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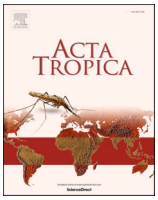

An integrative approach to explore species limits in *Laelaps mazzai* Fonseca, 1939 (Mesostigmata, Laelapidae), a South American widespread mite parasitizing the cricetid *Calomys* Waterhouse, 1837

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ABSTRACT

Laelaps mazzai Fonseca, 1939 (Mesostigmata, Laelapidae) parasitizes several species of the widespread South American rodent genus *Calomys* Waterhouse, 1837. Morphological variation has been noticed within this laelapid but has yet to be analyzed. Since several other species of laelapids that initially were considered generalists have resulted in host-specific species, after further analyses, herein we explored, through morphology and genetics, the variation of this parasite across six species of *Calomys*, trying to establish if it constitutes a polymorphic species or a complex of cryptic host specific-species. An integrative approach was applied, including principal component and discriminant analyses of females and males and DNA sequences (nuclear region ITS and the COI gene). The obtained results indicate that female mites tend to differentiate only the sizes of their dorsal shield among host species but with extensive overlapping. At the same time the males lack metrical differentiation, and the genetic evidence failed to resolve specific-species clades. We conclude that *L. mazzai* is a single widespread mite with little genetic and phenotypic differentiation.

1. Introduction

Historically, species were delimited exclusively based on their morphological characteristics. A more integrative approach is currently used, incorporating other data obtained from using different methodologies such as morphometric, ecological, and genetic tools, to support the morphological evidence (Dayrat, 2005). Within a species, morphological variations could be associated with the environmental context, while in parasitic arthropods, the host also should be considered an environment that could differentiate morphological characteristics (Morand et al., 2006). In this context, Mesostigmata mites are convenient to study models to test morphological variation since they are morphologically and ecologically diverse (Dowling and OConnor, 2010). Within Mesostigmata mites, Laelapidae includes "free-living" species and parasitic ones associated with invertebrates or vertebrates. For the latter, cricetid rodents are the most common hosts (Strandtmann and Wharton, 1958; Dowling and OConnor, 2010).

Morphological variations were reported for various parasitic species of the Laelapidae (Evans and Till, 1966; Furman, 1972a; Till, 1963). Some of these species were initially considered generalists, but further analysis resulted in different species, each specific to another host species (e.g., Gettinger, 1992a; Lareschi and Galliari, 2014). For example, *Androlaelaps rotundus* (Fonseca, 1936), considered a generalist mite, later turned out to be a complex of cryptic species identified and described as new host-specific species (e.g., Lareschi, 2011, 2020; Lareschi and Galliari, 2014). Something similar happened in the genus *Laelaps* Koch, 1836. With the support of molecular and morphometric tools, three new species previously included in *Laelaps manguinhosi* sensu latto Fonseca, (1936) were described (Savchenko and Lareschi, 2022). However, in other cases, the morphometric variations within the same species were insufficient to distinguish different species and were considered intraspecific variations. For example, in *Laelaps*

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clethrionomydis Lange, 1955, variations have been found among the mites associated with arvicoline rodents (Rodentia: Cricetidae: Arvicolini) of different genera, but not when the hosts are congeneric (Korallo-Vinarskaya et al., 2015). On the contrary, *Gigantolaelaps vitzthumi* Fonseca, (1939) presented morphometric differences among mites associated with the same host, *Cerradomys* (Weksler et al., 2006) (Cricetidae: Oryzomyini), but in different locations in Brazil (Martins-Hatano et al., 2012). Likewise, *Androlaelaps fahrenholzi* (Berlese, 1911) showed variations in its measurements depending on the host species (Rodentia: Cricetidae: Phyllotini) and locality (Silva de la Fuente et al., 2020).

Laelaps mazzai Fonseca, (1939) (Mesostigmata: Laelapidae) is one of the few species of the genus characterized by females and males with a hypertrichous dorsal shield, and males with the anal shield separated from the sternoventral shield (Fonseca, 1939, 1958). *Laelaps mazzai* has been reported to be associated mostly with species of *Calomys* Waterhouse, 1837 (Cricetidae, Sigmodontinae) from Argentina, Brazil, Paraguay, and Venezuela. Morphological variation has been noticed within *L. mazzai* (Furman, 1972a), but most of the literature reports host and/or locality association of this mite and does not analyze its intraspecific variation (e.g., Botelho et al., 1981; Whitaker and Abrell, 1987; Whitaker and Dietz, 1987; Gettinger, 1992b; Lareschi and Mauri, 1998; Lareschi et al., 2006; Nava and Lareschi, 2012; Sponchiado et al., 2015).

Species of *Calomys* are an emblematic component of the tribe Phyllotini, widely distributed in the Neotropical Region (Salazar-Bravo, 2015; Pardiñas et al., 2017;). Of the thirteen known *Calomys* species, *L. mazzai* was reported to be associated with *C. callidus* Thomas, 1916, *C. laucha* (Fischer, 1814), *C. musculinus* (Thomas, 1913), and *C. venustus* (Thomas, 1894) in central and northeastern Argentina (Lareschi and Mauri, 1998; Lareschi et al., 2006; Nava and Lareschi, 2012), with *C. laucha* in an undefined area of Paraguay (Whitaker and Abrell, 1987), with *C. hummelincki* (Husson, 1960) in eastern and western Venezuela (Furman, 1972a) and with *C. callosus* (Rengger, 1830) and *C. tener* (Winge, 1888) in eastern and central Brazil (Botelho et al., 1981; Whitaker and Dietz, 1987; Gettinger, 1992b; Sponchiado et al., 2015). However, the association with *C. tener* in Minas Gerais State (Whitaker and Dietz, 1987) must be revised, since later Gettinger (1992a) described a close species, *Laelaps valdevinoi* Gettinger, 1992, associated with this rodent in the Brazilian Federal District.

Since *L. mazzai* parasitizes several *Calomys* species in a wide area, this study aimed to analyze if this mite's morphology and genetic characterization are consistent across six different host species from Argentina or if it is a complex of cryptic host-specific species.

2. Materials and methods

The study was carried out based on 945 mites collected from rodents identified as *C. callidus, C. callosus, Calomys fecundus* (Thomas, 1926), *C. laucha, C. musculinus*, and *C. venustus* from the following Argentinean localities (Fig. 1, Table 1): 32 km SW La Unión (Salta Province) (32 U), Estación de Animales Silvestres Guaycolec (Formosa Province) (ESG), Reserva El Bagual (Formosa Province) (REB), 5 km NW Puerto Las Palmas (Chaco Province) (5PP), 7 km S Puerto Las Palmas (Chaco Province) (7PP), Estancia Cimarrón (Corrientes Province) (ECI), Esperanza (Santa Fe Province) (ESP), Establecimiento La Luisiana (Córdoba Province) (ELL), Establecimiento La Esperanza (Córdoba Province) (ELE), Arroyo Ana (Entre Ríos Province) (AAN), Olmos (Buenos Aires Province) (OLM), Estación Experimental de Agronomía Julio Hirschhorn (Buenos Aires Province) (EEA), Arana (Buenos Aires Province) (ARA), and Cabo Raso (Chubut Province) (CRA).

