Changes related to gender, geographic population and habitat in the antennal phenotype of *Triatoma patagonica* Del Ponte, 1929 (Hemiptera: Reduviidae)

Claudia S. Rodríguez[a,*], Liliana Crocco[a], Alejandra Altamirano[a], Silvia Catalá[b]

[a] Cátedra de Introducción a la Biología, Instituto de Investigaciones Biológicas y Tecnológicas (IIByT/CONICET), Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Avda. Vélez Sarsfield 299, piso 5. X5000JJC Córdoba, Argentina
[b] Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja (CRILAR/CONICET), Anillaco, 5301 La Rioja, Argentina

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ABSTRACT

Triatomines undergo morphological changes as an adaptive response to different habitats (wild, peridomestic, domestic, laboratory). The characterization of the antennal phenotype provides information on intraspecific variation caused by geographical origin and/or habitat. *Triatoma patagonica* Del Ponte, 1929 is known to occur in peridomiciles of rural areas in Argentina, where it also invades non-colonized dwellings. Here we describe and compare the antennal phenotype of *T. patagonica* in populations of different geographic origin, and explore possible modifications induced by laboratory rearing with the aim of investigating the range of phenotypic variation of the species for the first time. Sixty antennas of adult males and females of *T. patagonica* belonging to two peridomiciliary populations of different geographical origin were analyzed. Four types of *sensilla* were observed in three antennal segments, showing sexual dimorphism in the species. The multivariate analysis separated the populations of similar habitat (peridomicile) but different geographical origin, without showing differences between the peridomiciliary and laboratory populations of the same geographical origin. These results suggest phenotypic plasticity in *T. patagonica*, which would allow the species to adapt to a wide range of habitats without having a close association with a given host and its environment. The range of antennal phenotypic variation of *T. patagonica* would also be an indicator of its current stage of adaptation to the human environment.

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1. Introduction

Triatominae (Hemiptera: Reduviidae) are blood-sucking insects, vectors of *Trypanosoma cruzi* (Chagas, 1909) (etiological agent of Chagas disease). They are widely distributed in Latin America from 46° N (northeastern USA) to 46° S (Argentine Patagonia) (Carcavallo et al., 1999; Schofield and Galvão, 2009). These insects occur in a vast diversity of habitats; although they are of wild origin, with a large number of species inhabiting silvatic habitats, some species have developed a close relationship with humans, occupying the domicile and the peridomicile (Zeledón, 1976; Schofield, 1988; Schofield et al., 1999).

In Argentina, 18 species belonging to three genera of Triatominae are present, showing a wide geographic distribution and different epidemiological importance that varies with the habitats where they occur (Galvão et al., 2003). Of those species, *Triatoma infestans* (Klug, 1934) is the only domiciliated triatomine of epidemiological importance. Other species, such as *Triatoma*

guasayana Wygodzinsky & Abalos, 1949, *Triatoma sordida* (Stål, 1859), *Triatoma eratyrusiformis* Del Ponte, 1929, *Triatoma patagonica* Del Ponte, 1929, and *Triatoma garciabesi* Carcavallo, Cichero, Martínez, Prosen & Ronderos, 1967, are considered secondary vectors because, while they maintain their wild condition, they show synanthropic trends, colonizing the peridomiciles and frequently invading the household where they sometimes establish colonies (Canale, 2005).

T. patagonica is the triatomine present in wild and peridomestic habitats of southernmost distribution; it has been reported only for central, western and southern provinces of Argentina, of which the Patagonian province of Chubut represents its southernmost distribution limit (Virla de Argüello, 1984; Galvão et al., 2003). This species does not show feeding preference; it is mainly associated with rodents in the wild and establishes important colonies in peridomestic ecotopes, such as chicken and pigeon coops, goat and pig corrals, and resting places of cats and dogs (Virla de Argüello, 1984; Carcavallo and Martínez, 1985; Wisnivesky-Colli et al., 2003). In addition, although records of intradomicile colonization are scarce, Ferrero et al. (1999) and Giraldez et al. (2009) reported *T. patagonica* as the only species found colonizing both rural peridomestic and intradomestic environments in the

Table 1
Code, geographical localization and number of specimens of *Triatoma patagonica* analyzed in this study.

