically related, speciating in the process (host switching) (Page 2001; Hoberg and Brooks 2010). When host switching takes place, phylogenetic trees of hosts and mites have independent histories (Ronquist 2001).

Host rodents considered in the present study are in the same tribe (Akodontini), but they belong to different clades: *Deltamys* and *Akodon* are sister genera (D'Elía 2003; D'Elía et al. 2003; Smith and Patton 2007; Müller et al. 2013), but *Thaptomys* belongs to another clade containing *Thalpomys* and *Necromys* species (D'Elía 2003), or is the sister group of "*Akodon*" *serrensis* (Barros et al. 2009; Coyner et al. 2013). Mites belonging to the *An. rotundus* group associated with *Necromys* species and "*Ak.*" *serrensis* have been examined and differ from mites considered in the present study (see characteristics of the group below) (Lareschi and Barros-Battesti 2010; Lareschi pers. obs.). Although many potentially closely related mites, and too many important hosts, are missing from the study, based on our analyses we propose that probably host switching of mites among rodents has taken place, followed by speciation. This postulation is in accordance with the evolutionary lineages to parasitism in many laelapids, assuming that species which inhabit the nests have good possibilities to colonize new hosts who share those nests (Dowling 2006). Perhaps if the nest is not the colonizing point, the species of rodents sharing part of their geographic range could undergo the same colonizing process. The rodents considered in the present study share part of their geographic range (Bonvicino et al. 2002; Pardiñas et al. 2005), and they are in sympatry at some localities. In the present time, *Ak. montensis*, *Ak. cursor* and *T. nigrita* are species restricted to the Atlantic Forest or Mata Atlantica, where they overlap their distribution, whereas *D. kempi* (and another unnamed species of this genus) range from Rio Grande do Sul in Brazil, through Uruguay to East Argentina, and inhabits marshy environments, especially edges of wetlands, usually without trees (González and Pardiñas 2002). Although there is no evidence that *D. kempi* occurs in sympatry with any of the other three species, it is known that its range overlaps that of *Ak. montensis* and *T. nigrita* at the north shore of Lagoa dos Patos and in the neighborhoods of Porto Alegre in Rio Grande do Sul, Brazil (Patton et al. 2008; Pardiñas et al. 2008; Queirolo et al. 2008). *A. cursor* is known to be sympatric in Brazil with *Ak. montensis* at middle altitude in the Itatiaia National Park, Rio de Janeiro (Geise et al. 2004), at sea level in Iguapé, São Paulo (Geise et al. 2005), and with *T. nigrita* in Serra do Brigadeiro State Park, Minas Gerais (Moreira et al. 2009), Caparaó National Park, Minas Gerais, and Espirito Santo States (Bonvicino et al. 2002). *Akodon montensis* is known to be sympatric with *T. nigrita* in Brazil at Morro de Elefante, Rio Grande do Sul (Lima et al. 2010), Caucaia do Alto, São Paulo (Püttker et al. 2006), Serra da Fartura, São Paulo (de Moraes et al. 2003), in Argentina at Reserva del Valle del Cuña Pirú, Misiones (Cirignoli et al. 2011), Parque Nacional Iguazú, Misiones (Crespo 1982), and in Paraguay at Parque Nacional San Rafael and Puerto Pirapó, Itapúa (Myers and Wetzel 1979), and at Limoy Biological Reserve, Alto Paraná (de la Sancha 2014).

In accordance with many species of laelapids, in the present study only females were collected from the fur of the hosts (Radovsky 1985). Probably males and immature stages may occur in the nests of their hosts or on the soil, with good possibilities for colonizing new hosts and then speciate. Although more studies are necessary, the results obtained lead to further insights into the complexity of inferring the history of an association between a parasite and its host. Our assumption of host switching is exclusively for the four laelapid species considered in the present study. Probably coevolution has taken place between other laelapid mites and their mammal hosts.

Although sympatry among the four species of rodent hosts in the past may have allowed a single mite species to colonize other host species and speciate into four mite species, at present the four mite species considered are highly host specific. Evidence of this is the sample carried out in Reserva Privada de Usos Múltiples Valle del Cuña Pirú during a natural 'cycle' characterized by the increase of native populations of rodents locally known as 'ratada' (Hershkovitz 1955). During 'ratadas', rodents multiply rapidly and overlap their microhabitats. Usually, these events benefit exchange of ectoparasites (Gettinger and Ernst 1995; Nava et al. 2003). However, no exchange of mites *An. misionalis* and *An. navonae* n. sp. was observed among rodents in Cuña Pirú. Moreover, other akodontines have been captured in addition to *Ak. montensis* and/or *T. nigrita* (e.g. *Necromys* spp.), but *An. misionalis*-like species were not found parasitizing them, nor other rodents from nearby localities (e.g. *Ak. philipmyersi*, *Brucepattersonius* sp., etc.).