2.1. Molecular procedures

Out of the 945 mites, a subsample of 33 of both sexes was selected for DNA extraction as detailed: from *C. fecundus* (1 female and 1 male), *C. callidus* (3 females and 3 males), *C. callosus* (3 females and 3 males),

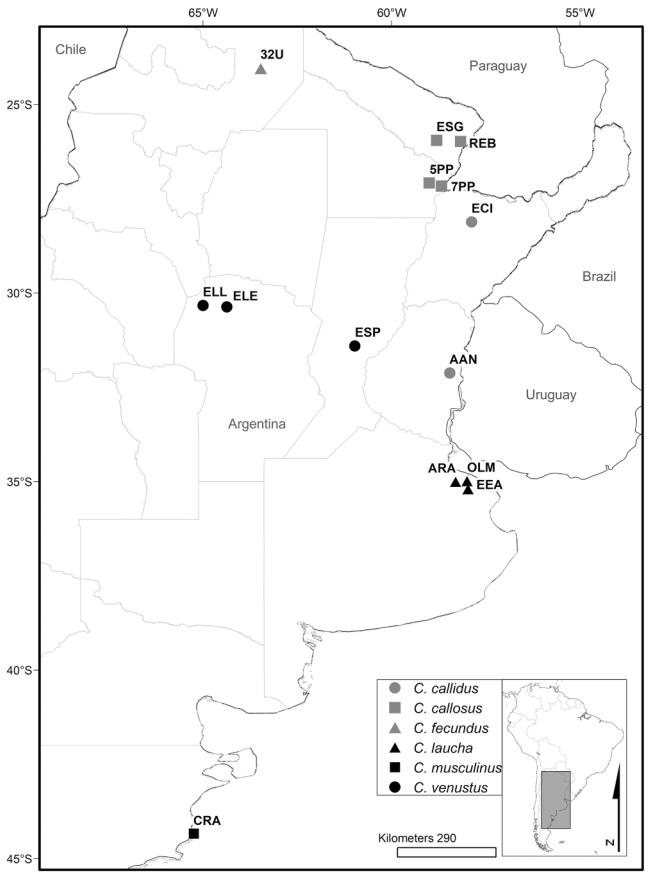

Fig. 1. Localities included in this study: 32 km SW La Unión, Salta Province (32 U); Estación de Animales Silvestres Guaycolec, Formosa Province (ESG); Reserva El Bagual, Formosa Province (REB); 5 km NW Puerto Las Palmas, Chaco Province (5PP); 7 km S Puerto Las Palmas, Chaco Province (7PP); Estancia Cimarrón, Corrientes Province (ECI); Esperanza, Santa Fe Province (ESP); Establecimiento La Luisiana, Córdoba Province (ELL); Establecimiento La Esperanza, Córdoba Province (ELE); Arroyo Ana, Entre Ríos Province (AAN); Olmos, Buenos Aires Province (OLM); Estación Experimental de Agronomía Julio Hirschhorn, Buenos Aires Province (EEA); Arana, Buenos Aires Province (ARA); and Cabo Raso, Chubut Province (CRA).

C. laucha (2 females), *C. musculinus* (4 females), *C. venustus* (12 females and 1 male). DNA was isolated individually from each mite using Chelex®100 following a non-destructive method for mites, that consisted of individual mites being punctured with a minute pin in the posterior region of the integument, the exoskeleton and the internal fluid obtained were transferred directly to the final Chelex-solution (Savchenko and Lareschi, 2019). After DNA isolation, the exoskeleton of each mite was recovered and prepared for its study using light microscopy (see Section 2.2). A PCR was performed to amplify the nuclear region Internal Transcribed Spacer 1 and 2 (fragment: 18S-ITS1–5.8S-ITS2) (De Rojas et al., 2002), and the mitochondrial gene Cytochrome Oxidase I (COI) (Folmer et al., 1994). The PCR protocol for the ITS region was an initial denaturation of 10 min to 95 °C, then 35 cycles of denaturation for 20 s to 95 °C, annealing for 30 s to 51 °C, extension for 90 s to 72 °C, and a final extension of 10 min to 72 °C. The protocol was similar for COI, but the annealing temperature was 50 °C. The final products of PCR were sequenced in Macrogen (Seoul, Korea).

2.2. Preparation and identification of mites

All mites were cleared in lactophenol and mounted individually in Hoyer's medium (Strandtmann and Wharton, 1958) for their identification by using a light microscope. For all mite identifications we

Table 1
Number of females and males of *Laelaps mazzai* obtained from every *Calomys* species and sampled locality, and subsample selected for morphometric and genetic analyses.

Host species	n hosts	Acronym	Locality	Geographic coordinates	*Laelaps mazzai*		Subsample for morphometric and genetic analyses	
					females	males	females	males
C. callidus	2	ECI	Estancia Cimarrón, Corrientes	28°6′53.5″ S; 57°52′28.3″ W	48	14	5	4
	8	AAN	Arroyo Ana, Entre Rios	32°7′16.3″ S; 58°26′60″ W	235	50	5	4
C. callosus	4	ESG	Estación de Animales Silvestres Guaycolec, Formosa	25°58′49.5″ S; 58°9′49.2″ W	59	7	3	0
	16	REB	Reserva El Bagual, Formosa	25°58′51.6″ S; 58°10′3.9″ W	187	46	7	6
	2	5PP	5 km NW Puerto Las Palmas, Chaco	27°4′45″ S; 58°40′6.3″ W	16	2	2	0
	1	7PP	7 km S Puerto Las Palmas, Chaco	27°9′40.5″ S; 58°40′27.3″ W	24	4	1	0
C. fecundus	4	32U	32 km SW La Unión, Salta	24°2′43.5″ S; 63°28′12.1″ W	64	14	6	8
C. laucha	3	OLM	Olmos, Buenos Aires	34°59′10.2″ S; 57°59′56″ W	1	0	1	0
	13	EEA	Estación Experimental de Agronomía Julio Hirschhorn, Buenos Aires	34°59′10.2″ S; 57°59′56″ W	101	12	10	4
	2	ARA	Arana, Buenos Aires	35°0′25.3″ S; 57°54′33.6″ W	3	2	1	2
C. musculinus	3	CRA	Cabo Raso, Chubut	44°20′23″ S; 65°14′59″ W	8	0	7	0
C. venustus	7	ELL	Establecimiento La Luisiana, Córdoba	30°22′ S; 64°22′ W	11	2	10	2
	4	ELE	Establecimiento La Esperanza, Córdoba	30°12′ S; 64°30′ W	9	0	6	0
	3	ESP	Esperanza, Santa Fé	31°24′20″ S; 60°58′16″ W	23	3	5	2
TOTAL	**72**				**789**	**156**	**69**	**32**

followed Furman (1971, 1972a), as well as characteristics provided by Tipton (1960), and *L. mazzai* original description and figures presented in Fonseca (1939). The identifications were complemented by comparing with the *L. mazzai* female lectotype (IBSP604c), the allotype (IBSP604[1/3]), and one male paratype (IBSP604[2/3]) (Coleção Acarológica do Instituto Butantan, SP, Brazil), all of them collected from an unidentified rodent from an unspecified locality in the Province of Salta, Argentina. Voucher mites collected from every host species will be deposited at División Zoología de Invertebrados, Museo de La Plata (MLP; La Plata, Buenos Aires, Argentina). Salazar-Bravo (2015) was followed for host rodent taxonomy; rodents were housed at the Colección de Mamíferos del Centro Nacional Patagónico (CNP; Puerto Madryn, Chubut, Argentina), except for those from ESP, which are deposited at the collection of Laboratorio de Ecología de Enfermedades