Code	Province (department)	Locality	Specimens		Habitat	Coordinates Long./Lat.
			F	M		
PSL	San Luis (Junín)	Santa Rosa de Conlara	12	12	Peridomestic (chicken coops)	65°21′W/32°15′S
PSF	Santa Fe (9 de julio)	San Bernardo	7	7	Peridomestic (chicken coops)	61°32′W/28°39′S
LSF	Santa Fe (9 de Julio)	Montefiore	11	11	Laboratory	61°52′W/29°40′S

F: females; M: males; Long./Lat.: longitude and latitude.

departments of Pichimahuida (province of Río Negro) and San Cristóbal (province of Santa Fe).

Susceptibility of *T. patagonica* to infection with *T. cruzi* has been demonstrated experimentally in the laboratory (Mazza, 1937) and in the field (Abalos and Wygodzinsky, 1951). However, Wisnivesky-Colli et al. (2003) examined for *T. cruzi* 67 bugs of this species collected in peridomicilies of Chubut province, and none of them was infected. In addition, females and fifth-instar nymphs of *T. patagonica* would be efficient vectors of the protozoan, because they defecate during or immediately after feeding (Nattero et al., 2002; Rodríguez et al., 2008).

Because of its habits, *T. patagonica* may become increasingly important as secondary vector of *T. cruzi* in Argentina; indeed, *T. patagonica* would be in process of adaptation to the human environment and would replace *T. infestans* in those areas where the latter has been eliminated. Knowing aspects of the biology, evolution and genetics of these species of peridomestic habits is important both to evaluate vector efficiency of *T. cruzi* and to contribute with important data for the success of triatomine surveillance and control strategies in the human environment (Arévalo et al., 2007).

Dujardin et al. (2000, 2009) indicated that genetic and environmental characteristics can modulate the morphology of triatomines. These bugs can undergo rapid morphological changes as an adaptive response to the different geographical regions and habitats they occupy (wild, peridomestic, domestic). The antennal phenotype has been used to identify genera, species and sex of triatomines and is currently employed as an indicator of intraspecific variation caused by geographical origin and habitat (Catalá and Dujardin, 2001; Catalá et al., 2005; Esteban et al., 2005; Villela et al., 2005). Accordingly, Hernández et al. (2008, 2010) and Abrahan et al. (2008) demonstrated a strong association between macroconditions and micro-environments, chromosomal cytotypes and antennal phenotype of *T. infestans*.

Gorla et al. (1993) first analyzed the antennal phenotype of *T. patagonica* based on the density of *sensilla* present in the pedicel of two individuals. As a first step in the study of the range of phenotypic variation of this species, the present work analyzed and compared the antennal phenotype of *T. patagonica* in two populations of different geographical origin and explored possible modifications related to laboratory rearing.

2. Materials and methods

2.1. Insects

The antenna of 60 adults of *T. patagonica* of both sexes was analyzed. Included were specimens from two peridomestic populations of different geographical origin in Argentina (collected of San Luis and Santa Fe provinces in 2006 and 2010 respectively), as well as laboratory specimens reared for seven generations in the Laboratory of Coordinación Nacional de Control de Vectores, Córdoba, Argentina. The population of laboratory had been established with insects collected from chicken coops of the locality of Monte Fiori, of 9 de Julio Department, province of Santa Fe (Table 1).

The colony reared in the laboratory was kept in glass bottles (100 cm^3), containing 25 adults (males and females) per bottle,

under varying environmental conditions. When there had been no demand for these insects, they were maintained at ambient temperature (12–24 °C) and offered a blood meal at monthly intervals. However, on occasions when it was necessary to increase the size of the colony, the temperature was increased to 27 °C and blood meal was offered at intervals of 10–15 days.

All the insects were conserved in 70% alcohol until processed in the laboratory.

2.2. Analysis of the antennal phenotype

The antennas of each insect were cut from the head at the level of the scape (basal or first segment), processed with 4% NaOH and neutralized with 5% glacial acetic acid. This procedure allowed cuticle diaphanization and further identification and counting of *sensilla* using a light microscope (Olympus BX 40, 40X) connected to a camera lucida (Olympus U-DA). The antennae were preserved in individual Eppendorf tubes containing 87% glycerin until analysis. For analysis, they were mounted *in toto* using glycerin.