Our results support the fact that there are still cryptic species in the *An. rotundus* species group which are necessary to study and unveil potential hidden new species. Cryptic species are known to be prevalent among laelapids (Furman 1972; Gettinger and Owen 2000; Dowling 2006; Lareschi 2011) and we support the value of using multivariate analyses in disclosing hidden diversity and understanding the dynamics of parasite speciation.

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Appendix 1: Characters and their acronyms measured from the mites and used in morphometric analyses

Dorsal shield length (LDS); dorsal shield width at midlevel (WDS); distance between *j5* setae (*j5–j5*); distance between *z5* setae (*z5–z5*); length of *j5* (*Lj5*); length of *z5* (*Lz5*); distance between dorsal setae *j6* (*j6–j6*); length of idiosoma (*Lid*); length of seta *j6* (*Lj6*); distance between *J5* setae (*J5–J5*); distance between *Z5* setae (*Z5–Z5*); length of *J5* (*LJ5*); length of *Z5* (*LZ5*); distance between gnathosomal setae (*gn–gn*); length of gnathosomal seta (*Lgn*); length of hypostomal seta *h3* (*Lh3*); distance between gnathosomal and hypostomal seta *h3* (*gn-h3*); length of sternal shield (*LSS*); width of sternal shield at level of second sternal setae (*WSS*); distance between first sternal setae (*st1–st1*); distance between third sternal setae (*st3–st3*); length of anterior sternal setae (*Lst1*); length of third sternal setae (*Lst3*); length of epigynal shield (*Les*); distance between epigynal setae (*st5–st5*); greatest width of epigynal shield (*>Wes*); length of metasternal seta (*Lst4*); length of epigynal setae (*Lst5*); length of paranal (*paa*) setae (*Lpaa*); length of postanal (*poa*) seta (*Lpoa*); distance from postanal seta to anterior midline of anal shield (*pst-edge*); distance

between paranal setae (*paa–paa*); greatest width of anal shield (>*Was*); length of proximal seta of coxa I (*LpscI*); length of distal seta of coxa I (*LdscI*); length of posterior seta of coxa II (*LpscII*); length of posterior seta of coxa III (*LpscIII*); length of seta of coxa IV (*LscIV*); length of seta *ad1* in femur I (*Lad1*); length of *ad3* in genu I (*Lad3*).

Appendix 2: Mites included in multivariate analysis (acronyms, number of specimens, host species and locality)

TK129542-1/2: 2 mites, *A. montensis*, Limoy, Alto Paraná, Paraguay (24°46′57″S, 54°26′20″W). LTU391-1/10: 10 mites, *A. montensis*, Salto El Paraíso, Misiones, Argentina (27°13′49″S, 54°02′24″W). JN509-1/2: 2 mites, *A. montensis*, Cuña Pirú, Misiones, Argentina (27°05′17″S, 54°57′09″W). CNP1835: 1 mite, *A. montensis*, Cuña Pirú, Misiones Province, Argentina. CG38-1/2: 2 mites, *A. montensis*, Parque Provincial Urugua-í, Misiones, Argentina (25°51′10.29″S, 54°10′41.53″W). LTU594-1/2: 2 mites, *A. montensis*, 7 km S Puerto Las Palmas, Chaco (27°09′40.53″S, 58°40′27″W). MZUFV3949-1/7: 7 mites, *A. cursor*, Mata do Paraíso Research Station, Viçosa, Minas Gerais, Brazil (20°46′S, 42°51′W). MZUFV2971-2: 2 mites, *A. cursor*, Mata do Paraíso Research Station, Viçosa, Minas Gerais, Brazil. MZUFV3950-1: 1 mite, *A. cursor*, Mata do Paraíso Research Station, Viçosa, Minas Gerais, Brazil. CNP1926-1/2: 2 mites, *T. nigrita*, Cuña Pirú, Misiones Province, Argentina. CNP1791-1/6: 6 mites, *T. nigrita*, Cuña Pirú, Misiones Province, Argentina. CNP1926-4: 1 mite, *T. nigrita*, Parque Provincial Urugua-í, Misiones Province, Argentina. CNP4262-1/2: 2 mites, *T. nigrita*, Parque Provincial Urugua-í, Misiones Province, Argentina.

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