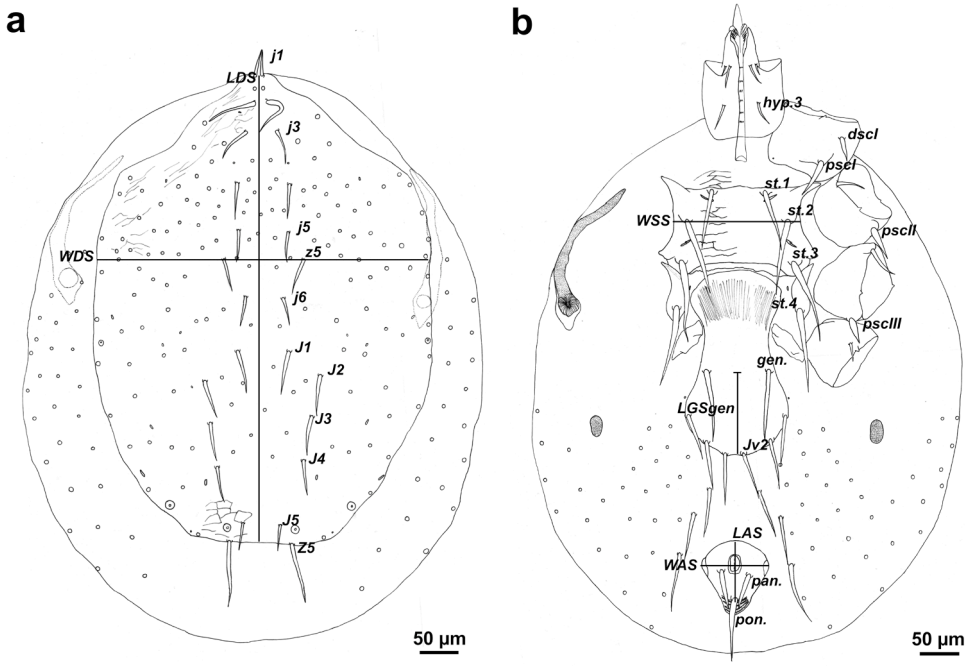

Fig. 2. Dorsal (a) and ventral view (b) of a female of *Laelaps mazzai* collected from *Calomys callosus* in REB. Shields and setae nomenclature used in morphometrics are indicated.

(LEcEn-ICIVET, Esperanza, Santa Fe, Argentina).

2.3. Linear morphometrics

Out of the 945 mites, a subsample of 69 females and 32 males obtained from each *Calomys* species were selected for linear morphometrics analyses (Table 1). Thirty-seven measurements of the females (Fig. 2a, 2b, Table 2) and 29 of the males (Fig. 3a, 3b, Table 3) were taken of different structures and setae of the idiosoma, gnathosoma and legs. Evans and Till (1965, 1979) were followed for chaetotaxy and shields nomenclature. Measurements were taken using Leica Application Suite software (LAS V.4.12), provided in micrometers (μm). The results were presented in the text and tables as the average measure followed by minimum and maximum values between brackets. A Principal Components Analysis (PCA) based on the covariance matrix was carried out to reduce the dimensionality of the morphometric data. A Discriminant Analysis (DA) was performed to evaluate the association between host species. PCA and DA were performed for females and males separately on JMP7.0.1. (SAS Institute). Ellipses showed the 95% confidence region to contain the true mean of group.

2.4. Phylogenetic analyses

Sequences of ITS and COI were edited and aligned in CodonCode Aligner (CodonCode Corporation) with GenBank sequences of *Laelaps muricola* (Träghardh, 1910), *Laelaps giganteus* (Berlese, 1918), *Laelaps schatzi* Lareschi and Savchenko, 2021, *Laelaps agilis* (Koch, 1936) (just for COI) and as an outgroup *Androlaelaps marshalli* (Berlese, 1911). The phylogenetic tree was constructed with MrBayes 3.2.6 after 10 million of generations using a GTR+*G* model of substitution. The trees were visualized with FigTree v.1.4.4. The Bayesian posterior probabilities were transformed into percentages and indicated on the nodes of phylogenetic trees. GenBank access numbers of sequences obtained in this study were indicated on labels of phylogenetic trees (ITS:

Table 2
Character measurements (μm) of females of *Laelaps mazzai*. Results are presented as average followed by minimum and maximum values between brackets. Number of mites (n) measured are indicated for each rodent species. Measurements of the *Laelaps mazzai* lectotype were obtained from direct observation. Measurements of *Laelaps mazzai* from *Calomys hummelincki* were obtained from literature.

Characters	*Calomys callidus* $n = 10$	*Calomys callosus* $n = 13$	*Calomys fecundus* $n = 6$	*Calomys laucha* $n = 12$	*Calomys musculinus* $n = 7$	*Calomys venustus* $n = 21$	*Laelaps mazzai* lectotype	*Laelaps mazzai* from *Calomys hummelincki* (Furman, 1972a)
LDS	640 [632–645]	623 [611–638]	597 [590–610]	608 [597–616]	659 [645–686]	629 [616–645]	592	725 [697–752]
WDS	466 [454–479]	452 [441–470]	439 [426–450]	432 [422–445]	467 [450–485]	464 [448–478]	458	475 [440–510]
WSS	181 [176–188]	179 [172–187]	174 [169–181]	173 [168–182]	176 [164–187]	181 [171–191]	180	175 [172–180]
st.1-st.1	78 [72–81]	75 [69–79]	73 [70–75]	73 [70–76]	72 [67–78]	75 [72–81]	72	–
st.2-st.2	146 [139–154]	145 [139–150]	142 [138–148]	141 [137–144]	142 [138–146]	144 [139–153]	144	–
st.3-st.3	163 [155–170]	161 [152–170]	158 [152–165]	158 [152–167]	160 [151–158]	161 [155–168]	161	–
st.4-st.4	177 [164–187]	175 [160–190]	174 [159–188]	168 [151–184]	160 [143–169]	178 [169–196]	171	–
LS4	120 [115–126]	118 [112–128]	118 [112–125]	115 [108–121]	118 [112–123]	118 [114–124]	118	–
gen.-gen.	90 [85–101]	88 [79–96]	85 [79–91]	83 [78–90]	95 [89–103]	88 [83–93]	83	74 [70–77]
gen.	100 [95–108]	102 [94–109]	101 [96–109]	96 [90–101]	102 [95–110]	103 [99–112]	110	–
LGSgen	126 [120–129]	124 [117–132]	125 [122–127]	121 [111–130]	134 [131–140]	128 [121–135]	129	156 [145–166]
Jv2-Jv2	41 [35–49]	39 [27–48]	34 [29–42]	36 [29–40]	39 [30–44]	38 [32–47]	44	–
Jv2	77 [73–84]	76 [71–82]	77 [73–80]	76 [69–82]	83 [74–89]	74 [66–79]	–	–
LAS	83 [78–86]	82 [76–88]	79 [72–86]	79 [74–85]	90 [87–97]	85 [79–96]	79	107 [98–115]
WAS	89 [83–95]	93 [82–103]	91 [81–95]	88 [78–95]	96 [88–103]	93 [83–99]	99	107 [103–110]
Lpan.	54 [51–59]	54 [48–66]	51 [49–55]	49 [42–55]	52 [46–58]	54 [49–60]	–	53 [50–56]
Lpon.	91 [83–98]	87 [79–96]	85 [80–95]	78 [74–82]	80 [74–82]	88 [80–95]	–	88 [80–96]
Lhyp.3	32 [29–36]	31 [26–36]	31 [29–33]	31 [28–33]	27 [22–32]	31 [22–34]	–	40 [36–43]
LpscI	49 [46–50]	47 [43–50]	45 [41–49]	46 [43–49]	53 [51–55]	46 [28–51]	45	42 [40–43]
LdscI	33 [31–36]	33 [30–36]	31 [30–35]	28 [24–32]	35 [33–37]	33 [29–38]	–	36 [33–38]
LpscII	52 [48–57]	50 [47–55]	45 [44–47]	46 [43–48]	50 [45–53]	50 [46–54]	45	–
LpscIII	36 [32–38]	36 [34–38]	32 [29–34]	33 [30–35]	34 [32–37]	35 [32–39]	33	–
lj1	36 [27–45]	34 [27–39]	33 [31–37]	33 [31–38]	37 [30–41]	36 [29–40]	29	–
j3-j3	45 [41–50]	46 [40–49]	46 [45–48]	44 [40–49]	49 [46–51]	48 [43–52]	43	–
z5-z5	119 [108–125]	117 [111–124]	119 [112–126]	117 [114–125]	125 [121–130]	122 [114–137]	117	–
lz5	49 [47–53]	52 [44–59]	54 [51–58]	48 [44–52]	56 [52–61]	55 [50–60]	–	–
j5-z5	52 [42–60]	51 [44–61]	48 [47–50]	48 [43–53]	51 [46–57]	53 [47–60]	54	–
j6-j6	68 [57–77]	60 [48–70]	58 [49–65]	58 [51–68]	60 [57–64]	63 [52–74]	63	–
lj6	45 [40–50]	51 [48–54]	50 [48–52]	46 [41–53]	53 [50–58]	52 [51–53]	–	–
J1-J1	69 [64–74]	69 [63–74]	65 [62–68]	65 [60–72]	66 [61–72]	70 [62–75]	62	–
J2-J2	162 [147–171]	160 [151–175]	156 [151–166]	155 [146–163]	162 [147–172]	165 [154–173]	141	–
J3-J3	139 [127–155]	139 [126–153]	142 [132–154]	134 [119–141]	158 [150–167]	149 [135–155]	121	–
J4-J4	130 [115–147]	131 [119–147]	125 [117–136]	124 [113–140]	129 [114–147]	137 [118–155]	127	–
J5-J5	56 [51–60]	57 [51–67]	57 [55–59]	56 [53–60]	56 [54–60]	59 [54–64]	53	–
J5L	39 [37–41]	39 [36–41]	36 [33–38]	38 [33–44]	39 [36–45]	39 [34–42]	42	49 [45–52]
Z5-Z5	93 [89–97]	92 [84–106]	93 [90–97]	93 [89–101]	96 [89–102]	96 [90–104]	90	–
Z5L	95 [90–106]	95 [86–100]	91 [81–96]	93 [89–98]	104 [101–108]	96 [91–99]	–	114 [107–121]