One antenna of each individual was examined. The ventral side (Catalá, 1997) of the three distal segments of the antennae: Pedicel (P), Flagellar segment 1 (F1) and Flagellar segment 2 (F2) were drawn; four types of *sensilla* were identified and counted, following Catalá and Schofield (1994): bristles (BR), thin-walled trichoids (TH), thick-walled trichoids (TK) and basiconica (BA). These *sensilla* have shown geographical and habitat variations among other Triatominae species (Catalá and Dujardin, 2001; Catalá et al., 2004, 2005).

2.3. Data analysis

Mean and deviation values were obtained for each *sensillum* type in each antenna segment. Differences in antennal phenotype between males and females and among groups were explored with univariate and multivariate analyses. The Levene test was used to determine homogeneity of variances of the variables analyzed. Comparisons between sexes and groups were made using ANOVA or Student's *t*-test for those variables with homogeneous variances. The variables showing variance heterogeneity were analyzed using the Mann–Whitney *U* non-parametric test. Differences were considered significant at $p < 0.05$.

A principal component analysis (PCA) was performed with the 12 variables evaluated using Statistica 7 software (StatSoft Inc., 2007). The variables were grouped into four principal components obtained from a covariance matrix. These four new variables were used to perform a discriminant analysis (DA) using PADwin version 98 to obtain multivariate functions that identify the groups studied. PADwin software was developed by J.P. Dujardin (http://www.mpl.ird.fr/morphometrics) and is used to make discriminant analysis and calculate statistical significance (Wilks values and distances of values of Mahalanobis) of differences between groups using non parametric tests: permutation test and cross classification tests. The number of permutations used was 1000.

The univariate and multivariate analysis to compare the antennal phenotype between *T. patagonica* populations of different

Table 2
Mean number and standard deviation of antennal *sensilla* found by segment in females and males of *Triatoma patagonica* (*n* = 60). Student's *t*-test or Mann–Whitney *U* test were conducted to compare, for the different variables, between sex.

Antennal segment	Antennal *sensilla*	Females $n = 30x \pm$ SD	Males $n = 30x \pm$ SD	t[a] or U[b] value test	*p* Value
Pedicel	BR	65.06 ± 10.37	61.77 ± 1423	−1.03[a]	0.308
	TPF	86.60 ± 2656	120.77 ± 27.43	167.50[b]	**<0.001**
	TPG	23.33 ± 19.16	13.43 ± 9.44	301.50[b]	**0.028**
	BA	1.46 ± 2.88	0.57 ± 0.90	−1.63[a]	0.108
	Totals	176.47 ± 44.79	196.53 ± 33.38	1.96[a]	0.053
Flagellum 1	BR	10.96 ± 4.03	10.27 ± 3.19	−0.744[a]	0.459
	TPF	30.96 ± 13.18	39.87 ± 14.75	243.00[b]	**0.002**
	TPG	145.90 ± 52.49	118.03 ± 39.01	303.50[b]	**0.030**
	BA	5.40 ± 4.45	5.17 ± 3.13	0,23[a]	0.632
	Totals	193.23 ± 61.56	173.33 ± 54.05	−1.33[a]	0.188
Flagellum 2	BR	7.10 ± 3.03	6.83 ± 3.30	−0.32[a]	0.745
	TPF	14.03 ± 6.65	19.60 ± 11.50	315.50[b]	**0.046**
	TPG	81.10 ± 22.95	75.07 ± 24.12	−0.99[a]	0.325
	BA	6.23 ± 4.53	6.53 ± 4.34	0.26[a]	0.794
	Totals	108.47 ± 30.12	108.03 ± 35.59	−0.05[a]	0.960

a: Student's *t*-test; b: Mann–Whitney *U* test; *n*: number of specimens; *x*: average; SD: standard deviation; BR: bristles; TPF: thin walled trichoid; TPG: thick walled trichoid; BA: basiconica; bold values: differences significant.

geographical origin and similar habitat (*PSL* and *PSF*) and between populations of similar geographical origin and different habitat (*PSF* and *LSF*) were carried out separately for each sex due to the sexual dimorphism demonstrated above.

3. Results

3.1. General characteristics of the antenna of T. patagonica sexual dimorphism

The adults of *T. patagonica* (*n* = 60) analyzed presented the four types of *sensilla* (BR, TH, TK and BA) distributed over the Pedicel (P) and the two flagellar segments (F1 and F2). The mean number of *sensilla* in each segment for males and females, as well as the mean number of BR, TH, TK and BA per segment, are shown in Table 2. The univariate analysis (Student's *t*-test or Mann–Whitney test) showed significant differences between sexes. Males exhibited a higher number of TH on P, F1 and F2 than females, whereas, females had a higher number of TK on P and F1.