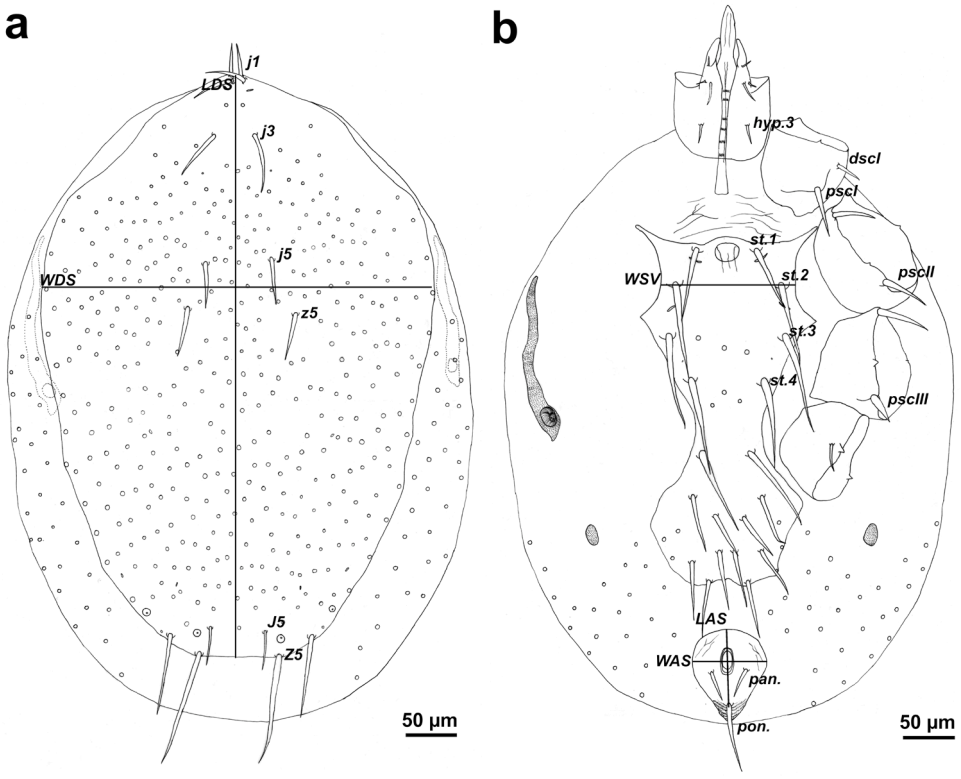

Fig. 3. Dorsal (a) and ventral view (b) of a male of *Laelaps mazzai* collected from *Calomys callosus* in REB. Shields and setae nomenclature used in morphometrics are indicated.

Table 3
Characters measurements (µm) of males of *Laelaps mazzai*. Results are presents as average followed by minimum and maximum values between brackets. Number of mites (n) measured are indicated for each rodent species. Measurements of *Laelaps mazzai* allotype and paratype were obtained from direct observation.

	Calomys callidus $n = 8$	*Calomys callosus* $n = 6$	*Calomys fecundus* $n = 8$	*Calomys laucha* $n = 6$	*Calomys venustus* $n = 4$	*Laelaps mazzai allotype*	*Laelaps mazzai paratype*
LDS	582 [561–613]	576 [557–613]	568 [557–575]	572 [553–599]	579 [572–586]	586	581
WDS	384 [368–404]	374 [347–404]	361 [347–380]	368 [358–381]	367 [365–368]	383	383
WSV	146 [141–156]	143 [136–156]	139 [136–140]	136 [129–140]	138 [135–140]	148	145
st.1-st.1	63 [59–73]	63 [59–73]	61 [59–63]	59 [56–62]	61 [60–61]	64	67
st.2-st.2	114 [111–124]	114 [108–124]	112 [108–114]	108 [105–112]	114 [112–116]	118	120
st.3-st.3	125 [121–135]	124 [118–135]	122 [118–124]	119 [115–126]	119 [115–122]	130	129
st.4-st.4	81 [79–88]	83 [80–86]	78 [75–81]	79 [73–87]	79 [74–85]	83	81
LS4	105 [96–111]	104 [96–111]	104 [102–104]	104 [100–110]	104 [103–104]	112	121
gen.-gen	50 [45–54]	50 [47–56]	52 [50–54]	48 [42–50]	48 [42–50]	73	73
gen.	88 [80–94]	86 [80–94]	85 [81–88]	87 [77–96]	88 [87–89]	62	62
Jv2-Jv2	39 [35–42]	39 [35–44]	40 [36–44]	42 [37–47]	40 [39–40]	39	36
Jv2	60 [49–67]	58 [49–67]	57 [53–60]	55 [48–59]	58 [57–58]	64	64
LAS	78 [72–81]	78 [72–81]	80 [78–81]	74 [68–77]	76 [75–76]	79	79
WAS	83 [79–93]	84 [79–93]	83 [79–85]	81 [76–83]	81 [80–81]	80	83
Lpan.	33 [31–38]	34 [31–38]	34 [31–36]	29 [27–32]	32 [31–32]	38	39
Lpon.	64 [61–72]	64 [61–72]	62 [61–63]	63 [61–63]	63 [62–63]	64	64
Lhyp.3	22 [21–25]	24 [22–26]	22 [20–26]	22 [19–24]	22 [19–24]	24	23
LpscI	46 [44–51]	47 [46–51]	44 [40–46]	46 [44–49]	46 [44–49]	52	55
LdscI	29 [27–31]	27 [22–31]	26 [22–30]	24 [21–27]	27 [26–27]	32	29
LpscII	52 [48–55]	50 [48–55]	49 [48–51]	47 [41–51]	49 [48–49]	49	54
LpscIII	30 [27–33]	28 [25–33]	27 [25–29]	27 [25–28]	28 [27–28]	31	33
lj1	32 [30–34]	30 [30–32]	30 [27–30]	28 [23–30]	30 [29–32]	38	32
j3-j3	43 [40–46]	43 [40–46]	43 [42–43]	44 [41–51]	43 [42–43]	47	41
z5-z5	106 [104–109]	105 [101–109]	105 [101–107]	106 [104–108]	106 [105–106]	104	107
j5-z5	53 [49–57]	53 [47–57]	54 [47–57]	54 [50–61]	53 [52–53]	35	37
J5-J5	55 [45–66]	54 [45–66]	54 [46–58]	51 [46–58]	53 [52–53]	52	60
J5L	42 [39–45]	41 [36–45]	40 [36–45]	39 [36–41]	40 [39–40]	45	45
Z5-Z5	83 [75–99]	84 [75–99]	83 [76–89]	74 [68–79]	79 [78–79]	81	86
Z5L	110 [103–115]	109 [103–115]	108 [107–109]	106 [94–111]	107 [106–107]	117	117