3.2. Changes on antennal sensilla number related to the geographic origin

Females from the *PSL* population had a lower number of BR on P and F1 (*F* = 4.67; *p* = 0.045, and *U* = 16.00; *p* = 0.06, respectively) and a lower number of TH and BA on both flagellar segments (*F* = 5.69; *p* = 0.028 and *F* = 6.77; *p* = 0.018 for TH and BA on F1; and *F* = 21.09; *p* < 0.001 and *F* = 8.19; *p* = 0.010 for TH and BA on F2) than *PSF* females (Fig. 1A). In turn, males from the *PSL* population exhibited a lower number of BR (*F* = 33.22; *p* < 0.001) and a higher number of BA (*U* = 18.00; *p* = 0.04) on P than males from the *PSF* population. All the other receptors analyzed exhibited a lower number on F2 in *PSL* males (*U* = 10.00; *p* = 0.006 for BR; *F* = 6.45; *p* = 0.021 for TH; *F* = 12.45; *p* = 0.002 for TK; and *F* = 19.17; *p* < 0.001 for BA) than in *PSF* males (Fig. 1B).

3.3. Changes on sensilla number related to habitat: peridomicile and laboratory

Females from the peridomestic population (*PSF*) showed a higher number of BR on P (*F* = 4.91; *p* = 0.041) and of BA on F1 (*F* = 10.16; *p* = 0.005) than females reared in the laboratory (*LSF*). Males from the peridomestic population (*PSF*) had a higher number of BR on P (*F* = 14.16; *p* = 0.001) and of TK on F1 (*F* = 6.06; *p* = 0.025) and F2 (*FU* = 14.00; *p* = 0.002) than *LSF* males.

3.4. Multivariate analysis of the antennal phenotype: changes related to the geographical origin and habitat

The multivariate analysis was performed for males and females separately, grouped by geographical origin and habitat: *PSL*, *PSF* and *LSF*. The two first canonical functions generated by the discriminant analysis were highly significant for both sexes (*F* = 3.049; *p* < 0.007 and *F* = 4.069; *p* < 0.0009, respectively). The first discriminant function separated individuals by geographical origin explained 87% of the total variation in females and 82% in males, whereas the second function explained 13% in females and 18% in males (Fig. 2A and B). Mahalanobis distances, calculated during the analysis showed that *PSL* individuals of both sexes were significantly different from *PSF* specimens, with no differences between individuals of similar origin but different habitat (*PSF* and *LSF*) (Table 3).

4. Discussion

The epidemiological risk for *T. cruzi* transmission increases with the possible incorporation of peridomestic triatomines to *T. cruzi* domestic cycle (Bos, 1988; Bar and Wisnivesky-Colli, 2001). Studying the changes involved during adaptation might help to understand the basic processes of intradomestic colonization by some triatomine species (Dujardin et al., 2000). *T. patagonica* colonizes peridomiciles of a wide geographical region in Argentina (Lent and Wigodzinsky, 1979; Virla de Argüello, 1984; Carcavallo and Martínez, 1985; Wisnivesky-Colli et al., 2003); a few records of intradomiciliary colonization have been provided (Ferrero et al., 1999; Giraldez et al., 2009). Hence, studying the range of antennal

Table 3
Mahalanobis distances and their significance (*P*) after Bonferroni correction, obtained from discriminant analysis of sensilla patterns of females and males of *Triatoma patagonica* of three populations of different geographical origin and habitat. Bonferroni test *p* < 0.0033. (a) Comparison between groups of different geographical origin. (b) Comparison between groups of different habitat (peridomestic and laboratory).

Population	Distance	*p* Value
(a) ♂-*PSL*/♂-*PSF*	2.62	**0.002**
♀-*PSL*/♀-*PSF*	2.32	**0.002**
(b) ♂-*PSF*/♂-*LSF*	1.55	0.094
♀-*PSF*/♀-*LSF*	1.22	0.25