OL514172-OL514179, ON847359-ON847361; COI: OL514185-OL514194, ON847362-ON847364). An analysis of genetic distances (number of base substitutions per site) was performed in MEGAX to evaluate genetic divergence between species; genetic distances were transformed intoa percentage.

3. Results

3.1. Identification and characterization of Laelaps mazzai

Females and males of *L. mazzai* were obtained from all host species, except from *C. musculinus*, which was associated only with female mites. Males of *L. mazzai* were not obtained for localities OLM, CRA, and ELE (Table 1). For every host species, mites were obtained for more than one locality, except for *C. fecundus* and *C. musculinus* (Table 1). All mites presented consistent characteristics with original descriptions for both sexes of *L. mazzai* and coherence with the female lectotype, allotype, and paratype, as well as with mites from Venezuela reported by Furman (1972a) (see measurements in Table 2). *Laelaps mazzai* females herein studied were recognized by the following diagnostic characters: the remarkably hypertrichy in the dorsal shield (60–74 pairs of setae) with accessory setae clustered in medial podonotal region, coxa I with strong setiform proximal seta and stout setiform distal seta, coxa II with a strong setiform posterior seta, and coxa III with spiniform posterior seta. Males of *L. mazzai* were recognized because of a denser hypertrichy backwards from the level of the second pair of legs and the anal shield separated from the sternoventral shield.

Concerning the measurements, in average, our samples of female *L. mazzai* from *C. callidus, C. callosus, C. fecundus, C. laucha, C. musculinus* and *C. venustus* are shorter (length of the dorsal shield, LDS $\leq$ 659 μm) than in *L. mazzai* from *C. hummenlincki* from Venezuela ($\geq$725 μm). However, when maximum/minimum values are considered, measurements are very similar ($\geq$697 μm in *C. hummenlincki* vs $\leq$ 686 μm in the remaining species). In addition, LDS of the lectotype (592 μm) was shorter than in those herein studied with the exception of *C. fecundus* ($\geq$590 μm). Something similar took place with the width of the dorsal shields (WDS) in mites associated with different host species which overlapped (Table 2). Concerning males of *L. mazzai*, no differences were observed among mites associated with different host species, as well as with the allotype, with overlapping in most of the measurements (Table 3).

3.2. Linear morphometrics

Our results indicated overlapping in most of the measurements of diagnostic characters of females and males of *L. mazzai* associated with different host species (Table 4). However, a tendency to separate mites associated with every host species was observed mainly in the length and width of the dorsal shield in females. In the PCA for females of *L. mazzai*, the first three principal components account for 67% of the

Table 4
Eigenvectors of each measure in the components 1 to 3 of the principal component analysis (PCA) of females and males of *Laelaps mazzai* collected of *Calomys* species. Cummulative variances of each component are presented in percentage in the last row.

Acroym	Character	Females			Males		
		PC1	PC2	PC3	PC1	PC2	PC3
LDS	Length of dorsal shield	**0.623**	**−0.538**	0.225	**0.683**	0.262	**−0.585**
WDS	Maximum width of dorsal shield	**0.552**	0.281	0.034	**0.644**	**−0.596**	0.307
WSS	Width of sternal shield at sternal setae 2 level (only in females)	0.135	0.098	0.169	–	–	–
WSV	Width of sternoventral shield at sternal setae 2 level (only in males)	–	–	–	0.120	0.105	0.274
st.1-st.1	Distance between insertion of sternal setae 1	0.046	0.050	0.098	0.030	0.207	0.118
st.2-st.2	Distance between insertion of sternal setae 2	0.075	0.119	0.121	0.095	0.186	0.117
st.3-st.3	Distance between insertion of sternal setae 3	0.089	0.078	0.171	0.089	0.132	0.210
st.4-st.4	Distance between insertion of metasternal setae 4	0.072	**0.549**	0.330	0.031	−0.034	0.233
LS4	Length of metasternal setae 4	0.043	−0.026	0.138	0.081	−0.023	0.094
gen.-gen.	Distance between genital setae	0.131	−0.047	0.006	0.019	0.188	−0.011
gen.	Length of genital setae	0.073	0.034	0.019	0.044	0.107	0.103
LGSgen	Distance from the middle point between genital setae until the posterior margin of genital shield (only in females)	0.128	−0.013	−0.157	–	–	–
Jv2-Jv2	Distance between setae Jv2	0.049	0.064	−0.018	0.014	0.051	−0.107
LJv2	Length of setae Jv2	0.046	−0.108	0.016	0.073	0.217	0.213
LAS	Length of anal shield	0.126	−0.051	−0.009	0.048	0.137	0.030
WAS	Maximum width of anal shield	0.093	0.037	−0.046	0.085	0.331	−0.012
Lpan.	Length of paranal setae	0.066	0.043	0.084	0.003	0.023	0.165
Lpon.	Length of postanal seta	0.069	0.108	0.207	0.040	0.111	−0.074
Lhyp.3	Length of hypostomal setae 3	−0.007	0.039	0.085	−0.004	0.063	0.057
LpscI	Length of proximal setae of coxa I	0.057	−0.107	−0.020	0.016	0.004	0.080
LdscI	Length of distal setae of coxa I	0.049	−0.055	0.010	0.046	0.070	0.167
LpscII	Length of posterior setae of coxa II	0.051	−0.029	0.123	0.061	0.066	0.167
LpscIII	Length of posterior setae of coxa III	0.033	−0.003	0.059	0.038	0.007	0.120
lj1	Length of setae j1	0.066	−0.010	0.011	0.035	0.042	0.164
j3-j3	Distance between setae j3	0.065	0.055	−0.061	0.029	0.014	−0.010
z5-z5	Distance between setae z5	0.071	−0.004	−0.144	0.010	−0.003	−0.082
lz5	Length of setae z5	0.064	0.031	−0.125	–	–	–
j5-z5	Distance between setae j5 and z5	0.058	0.043	0.024	−0.010	−0.014	0.052
j6-j6	Distance between setae j6	0.096	0.127	0.171	–	–	–
lj6	Length of setae j6	0.045	−0.005	−0.133	–	–	–
J1-J1	Distance between setae J1	0.055	0.065	0.084	–	–	–
J2-J2	Distance between setae J2	0.175	0.158	−0.067	–	–	–
J3-J3	Distance between setae J3	0.236	−0.019	**−0.619**	–	–	–
J4-J4	Distance between setae J4	0.209	**0.412**	−0.382	–	–	–
J5-J5	Distance between setae J5	0.027	0.059	−0.059	0.082	0.286	0.190
J5L	Length of setae J5	0.044	−0.031	0.010	0.065	0.036	0.072
Z5-Z5	Distance between setae Z5	0.047	0.028	−0.027	0.124	0.345	0.263
Z5L	Length of setae Z5	0.099	−0.125	0.021	0.152	0.111	0.161
	Cumulative variance (%)	47	60	67	60	69	77

variance in the original 37 variables (Table 4). For the first component, almost all loadings were positive with a high magnitude of the size of dorsal shields (LDS and WDS). For the second component, the highest load was positive for the distance between st.4 setae (st.4-st.4), and negative loading for the size of the dorsal shield (LDS), and positive for the distance between J4 setae (J4-J4). For the third component, most of the loading were positive, although the high value was negative for distance between J3 setae (J3-J3) (Table 4). The first and second components separated female mites collected from *C. musculinus* (because of the length and width of the dorsal shield) from those associated with the remaining *Calomys* analyzed (Fig. 4a, 4b). However, measurements of the female mites from *C. callidus, C. callosus* and *C. venustus* overlapped, as well as those associated with *C. fecundus* and *C. laucha* (Fig. 4, Table 2).

In the PCA for males of *L. mazzai*, the first three principal components account for 77% of the variance in the original 29 variables, with most of the loadings positive (Table 4). Like in the females, for the first component, the high magnitude was for the length of dorsal shield (LDS) and maximum width of dorsal shield (WDS). For the second component, the high magnitude was for the WDS with a negative loading. For the third component, the high value was negative for the LDS (Table 4). The PCA and DA for males did not show clear differences in size among mites associated with different host rodents (Fig. 5a, 5b).

3.3. Phylogenetic analyses

Eleven sequences for ITS regions and 13 sequences for the COI gene of the *L. mazzai* from all *Calomys* species, except from mites of *C. musculinus*, were obtained. Phylogenetic analyses retrieved a monophyletic *L. mazzai* group (Figs. 6, 7) with low genetic differentiation across different species of hosts (Table 5). For ITS regions and COI gene, the clade of *L. mazzai* was related to *L. schatzi* associated with the sigmodontine *Oligoryzomys flavescens* (Waterhouse, 1837) (Cricetidae) from Argentina. Another clade corresponded to *L. muricola* associated with *Micaelamys namaquensis* (Smith, 1834) (Muridae) and *L. giganteus* from *Lemniscomys rosalia* (Thomas, 1904) (Muridae), both from South Africa. For COI gene, *L. giganteus* and *L. muricola* were associated with *L. agilis* from the rodent *Apodemus sylvaticus* (Linnaeus, 1758) (Muridae) from the Czech Republic. The genetic distance of *L. mazzai* and other species of *Laelaps* was 8–13% for ITS regions. Differences were higher for COI (15–20%) (Table 5). Meanwhile, genetic distances between *L. mazzai* from different host populations ranged between 0 and 0.2% for ITS regions and were slightly higher for the COI gene (2–4%) (Table 5).

4. Discussion

All studied mites were morphologically similar and consistent with the original description and type specimens of *L. mazzai* and differed from close species, as follows. Females of *L. mazzai* were distinguished from the other hypertrichous *Laelaps* species by the number and location of accessory setae in the dorsal shield and shape of coxal setae. *Laelaps valdevinoi* Gettinger, 1992 has a similar number of dorsal setae (61 consistent pairs) as *L. mazzai*, but 3–5 unpaired accessory setae were located on medial opistonotum (versus in *L. mazzai* that are situated in the podonotum). *Laelaps navasi* Fonseca, 1939 differs from *L. mazzai* because of its dorsal shield with 85–100 pairs of setae, and coxa I with proximal and distal setae spiniform (in *L. mazzai* both setae are strong setiform). In addition, *Laelaps surcomata* Furman, 1972, was easily distinguished from *L. mazzai* because of its dorsal shield with 46–49 pair of setae with one pair of accessory setae between j3 and j4, several extra setae in the posterior central area of dorsal shield, and all coxal setae setiform (in *L. mazzai* posterior seta of coxa III is spiniform) (Fonseca, 1939; Furman, 1972b; Gettinger, 1992a). The males of *L. mazzai* also differed from males of *L. valdevinoi*, by the anal shield not fused in a holoventral shield (Fonseca, 1939), while males of *L. surcomata* and *L. navasi* are unknown.

The length and width of the dorsal shield of the females of *L. mazzai* herein studied were the only characteristics that showed a tendency to morphologically separate mites concerning the species of their hosts, with some overlapping. On the contrary, males of *L. mazzai* did not show differences in any measures. Thus, our results support that *L. mazzai* is a unique species with a wide range of variation in some of its measures in females. We interpret the tendency to different sizes of *L. mazzai* females among host species as phenotypic plasticity, which is the capacity of a determinate genotype to produce several phenotypes due to the exposition to different environments (Miner et al., 2005). In "free-living" species, the phenotype could be determined mainly by abiotic variables (e.g., geographic position). However, in parasites, the biotic environment, represented by the host, could play an indispensable role in the expression of a phenotype, and the abiotic environment where the host lives (Morand et al., 2006).

The morphological type of plasticity is a common way of expressing the phenotype, and it is easy to measure in organisms with hard cuticles, such as arthropods. In the case of *L. mazzai*, the rodent hosts characteristics (e.g., hair density, physiological traits) could be an essential biotic environment that directly influences the sizes of mites (Morand et al., 2006). In contrast, males of *L. mazzai* lack morphometric differences related to the host species. As in most of the parasitic laelapids, males are less abundant than females on the host (herein 17% of the total mites), because they spend more time in host burrows (Strandtmann and Wharton, 1958; Radovsky, 1994), where usually microenvironments are more stable than the external environment. Thus, this lack of selective pressure on male mites may be reflected in a lack of morphological variation. In contrast, females, which are more associated with the host