♀: females; ♂: males; *PSL*: San Luis peridomestic population; *PSF*: Santa Fe peridomestic population; *LSF*: Santa Fe laboratory population; bold values: differences significant.
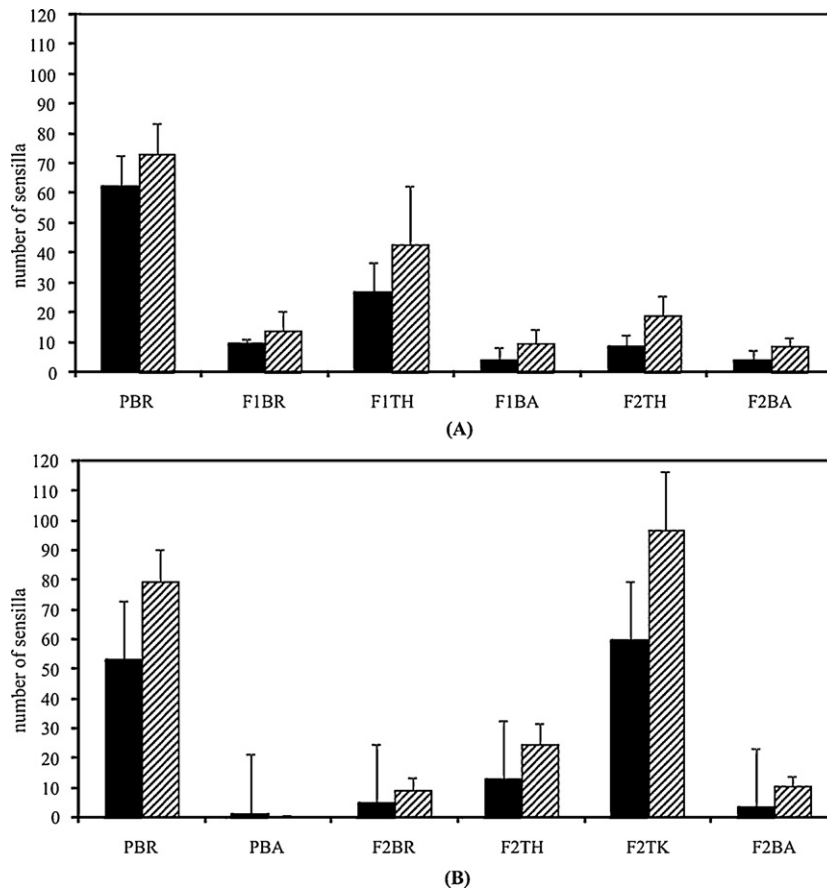
Fig. 1. Mean number of *sensilla* on *Triatoma patagonica* peridomestic populations of different geographical origin: San Luis (*PSL*) black solid bars and Santa Fe (*PSF*) cross bars. (A) Females and (B) males. PBR and PBA: bristles and basiconics of pedicel; F1BR, F1TH and F1BA: bristles, thin walled trichoids and basiconics of first flagellar segment; F2BR, F2TH, F2TK and F2BA: bristles, thin walled trichoids, thick walled trichoids and basicons of second flagellar segment.

phenotypic variation in *T. patagonica* and the possible modifications induced by laboratory rearing might provide some evidence of the current stage of *T. patagonica* adaptation to the human environment.

Antennal phenotype of insects reflects ancestral patterns modified by specific adaptations related to exploitation of different hosts and habitats (McIver, 1987). Comparative studies of the antennal phenotype of triatomines have revealed a clear taxonomic
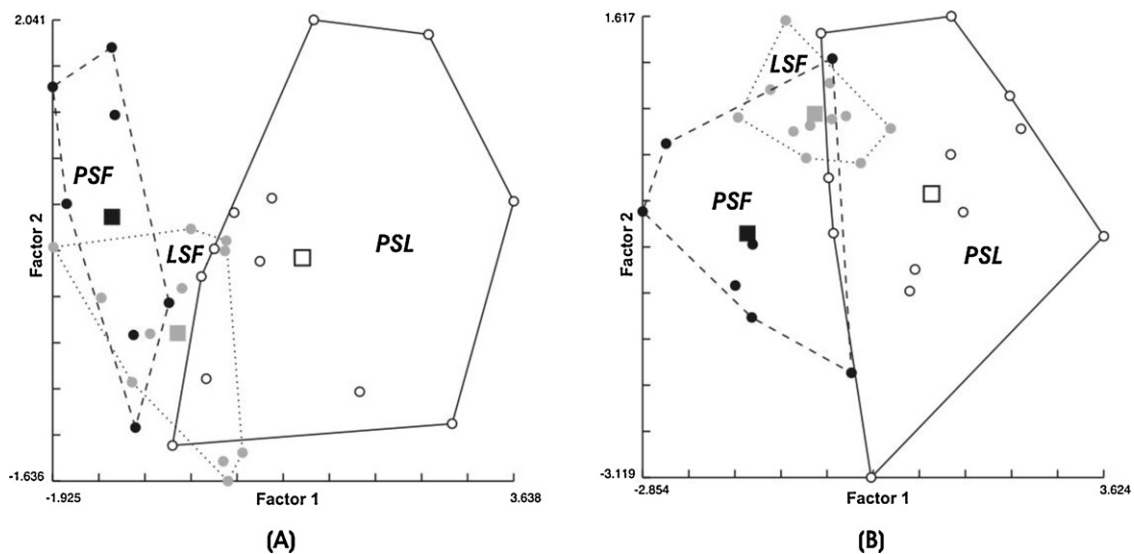

Fig. 2. Discriminant analysis from females (A) and males (B) of *Triatoma patagonica* of three populations of different geographical origin and habitat. *PSL*: San Luis peridomestic population; *PSF*: Santa Fe peridomestic population; *LSF*: Santa Fe laboratory population. Distances are significant between *PSL* and *PDF* for females and males.

difference as well as a correlation with the habitat range they occupy and their dispersal capacity (Catalá, 1997; Catalá and Dujardin, 2001; Abrahan et al., 2008; Carbajal de la Fuente et al., 2008; Hernández et al., 2008). The presence of the three most abundant types of chemoreceptors (TH, TK and BA) on the pedicel of *T. patagonica* adults would indicate the adaptation of this species to complex habitats such as peridomestic and wild habitats, which require greater sensory abilities than the domicile. Although all the species of the tribe Triatomini present the three types of *sensillum* on both flagellar segments (F1 and F2), TK and BA may not be present on P (Catalá, 1997). These variations would be related to the habitat range frequently used by the insect. Indeed, species like *T. guasayana*, *T. sordida*, *Triatoma pseudomaculata* Corrêa & Espínola, 1964 (Gorla et al., 1993; Catalá, 1997; Carbajal de la Fuente and Catalá, 2002), *Triatoma dimidiata* (Laterielle, 1811) (Arroyo et al., 2007), and *Triatoma maculata* (Erichson, 1848) (Carbajal de la Fuente et al., 2008), which usually occupy several types of habitats without being closely associated with a given host and its environment, have TH, TK and BA on P (Gracco and Catalá, 2000; Carbajal de la Fuente and Catalá, 2002); by contrast, species that exhibit only TH on P are adapted to more stable environments, associated with one habitat type, such as *T. infestans*, *Triatoma platensis* Neiva, 1913 and *Mepraia* sp. Mazza, Gajardo & Jörg, 1940 (Catalá, 1997; Carbajal de la Fuente and Catalá, 2002; Moreno et al., 2005).

Sexual dimorphism at the level of the antennal phenotype has been reported for several *Triatomini* species (Catalá and Dujardin, 2001; Carbajal de la Fuente and Catalá, 2002; Catalá et al., 2005; Moreno et al., 2005; Arroyo et al., 2007; Carbajal de la Fuente et al., 2008; Rodríguez Rodríguez et al., 2009). The principal sexual variations are related to the number and distribution of chemoreceptors involved in the reception of stimuli and associated with sexual behavior and active dispersal (Carbajal de la Fuente and Catalá, 2002). The univariate analysis showed significant differences between sexes in *T. patagonica*, with variations in the number of TK and TH on the three antennal segments (P, F1 and F2). The highest number of TK on both antennal flagella in *T. patagonica* females, observed also in *T. sordida* (Catalá, 1997) and *Triatoma brasiliensis* Neiva, 1911 (Carbajal de la Fuente and Catalá, 2002), would be related to specific reproductive activities, such as search of refuge and/or oviposition sites, since TK would be associated with perception of contact pheromones (Bernard, 1974) or with detection of molecules, primary in liquid phase (Catalá, 1997; Gracco and Catalá, 2000). Abundance of TH on the three antennal segments of *T. patagonica* males was also reported for other species, such as *T. infestans* (Catalá and Dujardin, 2001), *T. sordida* (Catalá, 1997), *T. pseudomaculata* (Carbajal de la Fuente and Catalá, 2002), *M. spinolai* Porter, 1934 and *M. gajardoi* Frias, Henry & Gonzalez, 1998 (Moreno et al., 2005), *T. dimidiata* (Arroyo et al., 2007), *Triatoma flavida* (Neiva, 1911), and *Triatoma bruneri* (Usinger, 1944) (Rodríguez Rodríguez et al., 2009). The high number of this chemoreceptor would be associated with sexual behavior, through perception of chemical signals produced by metasternal glands of females (Crespo and Manrique, 2007), which promote copulation and male aggregation around pairs (Catalá and Schofield, 1994; Catalá and Dujardin, 2001; Carbajal de la Fuente and Catalá, 2002; Moreno et al., 2005), and with host-seeking and refuge searching abilities and of particles released by the sweat and respiration of the host (Mayer, 1968; Bernard, 1974; Abrahan et al., 2008). Interestingly, the degree of sexual dimorphism in this species varies between geographical populations, suggesting a different expression of the adaptive pressure in males and females of different populations.