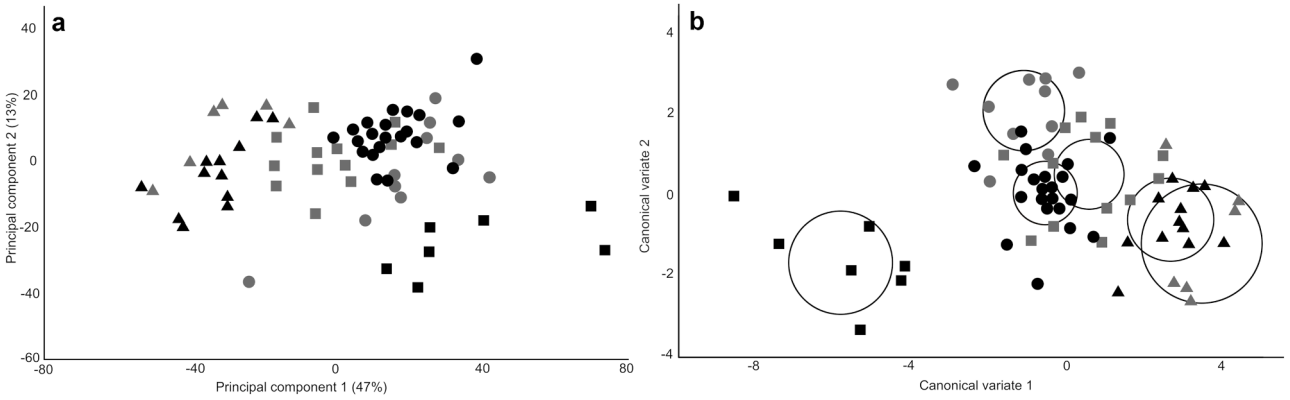

Fig. 4. Plots illustrating the first two principal component scores from PCA (a) and discriminant analysis (b) of *Laelaps mazzai* females collected from *Calomys fecundus* (gray triangle), *Calomys callidus* (gray dot), *Calomys callosus* (gray square), *Calomys laucha* (black triangle), *Calomys musculinus* (black square), *Calomys venustus* (black dot). Ellipses show the 95% confidence region to contain true mean of group.

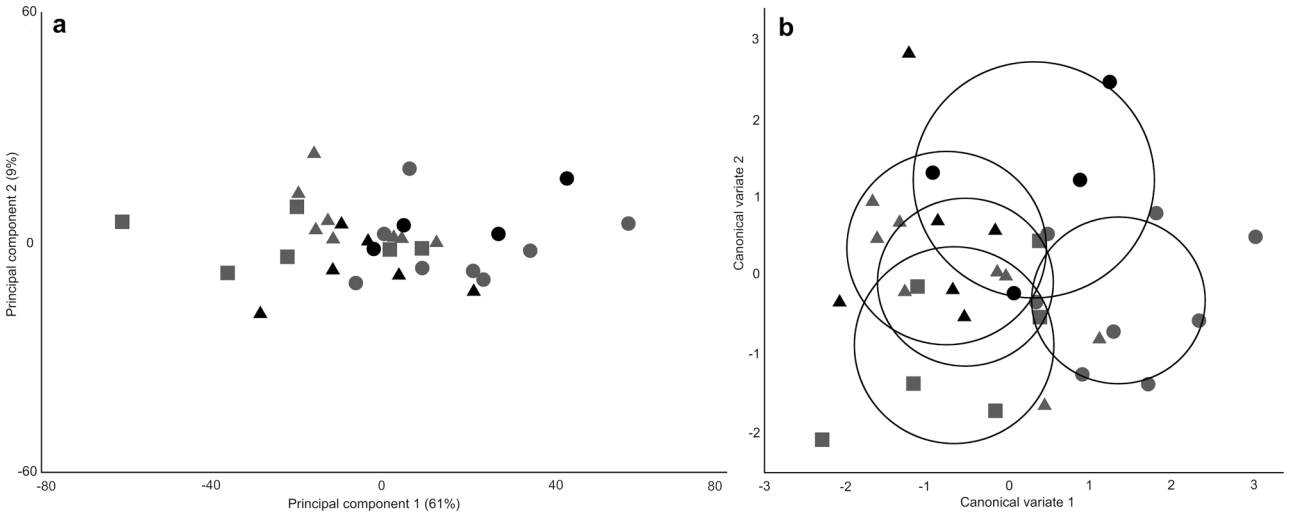

Fig. 5. Plots illustrating the first two principal component scores from PCA (a) and discriminant analysis (b) of *Laelaps mazzai* males collected from *Calomys fecundus* (gray triangle), *Calomys callidus* (gray dot), *Calomys callosus* (gray square), *Calomys laucha* (black triangle), *Calomys venustus* (black dot). Ellipses show the 95% confidence region to contain true mean of group.

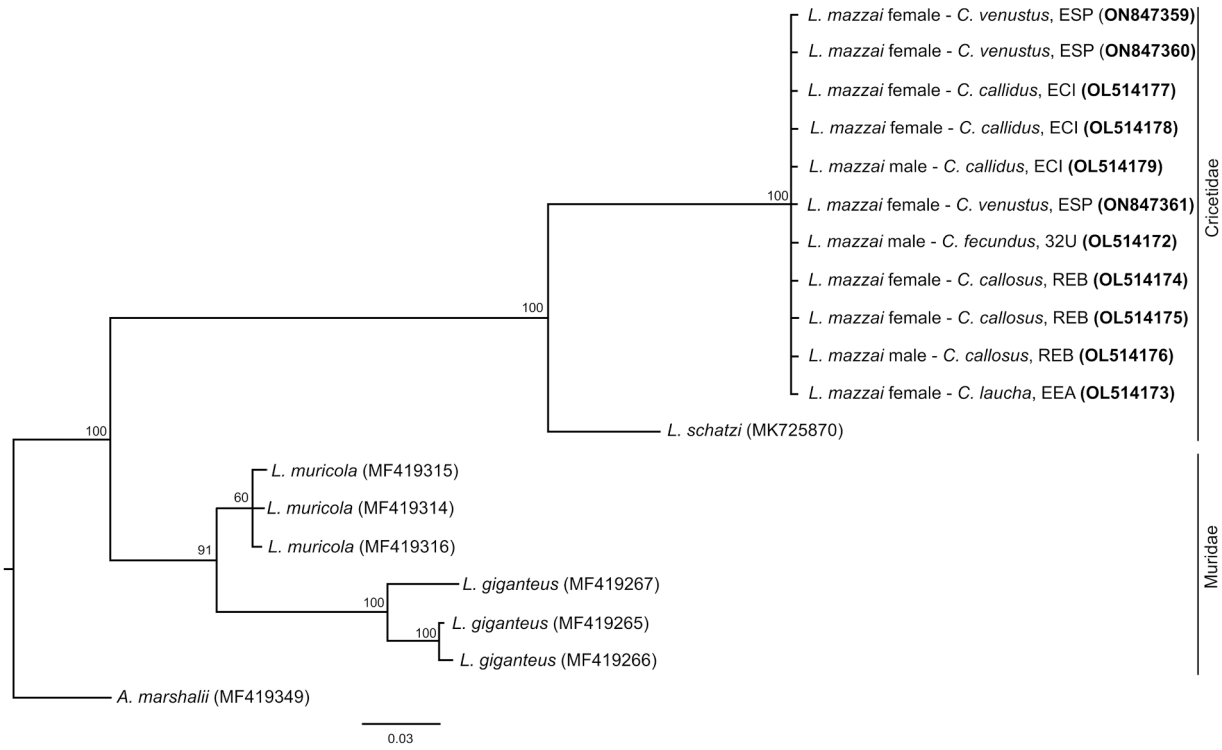

Fig. 6. Phylogenetic tree based on ITS region of *Laelaps mazzai*. Numbers on nodes shows Bayesian probabilities in percentage. Labels indicate mite species, sex of the mite, host, locality and GenBank access number in parenthesis. Families of rodents are showed on the right side. Sequences obtained in this study are indicated in bold.

body, reflect more variation in their size.

Furthermore, our results contrast with other studies where morphometric and molecular tools resolved cryptic species, each specific to a different host species, from a previous generalist laelapids species. For example, *Androlaelaps rotundus* (Fonseca, 1935) was originally described as a generalist species, and posteriorly several species were identified and described as new species-specific of their respective hosts (e.g., Lareschi, 2011, 2020; Lareschi and Galliari, 2014). Something similar occurs within *Laelaps* species. *Laelaps fonsecai* Gettinger, 1992 and *L. schatzi* were separated from the previous generalist species *L. paulistanensis* (Gettinger, 1992a, 1992b; Savchenko and Lareschi, 2019). In our study, *L. mazzai* did not show enough evidence to identify different species.