Catalá and Dujardin (2001) conducted the first study on intraspecific variation of the antennal phenotype of *T. infestans* in terms of geographical origin and habitat. This study and others (Catalá et al., 2005; Esteban et al., 2005; Villela et al., 2005) indicated that morphology of triatomines might be modulated by ecological factors that promote the existence of different phenotypes in populations of the same species developing in different geographical regions and/or habitats (wild, peridomestic, domestic and laboratory habitats). However, no general conclusions can be drawn about the increases or decreases in density of some *sensilla* as a function of the different habitats occupied by each triatomine species (Catalá et al., 2004).

The pattern of antennal *sensilla* of *T. patagonica* showed differences between populations of different geographical origin and similar habitat (*PSF* and *PSL*), the population from Santa Fe (*PSF*) having the highest number of TK and BA on F2 and BR on P (for both sexes). Considering that, in general, the function of BA is to detect particles released by the host during respiration (Bernard, 1974), and that TH would be related to the insect dispersal ability (Catalá, 1997; Moreno et al., 2005), the *PSF* population could be expected to have a greater range of habitats and a better ability to disperse and to seek for hosts.

On the other hand, a high density of insects in the habitat of *PSF* population might explain their higher number of BR than that of *PSL* populations (unpublished results); these mechanoreceptors receive tactile information related to the microhabitat (Catalá and Dujardin, 2001), showing susceptibility to population density (Catalá et al., 2004). Alternatively, a higher number of BR might indicate that *PSF* population would have greater amplitude of habitat than *PSL*, since Catalá and Dujardin (2001) indicated that the higher number of this mechanoreceptor in the pedicel of *T. infestans* might be involved with long-term adaptation to different habitats. The more extensive habitat of *PSF* population might be related to the presence and colonization of this species in the intradomiciles of Santa Fe province. In San Luis, *T. patagonica* has not been reported in intradomiciliary environments; hence, the species might have a lower degree of adaptation to human habitats, being present only in peridomiciles.

Considering that the laboratory is a novel habitat for triatomines, which can induce phenotypic changes in the populations, several authors have reported a reduction in some morphological characters (Zeledón, 1981; Dujardin et al., 1997, 1998, 1999; Jaramillo et al., 2002; Borges et al., 2005; Rodríguez Rodríguez et al., 2007). Regarding the antennal phenotype, Catalá et al. (2004) suggested that modifications in the *sensilla* pattern can occur in the laboratory because of the particular characteristics of this habitat. Those authors reported differences between specimens of populations of *T. infestans*, *Rhodnius prolixus* Stål, 1859 and *Rhodnius pallescens* Barber, 1932 reared in the laboratory, and those collected from their natural habitat. The *T. patagonica* population reared in the laboratory only exhibited a decrease in the number of BR and BA on pedicel. This result would be consistent with findings reported by Catalá et al. (2004), who indicated that more stable laboratory culture conditions might reduce the complexity of the antennal phenotype.

Overall, the present results provide the first complete description of the antennal phenotype of *T. patagonica*, and allow us to characterize the species as belonging to the peridomiciliary species group with an important intraspecific variability due to genetic drift. This high intraspecific variability would provide the species with a wide habitat range without having a close association with a given host and its environment.

Considering *T. patagonica* as a potential secondary vector of *T. cruzi* and taking into account that the antennal phenotype is a good indicator of habitat adaptation, further studies with individuals of different geographic origin are necessary to enhance the knowledge on phenotypic variation in this species, as well as studies on the morphological plasticity, which show relationships with the possible adaptation to the intradomiciliary environment.

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