Considering differences among *Calomys* species, two groups were proposed: a larger-bodied species group (including *C. callidus, C. callosus*, and *C. venustus*, among others), and a smaller-bodied species group (including *C. laucha* and *C. tener*) (Bonvicino et al., 2010). These groups could explain the similarity of median-sized *L. mazzai* from *C. callidus, C. callosus*, and *C. venustus*, and the tendency to separate smaller-sized *L. mazzai* from *C. laucha* and *C. fecundus*. However, these differences

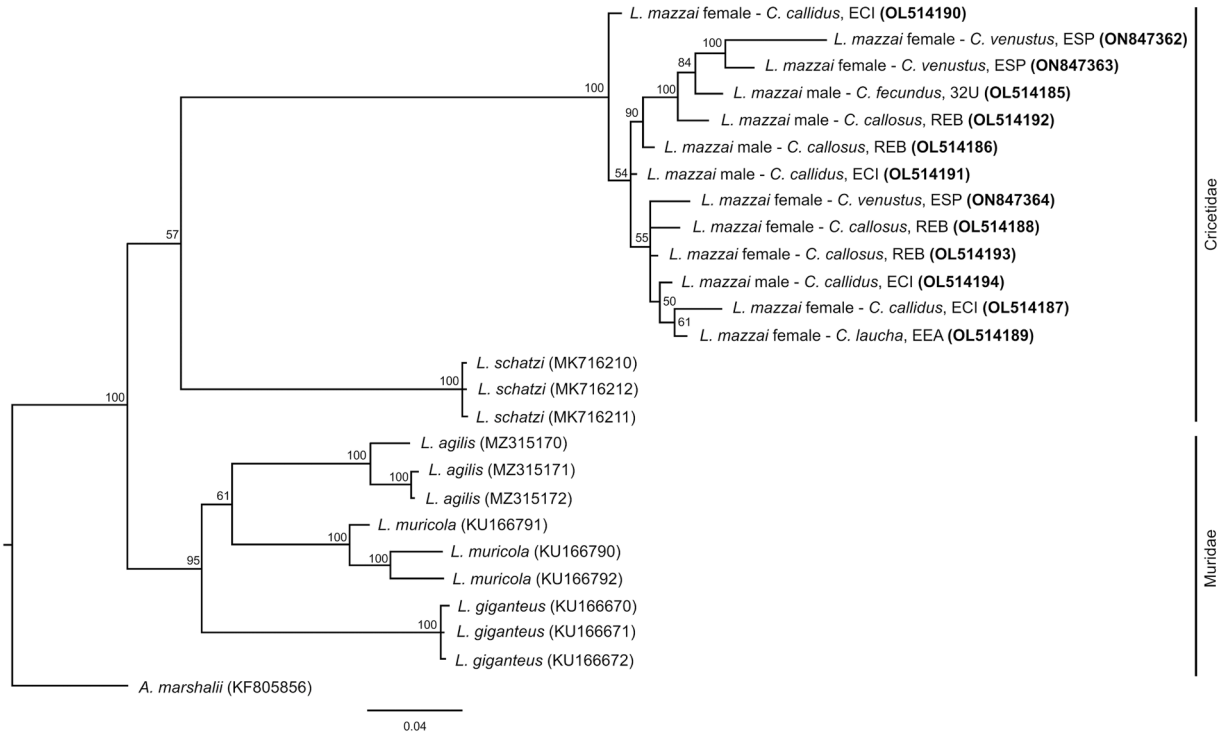

Fig. 7. Phylogenetic tree based on COI gene of *Laelaps mazzai*. Numbers on nodes shows Bayesian probabilities in percentage. Labels indicate mite species, sex of the mite, host, locality and GenBank access number in parenthesis. Families of rodents are showed on the right side. Sequences obtained in this study are indicated in bold.

Table 5
Genetic distances in percentage between different *Laelaps* species and L. *mazzai* from different *Calomys* species. Genetic distances for ITS region are showed above the diagonal and for COI gene, under diagonal.

	Mite species (rodent species; locality)	1	2	3	4	5	6	7	8	9
1	*L. mazzai* (*C. callidus*; ECI)		0.2	0.2	0.2	0.2	–	13	13	8
2	*L. mazzai* (*C. callosus*; REB)	2		0	0	0	–	13	13	8
3	*L. mazzai* (*C. fecundus*; 32 U)	3	3		0	0	–	13	13	8
4	*L. mazzai* (*C. laucha*; EEA)	2	2	3		0	–	13	13	8
5	*L. mazzai* (*C. venustus*; ESP)	4	4	4	4		–	13	13	8
6	*L. agilis*	17	18	19	17	19		–	–	–
7	*L. giganteus*	17	18	19	17	19	13		7	15
8	*L. muricola*	17	18	19	17	20	11	13		15
9	*L. schatzi*	19	20	18	20	15	15	15	15	

were only in the size of dorsal shields in female mites. We did not find morphological or genetic evidence to postulate that *L. mazzai* may be a complex of cryptic species. More samples of other *Calomys* species are needed (e.g., *C. hummelincki*), and probably other genetic markers to analyze a complete phylogenetic history of *L. mazzai*.

The phylogenetic analyses did not show differences among mites associated with the different host species. Phylogenetic trees of ITS region and COI gene show that obtained sequences of *L. mazzai* form a monophyletic group, separated from a clade that includes *L. muricola, L. giganteus*, and *L. agilis*. A phylogenetic analysis resolved different clades of *Laelaps* species from American rodents (Sigmodontinae) and Old-world rodents (Murinae) in agreement with Dowling and Oconnor (2010). In our study, genetic distances for COI were higher than ITS region, as shown in other studies on mesostigmatid mites, because of the higher rate of mitochondrial mutations against nuclear DNA fragments (De Rojas et al., 2007; Navajas et al., 1999). For example, in the genus *Dermanyssus* Dugès, 1834 (Mesostigmata: Dermanyssidae), COI provided 9–18% of divergence between species (up to 9% within species), and for ITS1 and ITS2 2–9% between species (up to 1% within species) (Roy et al., 2010). Our results indicate that *L. mazzai* had lower genetic distances for ITS and COI suggesting that it is only one species, and exclusively the females tend to present different sizes related to the host species.

In addition, in the original description of *L. mazzai* the host species was not indicated, only referring to the host as a "wild rat from Salta Province, Argentina". Interestingly, those female mites from *C. fecundus* that were collected in Salta Province were very similar in size to the lectotype. Thus, we postulate that the original host in which *L. mazzai* was described could be *C. fecundus*. Besides, *C. fecundus* and *C. callidus* are new hosts for *L. mazzai*, and *C. callosus* is reported for the first time in Argentina. We extend the known distribution of *L. mazzai* 1500 km to the south, to the province of Chubut (CRA), being the most austral record of this mite.

Author statement

MEC conducted field work, collected the material, identified the mites, designed and wrote the manuscript and discussed the results; CG, conducted field work, collected the material, identified the rodents, designed and wrote the manuscript and discussed the results; MCF conducted field work, collected the material, designed and wrote the manuscript and discussed the results; PMB designed and wrote the

manuscript and discussed the results; ML responsible for the obtaining of funds, conducted field work, collected the material, identified the mites, designed and wrote the manuscript and discussed the results.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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